RESEARCH ARTICLE

Reproductive Dynamics and Physiological Maturity of the Pronghorn Spiny Lobster *Panulirus penicillatus* in Eastern Visayas Region, Philippines

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ABSTRACT

The pronghorn spiny lobster, *Panulirus penicillatus,* is a high-value reef-associated species that supports small-scale fisheries and the live seafood trade in Eastern Visayas, Philippines. However, limited local reproductive information has constrained the implementation of science-based management measures for the species. This study assessed the reproductive dynamics and maturity patterns of *P. penicillatus* using fishery-dependent samples collected from five major lobster-producing areas from February 2018 to December 2019. A total of 8,549 individuals with valid sex records were analyzed, consisting of 4,415 males and 4,134 females. The overall sex ratio was slightly but significantly male-biased at 1:0.94 ($\chi^2 = 9.24$, df = 1, $p = 0.002$). Size distribution, based on 8,527 individuals with valid carapace length records, was dominated by small to intermediate individuals, with 57.2% occurring between 40 and 55 mm CL. Berried females were concentrated mainly within the 45–60 mm CL range, indicating that reproductively active females were present within commonly harvested size classes. Reproductive activity was extended but temporally variable, as shown by the occurrence of egg-bearing females, tarspot-bearing females, mature ovarian stages, and significant monthly variation in female gonadosomatic index. Berried female incidence peaked from April to August 2018, while ripe ovaries and elevated female GSI were prominent during February to June 2019. Histological examination identified six ovarian developmental stages: immature, developing, ripe, spawning, re-developing, and spent. Fecundity ranged from 41,962 to 446,782 eggs per female and increased significantly with CL, highlighting the greater reproductive contribution of larger females. Logistic maturity analysis estimated CL_{50} at 39.28 mm and CL_{95} at 42.33 mm based on physiological maturity. These values represent local biological maturity reference points and should not replace the national minimum legal size of 72 mm CL prescribed for *P. penicillatus* under Fisheries Administrative Order No. 265 s. 2020. The findings support strict enforcement of the national legal-size limit, year-round protection of berried females, inclusion of tarspot-bearing females in reproductive monitoring, and strengthened inspection at landing sites and live lobster trading points to reduce recruitment overfishing risk in Eastern Visayas.

*Corresponding Author: *cristan.campo@nfrdi.da.gov.ph*
Received: *November 16, 2025*
Accepted: *June 11, 2026*

Keywords: *Panulirus penicillatus; reproductive biology; fecundity; gonadosomatic index; size at sexual maturity; spiny lobster; Eastern Visayas*

1. INTRODUCTION

Spiny lobsters of the genus *Panulirus* support valuable small-scale and commercial fisheries across tropical and subtropical regions, particularly in the Indo-Pacific, where they contribute to coastal livelihoods, seafood trade, and local food systems. These fisheries are increasingly important within a global fisheries sector that faces growing pressure to balance production, biodiversity conservation, and sustainable resource governance (FAO 2024; Phillips et al. 2013). Among these species, the pronghorn spiny lobster *Panulirus penicillatus* is widely distributed from the western Indian Ocean to the central Pacific (Holthuis 1991) and is commonly associated with coral reefs, rocky substrates, crevices, and other structurally complex coastal habitats. Its high market value and demand as a live seafood commodity make it an important fishery resource in many island and coastal communities.

In the Philippines, spiny lobsters are harvested in several coastal regions and remain among

the high-value reef-associated fishery commodities traded in local and export markets. Recent work in Eastern Visayas showed that *P. penicillatus* is a dominant component of local spiny lobster landings and is harvested using compressor diving, gill nets, and traps, with live lobsters commonly sold outside the region (Campo et al. 2023). However, like many reef-associated invertebrates, spiny lobsters are vulnerable to overexploitation because of their habitat dependence, high catchability, market-driven fishing pressure, and the removal of juveniles and reproductive females before they have contributed sufficiently to the spawning stock (Bell et al. 2006; MacDiarmid and Lawler 1998; Phillips et al. 2013). These concerns are especially relevant in small-scale fisheries where monitoring is limited and biological reference points for management are poorly established.

National policy has recognized the conservation concern surrounding spiny lobsters. In the Philippines, Fisheries Administrative Order No. 265, series of 2020 regulates the catching, possession, transport, sale, trade, and export of puerulus, juvenile, and gravid spiny lobsters under the family Palinuridae (DA-BFAR 2020). The order also allows collection for research and academic purposes, provided that appropriate permits are secured. This regulatory framework highlights the need to protect early life stages and reproductive females, but its effective implementation requires locally generated biological information. In particular, size at sexual maturity, reproductive seasonality, fecundity, and the occurrence of egg-bearing and spermatophore-bearing females are essential for determining whether harvested individuals have had the opportunity to reproduce before capture.

Reproductive biology provides a foundation for assessing the vulnerability of exploited crustacean populations and designing appropriate harvest regulations. Parameters such as sex ratio, size distribution, gonadal development, gonadosomatic index, fecundity, spawning seasonality, and size at sexual maturity are widely used to guide minimum legal size limits, protection of berried females, closed seasons, and other harvest control measures (Atherley et al. 2021; Cruz et al. 2013; Thangaraja and Radhakrishnan 2017). Recent spiny lobster studies have also emphasized the importance of distinguishing physiological maturity, functional maturity, and morphological maturity because these indicators may produce different maturity estimates and management thresholds (Atherley et al. 2021). For species subject to continuous or prolonged spawning, such as many tropical *Panulirus* species, size-based regulations may be particularly useful because they can provide year-round protection to immature individuals and reproductive biomass.

In female spiny lobsters, reproductive activity may be assessed through several complementary indicators. Ovarian development and gonadosomatic index provide information on internal reproductive condition, while the presence of external eggs confirms recent spawning. The occurrence of an external spermatophore, commonly referred to as a "tarspot," is also biologically significant because it indicates recent mating and potential reproductive readiness. The spermatophoric mass is deposited externally by the male on the ventral thoracic region of the female and later used during fertilization when eggs are extruded (MacDiarmid and Sainte-Marie 2006; Matthews 1951). Therefore, the combined assessment of ovarian condition, egg-bearing status, and tarspot occurrence provides a more complete understanding of reproductive timing and maturity than any single indicator alone.

Although *P. penicillatus* has been studied in several parts of its range, available information remains geographically uneven. Studies from Taiwan, Hawaii, the Red Sea, Japan, and other Indo-Pacific localities have described aspects of its reproductive biology, including maturity, fecundity, sex ratio, and reproductive seasonality (Chang et al. 2007; Hogarth and Barratt 1996; Juinio 1987; MacDiarmid and Lawler 1998; Plaut 1993; Yamamoto 1960). However, reproductive traits in spiny lobsters can vary spatially in response to local fishing pressure, habitat quality, food availability, population density, temperature, and other environmental conditions. For this reason, maturity estimates and spawning patterns from other regions may not be directly transferable to Philippine populations, particularly those exposed to intensive small-scale fishing.

In Eastern Visayas, the need for local reproductive information is especially urgent. The region supports active reef-associated fisheries and has documented high exploitation of spiny lobsters, particularly *P. penicillatus* (Campo et al. 2023). The importance of Eastern Visayas as a spiny lobster fishing area has been recognized for several decades. Juinio and Gomez documented the spiny lobster fishery in Eastern Samar based on surveys conducted in the early 1980s, providing one of the earliest fishery baselines for the area. The persistence of spiny lobster landings in Eastern Visayas, together with recent evidence that *P. penicillatus* remains a dominant component of local lobster catches, underscores the need to update

historical fishery information with contemporary reproductive and maturity data. Yet management remains constrained by limited biological baselines for identifying appropriate minimum legal sizes, evaluating seasonal protection, and assessing the reproductive contribution of larger females.

This study therefore examined the reproductive dynamics and maturity patterns of *P. penicillatus* in Eastern Visayas, Philippines, based on extensive sampling from 2018 to 2019. Specifically, it assessed sex ratio, size distribution, incidence of ovigerous and tarspot-bearing females, gonad developmental stages, reproductive seasonality, gonadosomatic index, fecundity, and size at physiological maturity. By estimating the size at 50% maturity and identifying the size at which most females become mature, this study provides biological reference points needed to support science-based management, particularly the evaluation of maturity-based harvest regulations, enforcement of existing minimum legal size provisions, and protection of reproductive females in the Eastern Visayas spiny lobster fishery.

2. MATERIALS AND METHODS

2.1 Study sites and sample collection

Reproductive biology data for *Panulirus penicillatus* were collected from five major spiny lobster landing and production areas in Eastern Visayas, Philippines, from February 2018 to December 2019. The sampling sites were selected based on preliminary surveys conducted in January 2018 and represented key fishing grounds and landing areas where *P. penicillatus* was regularly observed in the catch. These sites included the municipalities of Silago and Hinunangan in Southern Leyte, San Policarpo and Guiuan in Eastern Samar, and San Jose in Northern Samar (Figure 1).

