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**RESEARCH ARTICLE**

# Population Dynamics and Relative Yield-Per-Recruit of Spiny Lobsters (*Panulirus* spp.) Using Size-Structured Models and Implications for Management in Eastern Visayas, Philippines

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## ABSTRACT

The sustainable management of tropical spiny lobster (*Panulirus* spp.) fisheries is constrained by limited biological data and monitoring systems, particularly in the Philippines. This study investigated the population dynamics and yield-per-recruit of six *Panulirus* species (*P. penicillatus*, *P. ornatus*, *P. versicolor*, and *P. femoristriga*) and the two subspecies of *P. longipes (P. l. longipes* and *P. l. bispinosus*) in Eastern Visayas using length-frequency data from 9,051 individuals sampled between February 2018 and December 2019. Size-based stock assessment models in FISAT II estimated a pooled asymptotic length ($L_\infty$) of 180.3 mm (males) and 169.8 mm (females), with a mean growth coefficient (K) of 0.16 $yr^{-1}$. Pooled total mortality (Z) averaged 1.00 $yr^{-1}$, and fishing mortality (F) was 0.74 $yr^{-1}$. Exploitation rates were high, with pooled estimates of 0.70 for males and 0.69 for females, and species-level values ranging from 0.53 to 0.79, exceeding the optimal $E_{max}$ in five of the six species. Beverton–Holt yield-per-recruit analysis revealed that current fishing practices result in suboptimal yields, with 47–90% of individuals landed below their size at first maturity. Negative allometric growth (b = 2.02–2.70) and low size at first capture, equivalent to 20–46% of $L_\infty$, further support evidence of growth overfishing. These findings highlight the urgent need for species-specific management interventions, including size-based harvest controls, effort regulation, and improved monitoring, to restore stock productivity and ensure long-term sustainability of spiny lobster fisheries in the region.

**Keywords:** *Panulirus spp., population dynamics, resource management, stock assessment, spiny lobster*
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# Dinamika ng Populasyon at Relatibong Ani-sa-Bawat-Rekrut ng mga Banagán (*Panulirus* spp.) Gamit ang mga Modelong Nakabatay sa Estruktura ng Laki at mga Implikasyon sa Pamamahala sa Silangang Visayas, Pilipinas

## ABSTRAK

Nalilimitahan ang sostenibleng pamamahala ng pangisdaan ng mga tropikal na banagán (*Panulirus* spp.) dahil sa kakulangan ng biyolohikal na datos at mga sistema ng monitoring, partikular sa Pilipinas. Sinuri ng pag-aaral na ito ang dinamika ng populasyon at ani sa bawat bagong indibidwal na pumapasok sa populasyong pinangingisdaan (yield-per-recruit) ng anim na species ng banagan o *Panulirus* (*P. penicillatus*, *P. ornatus*, *P. versicolor*, at *P. femoristriga*, *P. l. longipes* at *P. l. bispinosus*) sa Silangang Visayas gamit ang length-frequency data mula sa 9,051 banagan na nakolekta mula Pebrero 2018 hanggang Disyembre 2019. Gamit ang mga modelo ng pagtatasa ng stock na batay sa laki sa FISAT II, tinatayang 180.3 mm para sa mga lalaki at 169.8 mm para sa mga babae ang asimptotikong haba ($L\infty$) mula sa pinagsamang datos, at 0.16 $taon^{-1}$ ang karaniwang coefficient ng paglaki (K). Mula sa pinagsamang datos, ang karaniwang kabuoang mortalidad (Z) ay 1.00 $taon^{-1}$, at ang mortalidad dulot ng pangingisda (F) ay 0.74 $taon^{-1}$. Mataas ang mga antas ng labis na panghuhuli ng banagan na may pinagsamang pagtatayang 0.70 para sa mga lalaki at 0.69 para sa mga babae. Ang mga halaga para sa bawat species ay mula 0.53 hanggang 0.79, na lumampas sa pinakamainam na $E_{max}$ sa lima sa anim na species. Ipinakita ng pagsusuring Beverton–Holt ng yield-per-recruit na ang kasalukuyang mga gawi sa pangingisda ay nagreresulta sa ani na mas mababa sa pinakamainam, at 47–90% ng mga banagang nahuhuli at naidadala sa pampang ay mas maliit kaysa sa laki kung kailan sila unang nagiging ganap na reproduktibo. Ang negatibong alometrikong paglaki (b = 2.02–2.70) at maliit na laki sa unang pagkakahuli, na katumbas ng 20–46% ng

L∞, ay higit pang sumusuporta sa ebidensiya ng labis na panghuhuli bago makamit ng mga banagan ang laki na nagbibigay ng pinakamainam na ani (growth overfishing). Binibigyang-diin ng mga natuklasan ang agarang interbensiyon sa pamamahala na angkop sa bawat species, kabilang ang pagkontrol sa paghuli batay sa laki, regulasyon sa pangingisda, at pinahusay na monitoring, upang maibalik ang produktibidad ng naturang yamang-dagat at matiyak na pangmatagalan at sostenible ang panghuhuli ng mga banagan sa rehiyon.