Monthly samples were obtained from the landed catch of local fishers and from buying stations across the five sampling sites. Sampling for sex and size composition followed a fishery-dependent landing-site monitoring approach, consistent with the scheduling and enumeration procedures described in the National Stock Assessment Program methodology

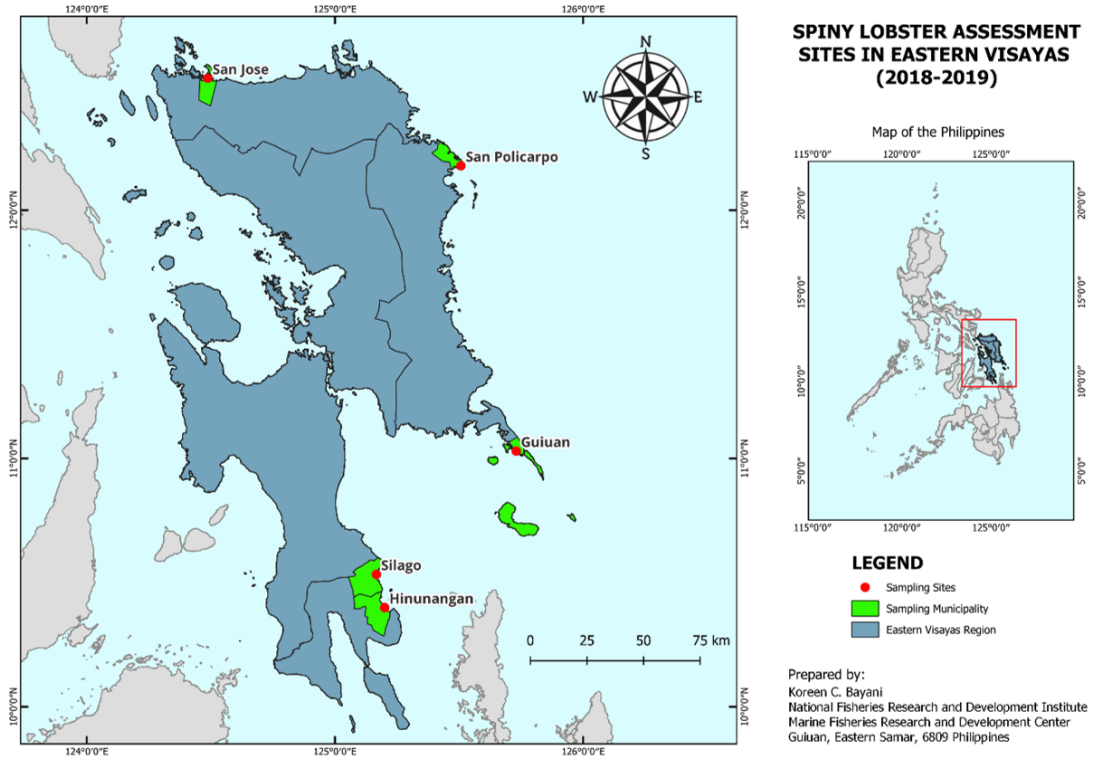

Figure 1. Map showing the spiny lobster assessment sites in Eastern Visayas, Philippines, from 2018 to 2019. Sampling sites are indicated in the municipalities of San Jose, Northern Samar; San Policarpo and Guiuan, Eastern Samar; and Silago and Hinunangan, Southern Leyte. Red points indicate sampling stations, green areas indicate sampling municipalities, and blue shading represents the Eastern Visayas region.

(Lopez 2017). In contrast, specimens used for gonadal examination were collected opportunistically from available landings, with 10 to 15 individuals randomly selected per sampling event depending on catch availability and the presence of suitable specimens for dissection.

2.2 Species identification and morphometric measurements

All specimens were identified as *P. penicillatus* based on external morphology. For each individual, sex, carapace length, body weight, reproductive condition, presence of external egg mass, and presence of spermatophore or "tarspot" were recorded (See Figure 3).

Sex was determined by examining the ventral morphology of the abdomen and swimmerets (Figure 2). Males were identified by the presence of single-layered swimmerets, whereas females were identified by double-layered swimmerets, with the inner layer appearing smaller and more setose.

Carapace length (CL) was measured to the nearest 0.1 mm using a Vernier caliper along the mid-dorsal line from the anterior margin between the postorbital spines to the posterior margin of the

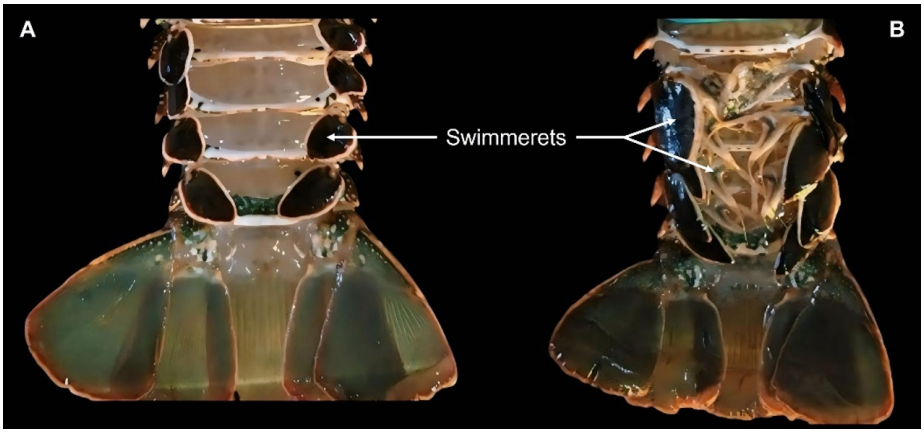

Figure 2. Ventral view of the abdomen of male and female *Panulirus penicillatus* showing the swimmerets used for sex identification. (A) Male with single-layered swimmerets. (B) Female with double-layered swimmerets, with the inner layer appearing smaller and more setose. Arrows indicate the position of the swimmerets.

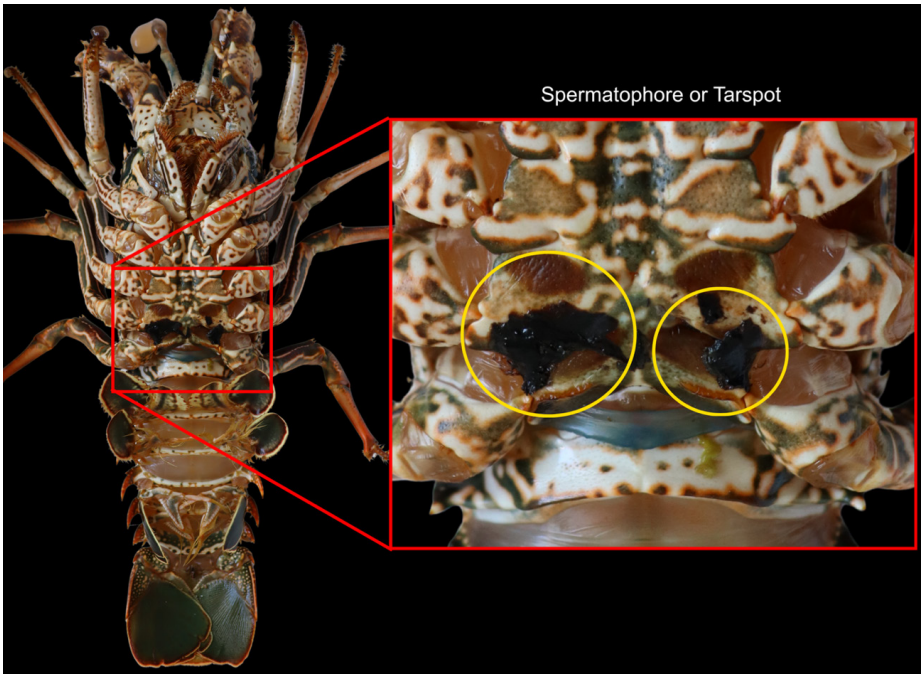

Figure 3. Ventral view of a female *P. penicillatus* showing the spermatophore mass (tarspot) attached to the sternum between the pereiopods following mating. The inset highlights the paired tarspots (yellow circles), which serve as an external indicator of recent mating and reproductive readiness prior to egg extrusion and attachment to the pleopods. Tarspot-bearing females were used as an indicator of reproductive activity in the present study.

carapace. Body weight (BW) was measured to the nearest gram using a 6-kg capacity weighing scale. For dissected specimens, gonad weight (GW) was measured to the nearest 0.01 g using an electronic pocket scale after removal of excess moisture.

2.3 Sex ratio analysis

Sex ratio was calculated monthly and for the total sample as the number of males relative to females and expressed as male:female ratio. For graphical presentation, monthly sex ratio was also expressed as the number of females per male, with a value of 1.0 representing the expected 1:1 ratio.

To determine whether the overall sex ratio deviated significantly from the expected 1:1 ratio, a chi-square goodness-of-fit test was performed using the observed numbers of males and females and expected proportions of 0.5 for each sex. Statistical significance was evaluated at $p < 0.05$.

2.4 Size distribution by sex and reproductive condition

Size distribution was examined using individuals with valid carapace length and sex records. Individuals were grouped into 5-mm CL classes. Each specimen was classified into one of three groups: male, non-berried female, or berried female. Berried females were defined as females carrying external egg masses attached to the pleopods, whereas non-berried females were females without visible external eggs at the time of sampling.

The number and percentage of individuals in each 5-mm CL class were calculated for each group and for the total sample. Size-frequency distributions were used to identify the dominant size classes in the sampled landings and to determine whether berried females occurred within commonly harvested size classes.

2.5 External reproductive indicators: berried condition and tarspot occurrence

Female reproductive condition was assessed using external reproductive indicators. Egg-bearing or berried females were identified by the presence of external egg masses attached to the pleopods. Egg masses were classified macroscopically based on color as bright orange, light orange to brown, or gray to black, representing progressive stages of embryonic development.

The presence of a spermatophore, locally referred to as a tarspot, was recorded when visible on the ventral thoracic region of females. Females were classified into three external reproductive categories: eggs only, tarspot only, or both eggs and tarspot. Monthly counts of these categories were used to describe the occurrence of reproductively active females through time.

Monthly incidence of berried females was calculated as:

$$Incidence\ of\ berried\ females = \frac{Number\ of\ berried\ females}{Total\ of\ females\ examined} \times 100.$$

The seasonal size distribution of berried females was examined by summarizing the number of berried females in each month and 5-mm CL class.

2.6 Gonad collection and macroscopic examination

A total of 169 gonad samples from male and female *P. penicillatus* of varying sizes were collected for macroscopic examination. Samples were obtained during May, July, August, and September 2018 and from January to December 2019 from Guiuan, San Jose, and San Policarpo.

Specimens were dissected using surgical scissors and forceps, and the gonads were carefully removed from the cephalothoracic cavity. Macroscopic characteristics of the gonads, including color, size, shape, texture, and degree of development, were recorded. The presence of oviposited eggs or spermatophores was also noted.