**Mga susing salita:** *Panulirus spp.; dinamika ng populasyon; pamamahala ng yamang pangisdaan; pagtatasa ng stock; banagan*

## 1. INTRODUCTION

Understanding population ecology is fundamental to sustainable fisheries management because it provides the biological basis for conservation planning, ecosystem-based management, economic optimization, and climate-resilient resource governance (Roberts et al. 2001; Pitcher et al. 2009; Pikitch et al. 2004; Costello et al. 2016; Worm et al. 2006; Keyl and Wolff 2008). Fishery status can be inferred from abundance indices, stock structure, and catch composition, while more advanced assessment approaches evaluate biomass trends, exploitation dynamics, and harvest strategies (Kirkwood et al. 1994; Pope et al. 2010; Smith and Addison 2003; Walters and Martell 2004; Dowling et al. 2015). However, the reliability of these assessments depends on data availability, data quality, and the life-history characteristics of the species being assessed (Dowling et al. 2015; Newman et al. 2015).

Traditional age-structured stock assessment models are widely used in finfish fisheries, where age can be estimated from otoliths and other calcified structures (Punt et al. 2013; Francis et al. 2016; Mapp et al. 2017). These approaches are less suitable for spiny lobsters and other crustaceans because molting, or ecdysis, removes the exoskeleton and produces discontinuous growth, making accurate age determination difficult (Foo and Wang 2013; Hosamani et al. 2017; Huntsberger et al. 2020). Consequently, size-structured models are more appropriate for crustacean fisheries because they use length-frequency data that can be routinely collected from landings and fishery-dependent monitoring. This approach is particularly useful for data-limited stocks, where biological information is scarce but size-composition data can still generate estimates of growth, mortality, exploitation, recruitment, and yield-per-recruit (Punt et al. 2013; Hodgdon et al. 2022).

Spiny lobsters are high-value crustacean resources that support artisanal fisheries, coastal livelihoods, and live seafood trade in many tropical regions (Holmyard and Franz 2006). In the Philippines, seven species and subspecies have been recorded: *Panulirus penicillatus*, *P. ornatus*, *P. versicolor*, *P. homarus*, *P. femoristriga*, and the two subspecies of *P. longipes, P. l. longipes*, and *P. l. bispinosus* (Juinio and Gomez 1986; Juinio-Meñez and Dantis 1996; Juinio-Meñez and Gotanco 2004). In Eastern Visayas, all have been confirmed except *P. homarus*, which appears to be rare in the region (Juinio and Gomez 1986; Campo et al. 2023). Despite their economic value, Philippine spiny lobsters remain poorly assessed, with limited species-specific information on growth, mortality, recruitment, exploitation, and size at first capture.

Philippine spiny lobsters contribute to subsistence fisheries, artisanal livelihoods, and aquaculture production, particularly in CARAGA, Bicol, Davao, Western and Eastern Visayas, and the Zamboanga Peninsula [Philippine Statistics Authority (PSA) 2017]. *P. penicillatus* and *P. ornatus* are among the most abundant and commercially important species. Lobsters are harvested mainly through hookah diving, although traps, spearguns, fish corrals, hook and line, and gillnets also contribute to catches (Juinio and Gomez 1986; Juinio-Meñez and Dantis 1996). Fry and juveniles are also collected in Eastern Visayas and Davao Oriental for grow-out culture in cages and pens (Macusi et al. 2019; Campo et al. 2023). The increasing demand for live lobsters has intensified fishing pressure because individuals of various sizes are accepted in local trade chains and transported to domestic and export markets.

Recent national fisheries reports indicate continuing pressure on Philippine fisheries production, with total fisheries output declining from 4.26 million MT in 2023 to 4.05 million MT in 2024, and quarterly declines reported in 2024 (PSA 2024, 2025). Although updated national species-specific lobster statistics remain limited, earlier records and field observations indicate declining lobster production and persistent exploitation of juveniles and subadults (Bureau of Agricultural Statistics 2012; PSA 2014; PSA 2017; Campo et al. 2023). Existing regulations, including the FAO No. 265 series of 2020 and the DILG Memorandum Circular No. 129 series of 2002, provide a policy basis for controlling the capture

and trade of undersized and gravid lobsters and for regulating compressor-assisted fishing. However, effective implementation requires updated biological and fishery-dependent evidence.

This study assessed the population dynamics and relative yield-per-recruit of six species and subspecies of spiny lobsters caught in Eastern Visayas, Philippines. Specifically, it examined relative abundance, size distribution, sex ratio, carapace length–body weight relationship, relative condition factor, growth parameters, mortality, exploitation rate, probability of capture, recruitment pattern, and relative yield-per-recruit. The findings provide evidence-based information to strengthen existing management measures and support species-specific conservation strategies for Philippine spiny lobster fisheries.

## 2. MATERIALS AND METHODS

### 2.1 Study site

Eastern Visayas is located in the east-central part of the Philippines (11° 14.0'N, 125° 0.0'E), bordered by the Philippine Sea to the east, the San Bernardino Strait to the north, the Camotes and Visayan Seas to the west, and the Surigao Strait to the south. The population dynamics of the spiny lobster were investigated in four key sites of the region: 1) San Jose, Northern Samar; 2) San Policarpo; 3) Guiuan, Eastern Samar; and 4) Silago-Hinunangan, Southern Leyte (Figure 1). These sites are primary contributors to spiny lobster production in the Eastern Visayas (Campo et al. 2023).

### 2.2 Data collection

Spiny lobster data were collected for 23 months, from February 2018 to December 2019, following the sampling scheme of the National Stock Assessment Program of the Department of Agriculture–National Fisheries Research and Development Institute (DA-NFRDI) (Santos et al. 2017). Sampling was conducted at lobster landing sites and buying stations for 20 days in a 30-day month and 21 days in a 31-day month.

Fishing activity in the study sites was primarily small-scale and artisanal, with hookah diving as the dominant method for collecting live spiny lobsters. Hookah diving is commonly used because it allows fishers to selectively collect live and undamaged lobsters from reef habitats, which is important in the live lobster trade where body integrity and survival condition strongly influence market value. However, this method may also introduce gear selectivity toward visible, accessible, and marketable size classes and species. Other gears, including traps, spearguns, fish corrals, hook and line, and gillnets, contributed to incidental catches. Standardized fishing-effort data, such as number of active fishers, fishing trips, fishing hours, or gear units per area, were not consistently recorded across sites during the study period.

A total of 9,051 live, undamaged, and healthy spiny lobsters were sampled, comprising *P. penicillatus* (n = 5,987), *P. ornatus* (n = 1,900), *P. versicolor* (n = 260), *P. femoristriga* (n = 345), *P. longipes longipes* (n = 447), and *P. longipes bispinosus* (n = 112). Species were identified using recognizable morphological characteristics following Motoh and Kuronuma (1980), Williams (1986), and Ravago-Gotanco and Juinio-Meñez (2002).

Only live, undamaged, and healthy lobsters were included in the biometric analysis to ensure reliable species identification, sex determination, carapace length measurement, body-weight measurement, and condition-factor estimation. Moribund, damaged, incomplete, or heavily injured individuals were excluded because broken carapaces, missing appendages, or poor body condition could bias length–weight relationships and relative condition factor estimates. Discards and rejected individuals were not consistently recorded at landing sites or buying stations and were therefore excluded from the analysis.

For each specimen, species, sex, body weight, and carapace length were recorded. Carapace length was measured from the anterior notch between the orbital spines to the posterior edge of the carapace using an electronic digital caliper, accurate to 0.01 mm [Eagletech, KDS, Philippines]. Body weight was measured using an electronic digital weighing scale, accurate to 0.01 g [Number One, NKS-6, Philippines].

### 2.3 Data analysis

#### 2.3.1 Relative abundance, size composition and sex ratio

Relative abundance was calculated as the percentage contribution of each species or subspecies to the total number of sampled spiny lobsters. Descriptive statistics of lobster CL and BW were determined and compared between male and female lobsters via Welch's t-test, with Cohen's D for the measure of effect size on IBM SPSS version 21. The variations in size-frequency distributions in CL and BW of lobsters were