2.7 Histological processing and gonad-stage classification

Whole gonads were preserved in 10% buffered formalin and processed for histological examination at the Parasitology Laboratory of Providence Hospital, Quezon City. Standard histological procedures were followed, including fixation, dehydration through graded alcohol, paraffin embedding, sectioning at 5 µm, and staining with hematoxylin and eosin. A total of 97 gonad samples were examined microscopically at 100× to 400× magnification. Photomicrographs were captured using a microscope-mounted camera.

Female ovarian developmental stages were classified based on macroscopic and histological characteristics following Juinio (1987), Minagawa and Sano (1997), Silva and Landim (2006), Chang et al. (2007), and Perez-González et al. (2009). Ovarian stages were categorized as immature, developing, ripe, spawning, re-developing, and spent.

Male gonadal stages were classified based on the descriptions of Matthews (1951), Minagawa (1997), and De Lima and Gesteira (2008), with maturity assessed according to the presence and relative abundance of spermatogonia, spermatocytes, spermatozoa, spherical bodies, and associated gonadal structures.

2.8 Reproductive cycle based on ovarian stages

The reproductive cycle of female *P. penicillatus* was assessed by calculating the monthly relative frequency of ovarian developmental stages. For each sampling month with histologically examined females, the number of individuals assigned to each ovarian stage was expressed as a percentage of the total number of females examined in that month.

Females with developing, ripe, spawning, re-developing, or spent ovaries were considered physiologically mature. Females with immature ovaries were considered immature. Monthly variation in ovarian stages was interpreted together with berried condition, tarspot occurrence, and GSI patterns to describe reproductive seasonality.

2.9 Gonadosomatic index

The gonadosomatic index (GSI) was calculated to evaluate temporal changes in gonad development and reproductive activity. For each dissected individual, GSI was computed as:

$$GSI = \frac{GW}{BW} \times 100$$

where GW is gonad weight in grams and BW is total body weight in grams.

Monthly mean GSI, standard deviation, standard error, minimum, and maximum values were calculated separately for males and females. Monthly differences in GSI were tested separately by sex using the Kruskal–Wallis rank-sum test because monthly sample sizes were unequal and GSI values were not assumed to meet parametric assumptions. For male GSI, months with only one observation were excluded from inferential monthly comparisons but retained in descriptive summaries and figures. When significant monthly differences were detected, pairwise Wilcoxon rank-sum tests with Benjamini–Hochberg adjustment were used for post-hoc comparisons. Statistical significance was evaluated at $p < 0.05$.

2.10 Fecundity estimation

Fecundity was estimated from 14 berried female *P. penicillatus* of varying sizes. Egg masses attached to the pleopods were carefully removed from fresh specimens and fixed in 10% formalin. Samples were transported to the laboratory and stored for 30 days to allow hardening of the eggs before counting.

Each egg mass was dried to constant weight, and the total dry weight was measured to the nearest 0.1 g using an electronic balance. Five 0.1-g subsamples were taken from each egg mass, and the number of eggs in each subsample was counted manually. The mean number of eggs from the five subsamples was used to estimate total fecundity by simple proportion:

$$F = \frac{W_t}{W_s} \times E_s$$

where F is estimated fecundity, W_t is the total dry weight of the egg mass, W_s is the dry weight of the subsample, and E_s is the mean number of eggs counted in the subsamples.

The relationship between fecundity and carapace length was evaluated using simple linear regression. Model fit was assessed using the coefficient of determination (R^2), and statistical significance was evaluated at $p < 0.05$.

2.11 Size at physiological maturity

Size at physiological maturity was estimated using an individual-level logistic regression model fitted to binary maturity status of female *P. penicillatus*. A total of 62 females with histologically examined ovaries and valid carapace length measurements were included in the analysis.

Females were classified as immature when ovaries were histologically immature and mature when ovaries were developing, ripe, spawning, re-developing, or spent. The probability of maturity was modeled as a function of carapace length using a binomial logistic model:

$$P(CL) = \frac{1}{1 + e^{-(a + bCL)}}$$

where P(CL) is the predicted probability of physiological maturity at a given carapace length, a is the intercept, b is the slope parameter, and CL is carapace length in millimeters.

The size at 50% physiological maturity (CL_{50}) was estimated as:

$$CL_{50} = -\frac{a}{b}$$

The size at 95% physiological maturity (CL_{95}) was estimated from the fitted logistic model as the CL at which the predicted probability of maturity was 0.95. The fitted maturity curve was used to estimate CL_{50} and CL_{95} as local biological maturity reference points. These estimates were interpreted in relation to previously published maturity estimates and the national legal minimum size for *P. penicillatus* under Fisheries Administrative Order No. 265 s. 2020.

2.12 Data analysis and visualization

Data encoding and initial cleaning were performed in a spreadsheet, while statistical analyses and graphical visualization were conducted in R. Figures were generated using the ggplot2 package. Graphical summaries were used to visualize monthly trends, size-frequency distributions, berried female incidence, external reproductive indicators, GSI patterns, fecundity relationships, and maturity curves. Statistical significance was evaluated at $p < 0.05$ for all tests

3. RESULTS

3.1 Sex ratio

Monthly sex ratio of *P. penicillatus* varied throughout the sampling period, ranging from 1:0.21 to 1:1.41 male:female (Figure 4). Most months showed a male-biased pattern, with female-per-male values below the expected 1:1 ratio. The strongest male bias was observed in February 2018, with a ratio of 1:0.21, followed by September 2018 at 1:0.46.

Female-biased months were also recorded, particularly in May 2018, August 2018, and from July to October 2019, as indicated by values above the 1:1 reference line. The highest female-biased ratio occurred in July 2019 at 1:1.41, followed by August 2018 at 1:1.34, September 2019 at 1:1.28, October 2019 at 1:1.23, and December 2019 at 1:1.21.

The raw dataset included 8,549 individuals with valid sex records, composed of 4,415 males and 4,134 females. This corresponds to an overall male:female ratio of 1:0.94, with males representing 51.6% and females 48.4% of the sample. The observed sex ratio differed significantly from the expected 1:1 ratio based on the chi-square goodness-of-fit test ($\chi^2 = 9.24$, df = 1, $p = 0.002$), indicating a slight but statistically significant male bias in the sampled landings.

3.2 Size distribution by sex and reproductive condition

The size structure of *P. penicillatus* was dominated by small to intermediate individuals (Figure 5). Of the 8,527 size-classified lobsters with valid carapace length records, most were concentrated between 40 and 55 mm CL, totaling 4,877 individuals or 57.2% of the sample. The modal size class was 45–50 mm CL, with 1,864 individuals or 21.9%, followed by 50–55 mm CL with 1,529 individuals or 17.9%, and 40–45 mm CL with 1,484 individuals or 17.4%.

Males showed the widest size range and dominated the larger size classes. Their highest abundance occurred at 45–50 mm CL, with 915 individuals or 20.7% of all males, followed by 50–55 mm CL with 808 individuals or 18.3%. Non-berried females followed a similar pattern, peaking at 45–50 mm CL with 877 individuals or 23.4% of all non-berried females, followed by 40–45 mm CL with 780 individuals or 20.9%.

Berried females were fewer and more concentrated in intermediate size classes. They were most abundant at 50–55 mm CL, with 78 individuals or 21.0% of all berried females, followed by 45–50 mm CL with 72 individuals or 19.4%, and 55–60 mm CL

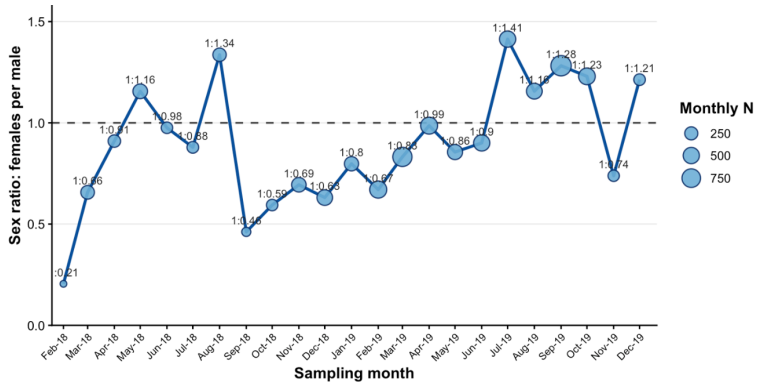

Figure 4. Monthly sex ratio of *Panulirus penicillatus* sampled from Eastern Visayas, Philippines, from February 2018 to December 2019. Sex ratio is expressed as the number of females per male, with values above each point shown as male:female ratio in the form 1:x. The dashed horizontal line indicates the expected 1:1 sex ratio. Points above the line indicate female-biased months, while points below the line indicate male-biased months. Bubble size represents the monthly sample size.

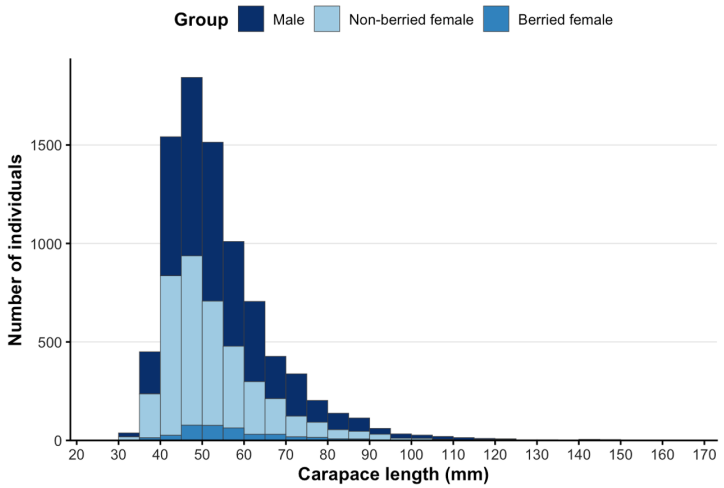

Figure 5. Size-frequency distribution of male, non-berried female, and berried female *Panulirus penicillatus* sampled from Eastern Visayas, Philippines, from February 2018 to December 2019. Bars show the number of individuals by 5-mm carapace length class, with ovigerous females presented as a subset of the female samples. N = 8,527 spiny lobsters with valid CL entries.

with 64 individuals or 17.2%. Together, berried females from 45 to 60 mm CL comprised 214 individuals or 57.5% of all berried females.

The sampled landings were concentrated within the same size range where berried females were most frequently observed. This overlap indicates that reproductively active females are routinely present in the catch, underscoring the need for strict protection of berried females and effective size-based monitoring at landing and trading points.

3.3 Incidence of berried females

The monthly incidence of berried female *Panulirus penicillatus* showed clear temporal variation from February 2018 to December 2019 (Figure 6). In 2018, berried females were first recorded in March, with an incidence of 9.7%, followed by a sharp increase in April (26.7%), May (34.7%), and June (33.8%). The highest incidence occurred in July 2018 and August 2018, when berried females comprised 51.2% and 52.9% of the monthly female samples, respectively. No berried females were recorded in February and September 2018, while low incidence values were observed from October to December 2018.

In 2019, berried females were recorded in all months, but at much lower levels compared with the 2018 peak. Monthly incidence ranged from 1.7% to 7.6%, with the highest value recorded in February 2019. Slight increases were observed toward the latter part of the year, particularly in November (6.5%) and December (5.5%).

Overall, the results indicate a pronounced egg-bearing period from April to August 2018, with peak berried incidence in July and August. The lower but persistent occurrence of berried females throughout 2019 suggests that reproductive activity was extended, although intensity varied between sampling years.

3.4 Seasonal size distribution of berried females

Ovigerous females were recorded across a broad size range, from approximately 30 to 110 mm CL. The seasonal size distribution is presented in Figure 7. The highest number of ovigerous females occurred in the 51–55 mm CL size class. The smallest ovigerous female measured 30.71 mm CL, indicating that some individuals may become reproductively active at relatively small sizes. However, the greatest concentration of egg-bearing females occurred at larger size classes than the smallest observed ovigerous individual.

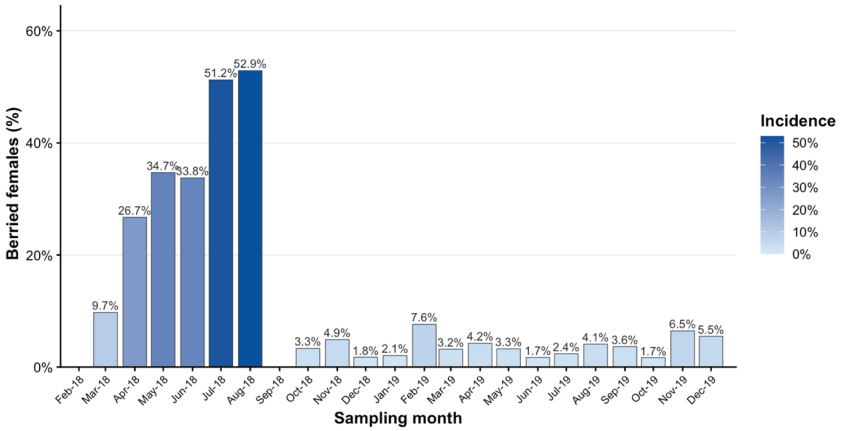

Figure 6. Monthly incidence of berried female *Panulirus penicillatus* sampled from Eastern Visayas, Philippines, from February 2018 to December 2019. Bars represent the percentage of female individuals carrying external egg masses relative to the total number of females examined each month. Color intensity indicates the magnitude of berried female incidence.

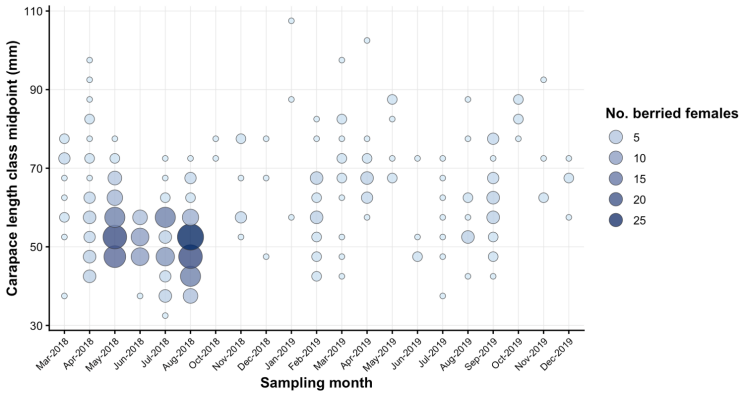

Figure 7. Seasoal size distribution of berried female *Panulirus penicillatus* sampled from Eastern Visayas, Philippines, from March 2018 to December 2019. Bubbles represent the number of berried females recorded in each sampling month and 5-mm carapace length class. Bubble size and color intensity indicate the number of berried females per month-size class combination.

Berried female *Panulirus penicillatus* were recorded across a wide size range, with carapace length class midpoints ranging from approximately 35 to 108 mm (Figure 6). The highest concentration of berried females occurred in the 45–60 mm CL size classes, particularly from April to August 2018, indicating a strong reproductive pulse during this period. The largest monthly aggregation was observed in August 2018, where berried females were most abundant around the 50–55 mm CL size classes.

In 2019, berried females were observed from January to December, but the monthly distribution was more dispersed across size classes and generally occurred in lower numbers compared with the 2018 peak. Berried females in 2019 were commonly recorded between 45 and 75 mm CL, with occasional larger individuals exceeding 90 mm CL. The presence of berried females across multiple months and size classes suggests an extended reproductive period, with a pronounced peak in 2018 and continued reproductive activity throughout 2019.

3.5 External reproductive indicators: eggs and tarspots

Reproductively active female *P. penicillatus* were recorded during most sampling months, based on the presence of external eggs, tarspot, or both eggs and tarspot (Figure 8). In 2018, reproductive activity was dominated entirely by females carrying eggs only. The highest number of reproductively active females was observed in May 2018, with 114 egg-bearing females, followed by August 2018 with 81 females, and June and July 2018 with 42 and 43 females, respectively. No reproductively active females were recorded in September 2018.

In 2019, reproductive activity was more diverse, with females recorded not only with eggs but also with tarspots and with both eggs and tarspots. Early 2019 showed relatively low numbers, although February 2019 included all three reproductive categories. A marked increase occurred from September to November 2019, when females with eggs, tarspots, or both were all present. September 2019 showed the highest reproductive activity in 2019, driven largely by females with tarspots and females with both eggs and tarspots.

The results indicate that egg-bearing females were most abundant during the major reproductive pulse in April to August 2018, while the occurrence of tarspot-bearing females in 2019, particularly from September to November, suggests continued mating activity and extended reproductive readiness beyond

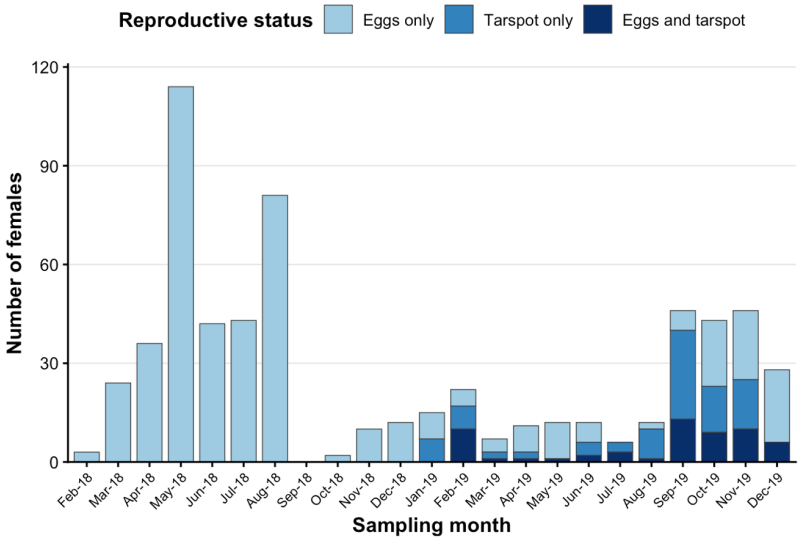

Figure 8. Monthly occurrence of reproductively active female *Panulirus penicillatus* sampled from Eastern Visayas, Philippines, from February 2018 to December 2019. Females were classified based on the presence of external eggs only, spermatophore or "tarspot" only, or both eggs and tarspot. Bars show the number of females recorded in each reproductive category per sampling month.

the months when egg-bearing females were most abundant.

3.6 Gonad morphology and histological stages

Macroscopic examination showed that the gonads of both male and female *P. penicillatus* were elongated and generally H-shaped, with paired anterior and posterior lobes joined near the central region (Figure 9). Gonad color, size, and texture varied with maturity stage.

Male gonads ranged from transparent or pale white in immature individuals to creamy white or yellowish in mature individuals. Immature male gonads were thin, soft, and difficult to distinguish from surrounding tissues, while mature gonads were larger, more compact, and more clearly visible within the cephalothoracic cavity.

Female ovaries showed more distinct maturity-related changes in color and size. Immature ovaries were thin, whitish, and poorly developed. As maturation progressed, ovaries became enlarged and changed from white or pale yellow to orange or dark orange. Ripe ovaries occupied a larger portion of the cephalothoracic cavity and appeared swollen and compact, while spent ovaries were reduced in size, pale, and flaccid.

Histological examination confirmed six ovarian developmental stages: immature, developing, ripe, spawning, re-developing, and spent (Figure 10 and 11; Table 1). Immature ovaries were characterized by previtellogenic oocytes and distinct connective tissue. Developing ovaries contained increasing numbers of vitellogenic oocytes. Ripe ovaries were dominated by large, mature oocytes that were closely packed. Spawning ovaries showed evidence of egg release, including spaces between oocytes, residual oocytes, and follicular structures. Re-developing ovaries contained both post-ovulatory structures and developing oocytes, while spent ovaries showed reconstituting connective tissue and reduced oocyte density.

Male gonadal development was classified into three histological stages. Stage 1 was characterized by the predominance of spermatogonia and limited development of sperm cells. Stage 2 showed increasing numbers of spermatocytes and developing sperm structures. Stage 3 was characterized by abundant spermatozoa, indicating advanced maturity.

3.7 Reproductive cycle

The monthly distribution of ovarian developmental stages showed temporal variation in the reproductive condition of female *Panulirus penicillatus* (Figure 12). Multiple gonadal stages were observed across the sampling period, indicating an extended reproductive cycle rather than a single, sharply defined spawning period.

In 2018, developing, ripe, and spent ovaries were observed from May to August. Developing ovaries were present in May and July, while ripe ovaries were recorded from May to August, suggesting active ovarian maturation during this period. Spent ovaries were also observed in May, July, and August, indicating that some females had recently spawned.

In 2019, ripe ovaries were prominent from February to June, with February, May, and June composed entirely of ripe-stage ovaries. Spawning ovaries were recorded in March and April, while re-developing ovaries were observed in March and July. Developing ovaries became more frequent from July to October and again in December, suggesting renewed ovarian development after spawning. Spent ovaries were dominant in January and November 2019 and were also present from July to October, indicating post-spawning or recovering females.

The occurrence of ripe, spawning, re-developing, developing, and spent ovaries across several months suggests that female *P. penicillatus* undergoes prolonged reproductive activity in Eastern Visayas. The high proportion of ripe ovaries from February to June 2019, together with the presence of spawning and spent stages in adjacent months,

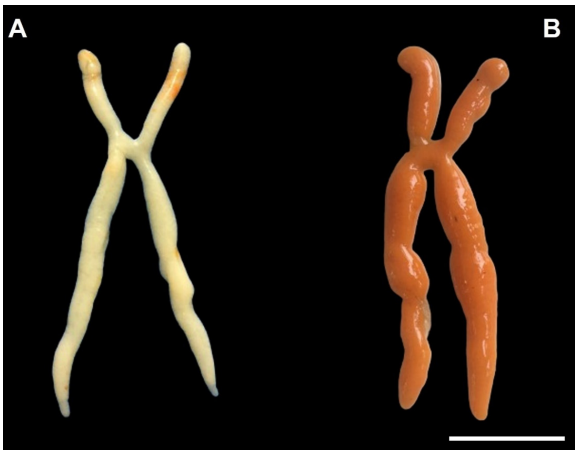

Figure 9. Gross morphology of the gonads of *Panulirus penicillatus*. (A) Mature male gonad showing a pale cream to whitish, elongated paired structure with slender lobes. (B) Mature or ripening female ovary showing an enlarged orange paired structure with well-developed anterior and posterior lobes. Scale bar = 20 mm.

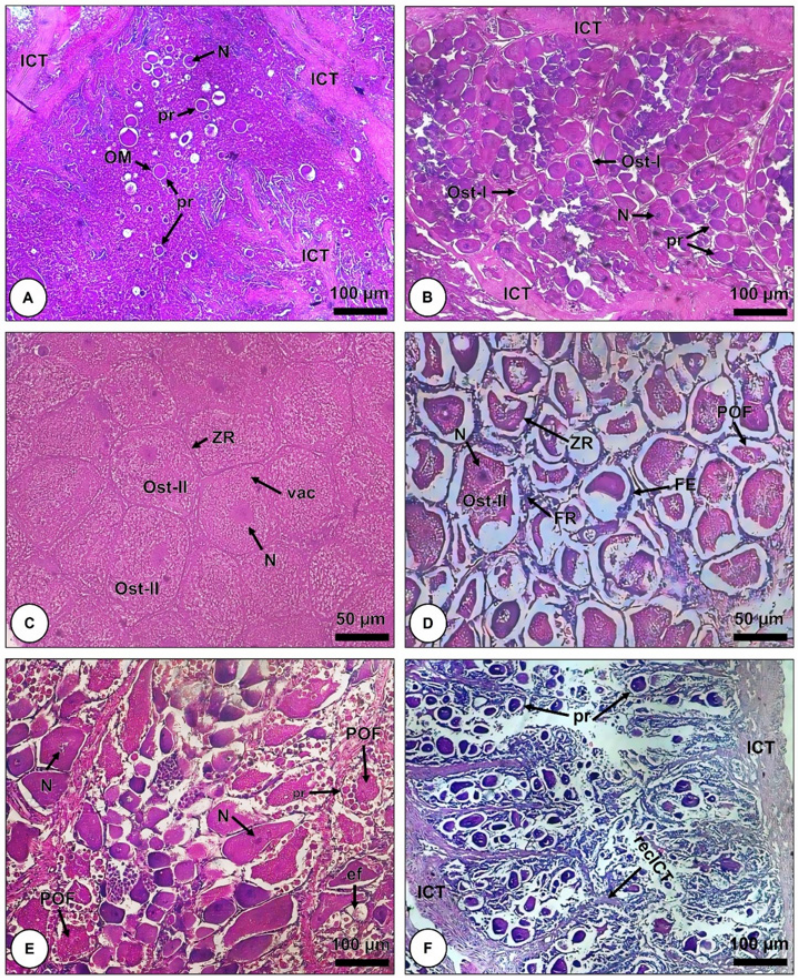

Figure 10. Histological sections of female *Panulirus penicillatus* ovaries showing different stages of ovarian development. (A) Immature ovary with previtellogenic oocytes and abundant interstitial connective tissue. (B) Developing ovary showing primary vitellogenic oocytes and remaining previtellogenic oocytes. (C) Ripe ovary dominated by large secondary vitellogenic oocytes with visible nuclei, zona radiata, and cytoplasmic vacuoles. (D) Spawning ovary showing follicular epithelium, post-ovulatory follicles, and follicles in resorption. (E) Re-developing ovary with post-ovulatory follicles, empty follicles, and developing oocytes. (F) Spent ovary showing reduced oocyte density and reconstituting interstitial connective tissue. Abbreviations: pr, previtellogenic oocyte; ICT, interstitial connective tissue; OM, oocyte membrane; Ost-I, primary vitellogenic oocyte; Ost-II, secondary vitellogenic oocyte; N, nucleus; ZR, zona radiata; vac, vacuole; FE, follicular epithelium; FR, follicle in resorption; POF, post-ovulatory follicle; ef, empty follicle; recICT, reconstituting interstitial connective tissue. Scale bars: A, B, E, and F = 100 µm; C and D = 50 µm.

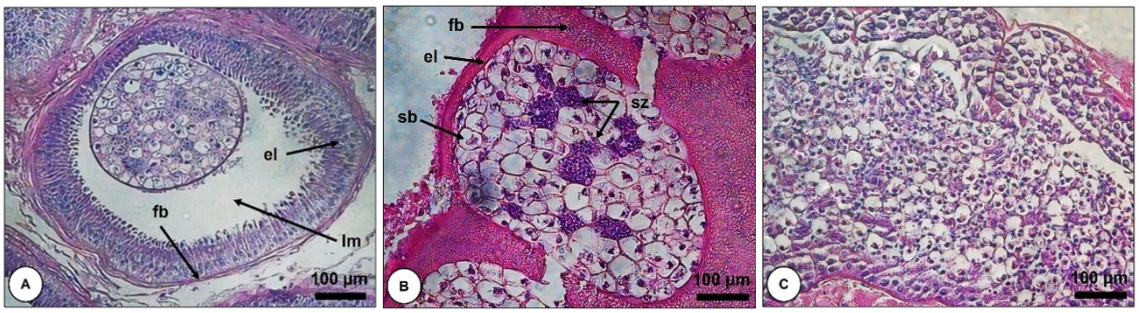

Figure 11. Histological sections of male *Panulirus penicillatus* testes showing different stages of testicular development. (A) Stage 1, early developing testis showing a distinct fibrous layer, epithelial layer, and lumen. (B) Stage 2, developing testis showing fibrous and epithelial layers, spherical bodies, and developing spermatozoa. (C) Stage 3, mature testis characterized by abundant spermatozoa and densely packed spherical bodies. Abbreviations: fb, fibrous layer or fibrocytes; el, epithelial layer; lm, lumen; sb, spherical bodies; sz, spermatozoa. Scale bars = 100 µm.

Table 1. Classification of gonad developmental stages found in female *Panulirus penicillatus*.

Ovarian Stage	Macroscopic Appearance	Histological Characteristics
Immature	Ovaries were thin, white to translucent, and rod-like, with slender anterior and posterior lobes occupying only a small portion of the cephalothoracic cavity. The ovaries were difficult to distinguish from surrounding tissues.	Ovarian tissue showed thick ovarian walls, abundant interstitial connective tissue, and small previtellogenic oocytes distributed mainly along the ovarian periphery.
Developing	Ovaries were enlarged, firm, and more visible within the cephalothoracic cavity. Color ranged from white or pale yellow to light orange as oocytes developed.	Ovaries contained numerous developing oocytes. Smaller early-stage oocytes were observed near the center, while larger vitellogenic oocytes were distributed toward the ovarian wall. The ovarian wall became thinner compared with the immature stage.
Ripe	Ovaries were fully developed, swollen, compact, and occupied much of the cephalothoracic cavity. Color ranged from orange to dark orange.	Ovarian tissue was dominated by large, mature vitellogenic oocytes that were densely packed. The ovarian wall was very thin or difficult to distinguish.
Spawning	Ovaries appeared slightly flaccid and less compact, with pigmented areas. Color ranged from light orange to pale yellow with orange patches.	Ovaries showed evidence of egg release, including spaces between oocytes, reduced oocyte compactness, residual oocytes, and thickened or ruptured ovarian walls.
Re-developing	Ovaries were thin to moderately developed and white to light yellow, indicating recovery and renewed ovarian development after spawning.	Ovarian tissue contained post-ovulatory structures together with young and developing oocytes. Developing oocytes were commonly observed near the ovarian wall, while remaining mature oocytes may still be present near the center. The ovarian wall was thickened.
Spent	Ovaries were shrunken, flaccid, and white to translucent. Some residual mature oocytes were occasionally visible macroscopically.	Ovarian tissue showed thick, folded ovarian walls, large empty spaces, reduced oocyte density, and reconstituting interstitial connective tissue, indicating post-spawning recovery.

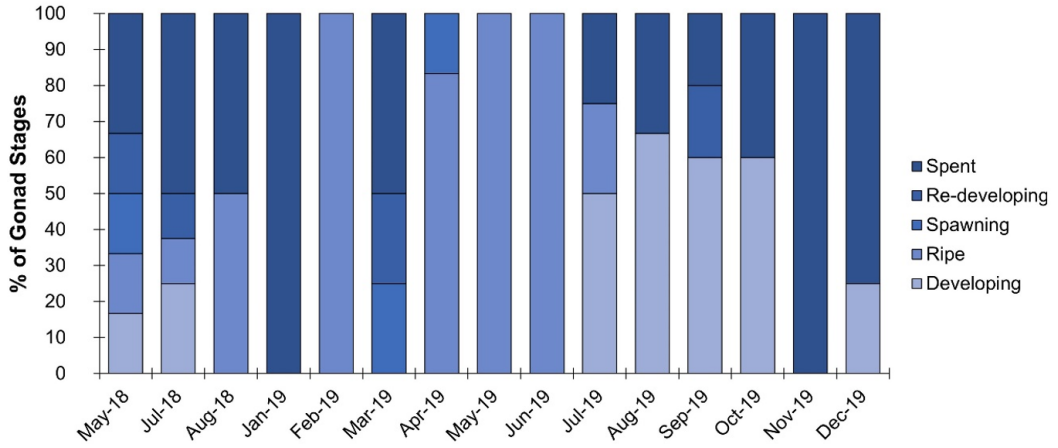

Figure 12. Monthly variation in the ovarian developmental stages of female *Panulirus penicillatus* sampled from Eastern Visayas, Philippines. Bars show the relative frequency of developing, ripe, spawning, re-developing, and spent ovaries by sampling month. The occurrence of multiple gonadal stages across months indicates an extended reproductive cycle.

indicates a major period of reproductive activity during the first half of the year, with continued ovarian redevelopment and post-spawning recovery in later months.

3.8 Gonadosomatic index (GSI)

The gonadosomatic index (GSI) of *P. penicillatus* varied by sex and sampling month (Figure 13). Female GSI showed pronounced temporal fluctuation, with monthly mean values ranging from 0.037 ± 0.010 in July 2018 to 3.082 ± 0.497 in February 2019. Monthly differences in female GSI were significant based on the Kruskal–Wallis test (χ^2 = 50.51, df = 12, $p < 0.001$), indicating substantial temporal variation in ovarian development.

Female GSI was relatively high in May 2018 (0.891 ± 0.222) and increased further in August 2018 (1.649 ± 0.797). In 2019, the highest female GSI was recorded in February (3.082 ± 0.497), followed by

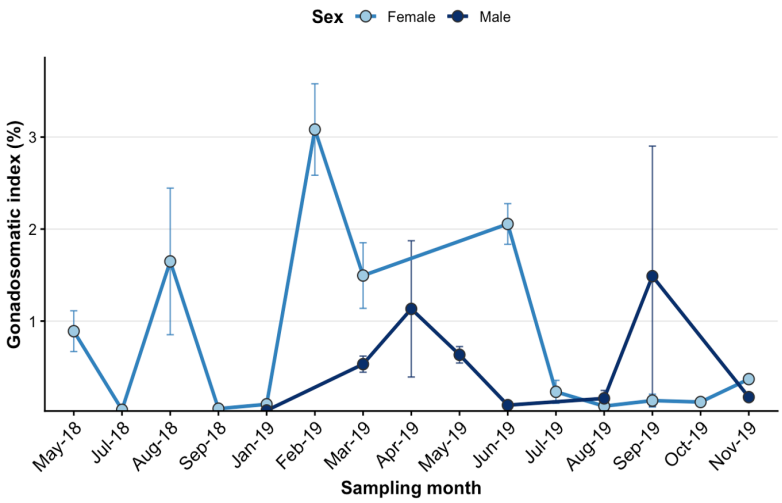

Figure 13. Monthly variation in the gonadosomatic index (GSI) of male and female *Panulirus penicillatus* sampled from Eastern Visayas, Philippines. Points represent mean monthly GSI values, and vertical bars indicate variation among individuals. Peaks in female GSI indicate periods of advanced ovarian development, while lower values correspond to spawning, spent, or developing stages.

June (2.056 ± 0.221) and March (1.495 ± 0.356). These elevated values indicate periods of advanced ovarian development. In contrast, low female GSI values were observed in July 2018 (0.037 ± 0.010), September 2018 (0.048 ± 0.026), January 2019 (0.096 ± 0.018), and from August to October 2019, when mean GSI values remained below 0.14. A slight increase was observed in November 2019 (0.370 ± 0.038), although this estimate was based on only two female samples.

Male GSI was generally lower than female GSI and was available for fewer sampling months. After excluding months with only one male observation, monthly differences in male GSI were significant (χ^2 = 14.40, df = 5, p = 0.013). Mean male GSI ranged from 0.087 ± 0.044 in June 2019 to 1.489 ± 1.413 in September 2019. Moderate male GSI values were also observed in March 2019 (0.532 ± 0.088), April 2019 (1.133 ± 0.741), and May 2019 (0.634 ± 0.089). However, pairwise post-hoc comparisons were not significant after adjustment, and the high value in September 2019 should be interpreted cautiously because of the small sample size and high variability.

The GSI pattern indicates that female *P. penicillatus* had distinct periods of increased gonadal investment, particularly in February and June 2019, with secondary elevation in August 2018. These peaks are consistent with periods of advanced ovarian maturation. Male GSI showed weaker and more variable monthly patterns, suggesting that female ovarian development provided a clearer seasonal signal of reproductive activity.

3.9 Fecundity

Fecundity was estimated from 14 berried female *P. penicillatus* with carapace lengths ranging from 43.30 to 66.02 mm CL. Estimated fecundity ranged from 41,962 to 446,782 eggs per female. Linear regression showed a positive relationship between fecundity and carapace length, indicating that larger females generally carried more eggs (Figure 14). The fitted model was F = 9,316.57CL − 330,906.24, with carapace length explaining approximately 37.5% of the variation in fecundity (R^2 = 0.375, p = 0.020). Although fecundity increased with size, variation was observed among females of similar

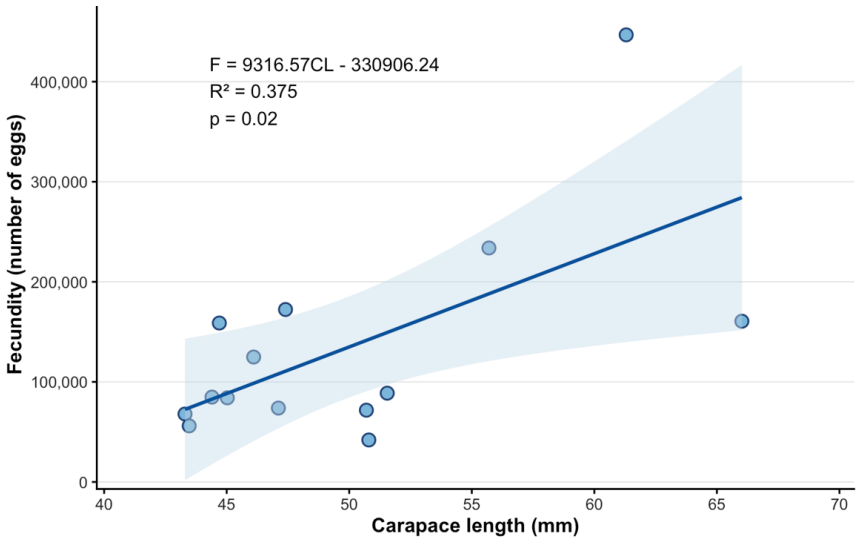

Figure 14. Size-fecundity relationship of berried female *Panulirus penicillatus* sampled from Eastern Visayas, Philippines. Points represent individual berried females, and the fitted line shows the linear regression between carapace length and estimated number of eggs. The shaded band represents the 95% confidence interval.

carapace length, suggesting that factors other than size may also influence egg production.

3.10 Size at physiological maturity

Size at physiological maturity was estimated from 62 female *P. penicillatus* with histologically examined ovaries and valid carapace length measurements. Of these, 5 females were classified as immature and 57 as mature based on ovarian developmental stage. Females used in the analysis ranged from 36.40 to 90.48 mm CL. The fitted logistic maturity model (Figure 15) showed that the probability of maturity increased sharply with carapace length. The estimated size at 50% physiological maturity was 39.28 mm CL, while the estimated size at 95% maturity was 42.33 mm CL. Nearly all females larger than approximately 42 mm CL were classified as physiologically mature, indicating that maturity is attained at relatively small sizes in the sampled population.

4. DISCUSSION

This study provides an updated assessment of the reproductive dynamics and maturity patterns of *Panulirus penicillatus* in Eastern Visayas, Philippines. By integrating fishery-dependent sex and size composition, incidence of berried females, external reproductive indicators, gonad morphology, histology, gonadosomatic index, fecundity, and logistic maturity analysis, the study provides biological reference points that are directly relevant to local management. The results indicate that *P. penicillatus* in Eastern Visayas exhibits an extended reproductive period, with clear temporal variation in egg-bearing incidence, ovarian development, and GSI. Reproductive females were recorded across several months and size classes, fecundity increased with carapace length, and females reached physiological maturity at relatively small sizes. These findings support precautionary management measures, particularly strict enforcement of the existing national minimum legal size, protection of berried females, and strengthened monitoring at landing and trading points.

4.1 Sex ratio, catch structure, and fishery-dependent sampling

The overall sex ratio of *P. penicillatus* was slightly male-biased, with 4,415 males and 4,134 females among 8,549 individuals with valid sex records. This corresponded to a male-to-female ratio of 1:0.94, with males representing 51.6% and females 48.4% of the sample. Although the numerical difference between sexes was small, the chi-square goodness-of-fit test showed a significant deviation from the expected 1:1 ratio. This result should be interpreted as a slight but statistically significant male bias in the sampled landings, rather than evidence of a strongly skewed natural population.

Monthly sex ratios varied considerably, ranging from 1:0.21 to 1:1.41. Most months were male-biased, but female-biased months were also observed, particularly in May and August 2018 and from July to October 2019. This temporal variability suggests that the sex composition of the catch may be influenced by seasonal behavior, spatial differences in fishing

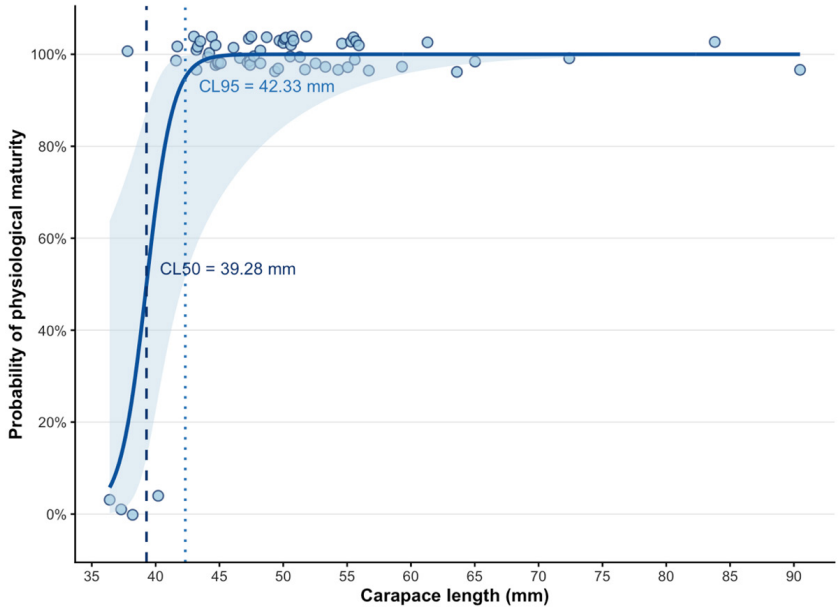

Figure 15. Logistic maturity curve showing the relationship between carapace length and probability of physiological maturity in female *Panulirus penicillatus* from Eastern Visayas, Philippines. Points represent individual females classified as immature or mature based on histological ovarian developmental stages. The solid line represents the fitted logistic model, and the shaded band indicates the 95% confidence interval. The dashed vertical line marks the estimated size at 50% maturity (CL_{50}), while the dotted vertical line marks the estimated size at 95% maturity (CL_{95}).

grounds, reproductive movements, or gear- and fisher-related selectivity. Since samples were obtained from fishery-dependent sources, including landed catch and buying stations, the observed sex ratio reflects the composition of the harvested population rather than a direct estimate of the unfished population.

Sex-ratio variation is common in spiny lobster fisheries and may be influenced by differences in habitat use, mobility, size, reproductive behavior, and vulnerability to fishing gears. In many panulirids, males may attain larger sizes than females, while females allocate more energy to ovarian development, egg production, brooding, and post-spawning recovery (MacDiarmid and Sainte-Marie 2006; Phillips 2013). The wider size range observed in males in this study is consistent with this general pattern and may partly explain why males were slightly more abundant in the landed catch. However, the occurrence of female-biased months also indicates that local fishing conditions and seasonal reproductive behavior likely contributed to the monthly variability in sex ratio.

4.2 Size structure and occurrence of reproductive individuals in the catch

The size distribution of *P. penicillatus* was concentrated mainly in the smaller to intermediate size classes. Males and non-berried females were most abundant within the 41–55 mm CL range, while berried females were most frequently observed within the 46–60 mm CL range. Males were represented across a wider size range and included the largest individuals recorded, whereas berried females were concentrated largely in intermediate size classes.

The overlap between the dominant size classes of the general catch and the size range of berried females is important because it shows that reproductive females are regularly captured by the fishery. Berried females were not restricted to large size classes; rather, many were recorded within the same size range that dominated the sampled catch. This indicates that fishing activities occur within the size range where females are already contributing to reproduction.

The smallest berried female recorded was 30.71 mm CL, showing that some females may become externally reproductive at relatively small sizes. However, the smallest berried individual should not be treated as the main maturity threshold. The presence of a single small berried female only indicates the minimum observed functional reproductive size, not the size at which most females in the population are mature. For management purposes, maturity ogives and population-level estimates such as CL_{50} and CL_{95} provide a more reliable basis than the smallest observed reproductive individual (Atherley et al. 2021; Thangaraja and Radhakrishnan 2017).

4.3 Incidence and seasonal size distribution of berried females

The monthly incidence of berried females showed strong temporal variation. In 2018, berried females were first recorded in March and increased sharply from April to August. The highest incidences were observed in July and August 2018, when berried females accounted for 51.2% and 52.9% of the monthly female samples, respectively. This pattern indicates a pronounced egg-bearing period during the middle of 2018.

In 2019, berried females were recorded throughout the year but at much lower monthly incidence, ranging from 1.7% to 7.6%. This suggests that egg-bearing activity persisted across months but with lower intensity compared with the 2018 peak. The difference between years may reflect real interannual variability in reproductive output, but it may also be influenced by sampling coverage, fishing grounds, or differences in the availability of reproductive females to the fishery. Because the data were fishery-dependent, caution is needed when interpreting interannual differences.

The seasonal size-distribution bubble plot further showed that berried females occurred across a wide size range, with CL class midpoints from approximately 35 to 108 mm. The highest concentration of berried females occurred within the 45–60 mm CL classes, especially from April to August 2018. In 2019, berried females were more widely distributed across months and size classes but generally occurred in lower numbers per size class. Together, these patterns indicate that egg-bearing activity is seasonal in intensity but extended across several months, with intermediate-sized females forming an important component of the reproductive catch.

4.4 External reproductive indicators: eggs, tarspots, and reproductive readiness

External reproductive indicators provided additional evidence that reproductive activity was not limited to egg-bearing females alone. Females with eggs only were most abundant in 2018, especially from April to August, with the highest number recorded in May 2018. In contrast, tarspot-bearing females and

females with both eggs and tarspots were mainly recorded in 2019, particularly from September to November.

The presence of tarspots is biologically important because the tarspot represents an externally attached spermatophoric mass deposited by the male during mating. In palinurid lobsters, the spermatophore is attached to the ventral thoracic region of the female and is later used during egg extrusion and fertilization (Matthews 1951; MacDiarmid and Sainte-Marie 2006). Therefore, females with tarspots but without eggs may represent recently mated females or individuals approaching oviposition. If only berried females are considered, reproductive activity may be underestimated.

The combined occurrence of eggs, tarspots, and eggs with tarspots supports the interpretation that *P. penicillatus* in Eastern Visayas has an extended reproductive period. Egg-bearing females were most abundant during the 2018 reproductive pulse, while tarspot-bearing females in 2019 indicated continued mating activity later in the year. This agrees with the broader view that multiple reproductive indicators should be considered when assessing spiny lobster reproductive dynamics because physiological, functional, and external indicators may not always coincide (Atherley et al. 2021).

4.5 Gonad morphology, histology, and reproductive cycle

Macroscopic and histological observations confirmed clear developmental changes in the gonads of *P. penicillatus*. Female ovaries changed from thin, whitish, and poorly developed structures in immature individuals to enlarged orange or dark orange ovaries in ripe individuals. Histological examination further confirmed six ovarian developmental stages: immature, developing, ripe, spawning, re-developing, and spent. These stages provided the basis for interpreting ovarian maturation and estimating physiological maturity.

The monthly distribution of ovarian stages indicated an extended reproductive cycle. In 2018, developing, ripe, and spent ovaries were observed from May to August, suggesting active ovarian maturation and recent spawning within the same general period when berried female incidence was high. In 2019, ripe ovaries were prominent from February to June, with February, May, and June composed entirely of ripe-stage ovaries. Spawning ovaries were recorded in March and April, while re-developing and developing ovaries appeared in later months. Spent ovaries were dominant in January and November 2019 and were present from July to October, indicating post-spawning or recovery phases.

This sequence of ripe, spawning, spent, re-developing, and developing stages suggests that reproduction is not confined to a single short season. Rather, *P. penicillatus* appears to undergo prolonged reproductive activity, with major reproductive signals in the first half of 2019 and a strong egg-bearing pulse in April to August 2018. Extended or multiple reproductive periods are common among tropical spiny lobsters, where seasonal environmental variation may be less restrictive than in temperate regions (MacDiarmid and Sainte-Marie 2006; Phillips 2013).

4.6 Gonadosomatic index and reproductive seasonality

The GSI results supported the histological interpretation of reproductive seasonality. Female GSI varied significantly among months, indicating temporal variation in ovarian development. The highest female GSI was recorded in February 2019, followed by June 2019 and March 2019, while a secondary elevation occurred in August 2018. These peaks correspond to months when ripe or advanced ovarian stages were observed, supporting their interpretation as periods of increased gonadal investment.

Low female GSI values were observed in July and September 2018, January 2019, and from August to October 2019. These lower values are consistent with spent, recovering, or early developing ovarian conditions. The slight increase in November 2019 may indicate renewed ovarian development, although this estimate was based on only two female samples and should be interpreted cautiously.

Male GSI showed weaker and more variable monthly patterns than female GSI. Although monthly differences in male GSI were statistically significant after excluding months with only one male observation, pairwise comparisons were not significant after adjustment. The high male GSI recorded in September 2019 was associated with high variability and a small sample size. Therefore, male GSI should be interpreted mainly as descriptive support, whereas female GSI provides a clearer seasonal signal of reproductive activity.

The combination of ovarian stage composition and GSI indicates that female *P. penicillatus* had distinct periods of advanced ovarian development, particularly in February and June

2019, with additional reproductive activity in August 2018. When considered together with berried female incidence and tarspot occurrence, these findings support the conclusion that reproductive activity is extended but varies in intensity through time.

4.7 Fecundity and reproductive value of larger females

Fecundity ranged from 41,962 to 446,782 eggs per female and increased significantly with carapace length. The fitted size-fecundity relationship showed that CL explained 37.5% of the variation in fecundity, indicating that size is an important but not exclusive predictor of egg production. This positive relationship is consistent with the general reproductive pattern in spiny lobsters, where larger females often contribute disproportionately to egg production (MacDiarmid and Sainte-Marie 2006; Phillips 2013). Similar size-related increases in fecundity have been reported for *P. penicillatus* from Taiwan, the Red Sea, and earlier Philippine work (Chang et al. 2007; Hogarth and Barratt 1996; Juinio 1987; Plaut 1993).

The moderate R^2 value suggests that factors other than CL also influence fecundity. Variation among females of similar size may be associated with nutritional condition, molting stage, ovarian condition, spawning history, egg developmental stage, or egg loss during capture and handling. Since egg masses were collected from landed individuals, some egg loss may have occurred before sampling, which could partly explain the observed variation.

From a management perspective, the positive size-fecundity relationship emphasizes the reproductive importance of larger females. Although many berried females occurred in intermediate size classes, larger females can contribute substantially more eggs. Therefore, management should not only aim to prevent the capture of immature individuals but also reduce unnecessary removal of berried females and larger reproductive females.

4.8 Size at physiological maturity, policy relevance, and local management implications

The logistic maturity analysis estimated CL_{50} at 39.28 mm CL and CL_{95} at 42.33 mm CL, indicating that female *P. penicillatus* in the sampled population attained physiological maturity at relatively small sizes. These values, however, should be interpreted as local biological maturity estimates based on ovarian histology, not as direct substitutes for the existing national legal-size limit. In this study, physiological maturity was determined from ovarian developmental stage, with females classified as mature when ovaries were developing, ripe, spawning, re-developing, or spent. This approach identifies whether the ovary has entered a mature developmental condition, but it does not necessarily confirm that a female has already spawned, brooded eggs, or contributed successfully to recruitment. Berried condition provides more direct evidence of egg-bearing at the time of capture, but it may underestimate maturity because mature females are not always carrying eggs when sampled.

Comparison with previous studies shows that reported maturity sizes for *P. penicillatus* vary among localities and maturity indicators (Table 2). The present CL_{50} and CL_{95} estimates are broadly comparable with reports from the Red Sea, where females were considered to mature around 40–50 mm CL, and with earlier Philippine observations indicating that many females were potentially mature at 45–49.9 mm CL. However, these biological estimates remain lower than the national regulatory reference under Fisheries Administrative Order No. 265 s. 2020, which identifies *P. penicillatus* as a regulated species and lists 7.2 cm CL, equivalent to 72 mm CL, as the carapace length at first sexual maturity or national minimum legal size.

This distinction is important for management. The 45 mm CL value, which is slightly above the estimated CL_{95}, may be discussed only as a local maturity benchmark; it should not be recommended as a replacement legal minimum size. The 72 mm CL national legal threshold remains more precautionary because it gives females greater opportunity to mature, spawn, brood eggs, and contribute to recruitment before becoming legally harvestable. This is especially important because fecundity increased significantly with carapace length, indicating that larger females have greater reproductive value.

The results also support strict protection of berried females and routine monitoring of tarspot-bearing females. Berried females were recorded across several months and size classes, and their capture directly removes embryos from the population. Tarspot-bearing females should also be monitored because tarspots indicate recent mating or potential spawning readiness. Because reproductive activity was extended, with egg-bearing females peaking from April to August 2018, ripe ovaries prominent from February to June 2019, and tarspot-bearing females recorded mainly from September to November 2019, a single closed season may not fully protect the reproductive stock if used alone. A more practical approach is year-round enforcement of the 72 mm

Table 2. Published maturity or reproductive-size indicators for *Panulirus penicillatus* and their relevance to the present study.

Study	Locality	Maturity or reproductive indicator	Reported size or key finding
Juinio 1987	Cagayan, Philippines	Reproductive condition and maturity observations	Most females were potentially mature at **45–49.9 mm CL**; male functional maturity was reported at approximately **70 mm CL.**
Chang et al. 2007	Taitung, southeastern Taiwan	Reproductive biology, sex ratio, GSI, fecundity, and maturity assessment	Examined *P. penicillatus* from **34.28–131.60 mm CL** and reported reproductive seasonality, fecundity, and maturity patterns for comparison with western Pacific populations.
Plaut 1993	Gulf of Eilat/Aqaba, Red Sea	Sexual maturity, reproductive season, and fecundity	Reported reproductive seasonality and fecundity patterns of *P. penicillatus* in a Red Sea population.
Hogarth and Barratt 1996	Red Sea	Size distribution, maturity, and fecundity	Reported that female *P. penicillatus* appeared to mature at approximately **40–50 mm CL**.
DA-BFAR 2020	Philippines	National regulatory reference under FAO No. 265 s. 2020	Lists the carapace length at first sexual maturity or national minimum legal size for *P. penicillatus* as 7.2 cm CL, equivalent to **72 mm CL**.
Present study	Eastern Visayas, Philippines	Histology-based physiological maturity using logistic maturity analysis	Estimated CL_{50} at 39.28 mm CL and CL_{95} at **42.33 mm CL**. These are local biological maturity reference points and should not replace the national 72 mm CL legal standard.

CL minimum legal size, strict protection of berried females, and regular monitoring at landing sites, buying stations, live lobster consolidation points, and transport checkpoints.

The present study supports the continued implementation of FAO No. 265 s. 2020 while providing local biological evidence to strengthen monitoring in Eastern Visayas. Measuring boards or calipers calibrated to the 72 mm CL legal threshold should be provided to fishers, traders, and enforcement personnel. Future work should expand histological sampling across more sites, months, years, and size classes, especially near the national legal threshold, to evaluate whether area-specific refinements may be warranted.

5. CONCLUSION AND RECOMMENDATIONS

This study provides robust local evidence on the reproductive biology of the pronghorn spiny lobster, *Panulirus penicillatus*, in Eastern Visayas, Philippines, and establishes biological information that can strengthen science-based fisheries management. The sampled population showed a slight but significant male bias, with monthly variation in sex ratio indicating that the composition of landings changes through time. Size distribution was concentrated mainly within the 41–55 mm CL range, while berried females were most commonly observed within the 45–60 mm CL range, demonstrating that reproductively active females are present within the size classes commonly represented in the catch.

Multiple lines of evidence indicate that *P. penicillatus* in Eastern Visayas has an extended reproductive period. Berried female incidence peaked from April to August 2018, particularly in July and August, while lower but persistent egg-bearing activity was observed throughout 2019. The occurrence of tarspot-bearing females, especially from September to November 2019, further suggests continued mating activity and reproductive readiness beyond the months of peak egg-bearing. Histological examination confirmed the presence of developing, ripe, spawning, re-developing, and spent ovaries across several months, while female GSI showed significant monthly variation, with peaks corresponding to periods of advanced ovarian development. Together, these indicators show that reproductive activity is not confined to a single short spawning season.

Fecundity increased significantly with carapace length, confirming the disproportionate reproductive value of larger females. This finding highlights the importance of protecting larger and egg-bearing females because their removal can reduce reproductive output and weaken recruitment

potential. The estimated size at physiological maturity was 39.28 mm CL for CL_{50} and 42.33 mm CL for CL_{95}, indicating that females in the sampled population become physiologically mature at relatively small sizes. However, these values should be treated as local biological maturity reference points, not as replacements for the national legal standard.

The findings strongly support the continued enforcement of Fisheries Administrative Order No. 265 s. 2020, which lists the carapace length at first sexual maturity or minimum legal size for *P. penicillatus* as 7.2 cm CL, equivalent to 72 mm CL, and prohibits the catching, possession, transport, sale, trade, and export of gravid spiny lobsters and juveniles below the prescribed size. The national 72 mm CL threshold remains more precautionary than the local physiological maturity estimates because it allows females greater opportunity to reproduce, brood eggs, and contribute substantially to spawning output before becoming legally harvestable.

Based on these findings, management should prioritize strict enforcement of the 72 mm CL national minimum legal size for *P. penicillatus*, together with year-round protection of berried females regardless of size. Tarspot-bearing females should also be incorporated into local reproductive monitoring because they indicate recent mating and potential spawning readiness. Enforcement should be strengthened at landing sites, buying stations, live lobster consolidation points, and transport checkpoints, where live lobsters can be inspected for carapace length, egg-bearing condition, and compliance with existing regulations. Standardized measuring boards or calipers calibrated to the 72 mm CL legal threshold should be provided to fishers, traders, and enforcement personnel to improve field implementation.

Continued reproductive monitoring is also recommended to refine local biological reference points and support adaptive management. Future studies should expand histological sampling across more months, years, sites, and smaller size classes; compare physiological maturity with functional maturity based on berried and tarspot condition; and evaluate whether reproductive peaks are consistent across fishing grounds. By linking reproductive biology with national policy implementation, this study provides a practical foundation for improving the sustainability of the *P. penicillatus* fishery in Eastern Visayas and reducing the risk of recruitment overfishing in this high-value reef-associated resource.

ACKNOWLEDGMENT

The authors thank the National Fisheries Research and Development Institute (NFRDI) for funding support, and Ricardo Loquias, Rene Lino Pore, Mark Lobos, and Michael Gayoso for their assistance in lobster data collection.

AUTHOR CONTRIBUTIONS

Campo CJM: Conceptualization, Methodology, Writing – original draft preparation, Data analysis, curation and visualization, Writing – Reviewing and Editing, Answering Reviewers Comments and Suggestions. **Boiser EB:** Methodology, Data collection, analysis, curation and visualization. **Salamida MTM:** Methodology, Data collection and analysis. **Bayani KC:** Methodology, Data collection and analysis. **Cabacaba NS**: Conceptualization, Writing – original draft preparation, Methodology, Supervision, Writing – Reviewing and Editing.

CONFLICTS OF INTEREST

The authors declare no conflict of interest exists.

ETHICS STATEMENT

Spiny lobsters were collected and sampled from local buying stations in accordance with local regulations and the exemption provided under Section 3(b) of Fisheries Administrative Order No. 265 (2020). Required permits were obtained from the respective Municipal Agriculture Offices. All specimens were handled following standard ethical guidelines for aquatic research, and no human subjects were involved.

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