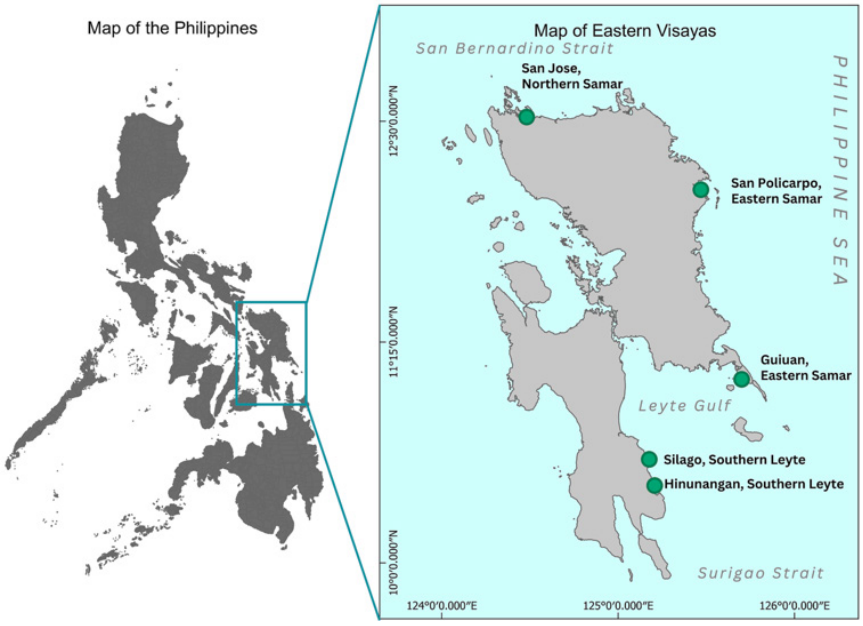


Figure 1. Spiny lobster assessment sites in Eastern Visayas, Philippines. Note: Green markers indicate the location of sampling site.

also determined for both lobster sexes. The monthly, quarterly, and monsoonal variations in sex ratio were also determined and analyzed using a one-way ANOVA with a 95% confidence interval.

### 2.3.2 Morphometric relationship and relative condition factor

The length-weight relationship for each male and female spiny lobster was analyzed using linear regression of the log-transformation of the potential model equation (Le Cren 1951):

$$W = aL^b$$

where $W$ is the BW, $L$ is the CL, $a$ is the intercept, and $b$ is the slope of the equation. The coefficient $b$ also represents the allometry of growth as observed in most crustaceans, including spiny lobsters (Fazhan et al. 2021; Waiho et al. 2021; de Carvalho-Souza et al. 2023), where $b = 3$ characterizes isometric growth, $b < 3$ characterizes negative allometric growth, and $b > 3$ characterizes positive allometric growth (Cusba and Paramo 2017). The allometry of $b$ coefficients was compared to the isometric value $b = 3$ using a Student t-test. The relative condition factor, $K_n$, of the six spiny lobster species was also estimated using the equation of Le Cren (1951):

$$K_n = W/W'$$

where $W$ represents the observed weight and $W'$ represents the estimated theoretical weight based on the carapace length-body weight relation established for each male and female lobster species. Statistical comparisons on relative condition factors among species were analyzed using one-way ANOVA, and within male and female spiny lobsters using independent-samples t-test.

### 2.3.3 Estimation of population parameters

The monthly data of male and female lobster CL-frequency distribution pooled for all Eastern Visayas were coded in FISAT II (Food and Agriculture Organization – International Center for Living Aquatic Resources Management Fish Stock Assessment Tool II) version 1.2.2 software to generate ecological data estimates on growth, mortality, exploitation levels, probability of capture, recruitment patterns, and relative yield-per-recruit (Gayanilo et al. 2005).

a. Growth parameters

We used the Powell-Wetherall Plot and ELEFAN I (electronic length frequency analysis) methods to estimate the length at infinity ($L_\infty$), growth coefficient ($K$), and growth performance index ($ø'$) of male and female spiny lobsters. The analysis for growth parameters assumed the von Bertalanffy growth function (VBGF) (Pauly 1984) with the formula (Sparre and Venema 1998) as follows,

$$L_t = L_\infty [1 - e^{-K(t-t0)}],$$

where $L_t$ is the length of the fish at age $t$, $e$ is the Naperian logarithm, and $t_0$ is the theoretical age that the fish would reach when it has a length of 0. The

value of $t_0$ was determined using the empirical formula of Pauly (1984):

$$log (-t_0) = 0.3922 – 0.2752 (log L_\infty) – 1.038 (log K).$$

The length-based growth performance index (ø') was also determined to test the gross accuracy of growth parameters such as $L_\infty$ and $K$ (Pauly 1979). This was calculated using the following empirical formula (Pauly 1979; Pauly and Munro 1984):

$$ø' = log (K) + 2 (log L_\infty).$$

Longevity, or $t_{max,}$ was estimated using the equation (Pauly 1983):

$$t_{max} = 3/K + t_0.$$

b. Mortalities and exploitation rate

The instantaneous mortality estimates can be described as $Z = F + M$, where $Z$ is total mortality, F is fishing mortality, and M is natural mortality, all expressed in $y^{-1}$. Total mortality $Z$ was determined using the length-converted catch curve of the Beverton and Holt (1956) equation:

$$Z = K [(L_\infty – L) / (L – L')],$$

where $L'$ is the initial length of the sample.

Natural mortality $M$ was estimated using the Pauly (1984) empirical formula, but with consideration of the clustering habit of spiny lobsters. For spiny lobsters, the $M$ value must be 20% lower than the true value (Sparre and Venema 1998):

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

$$M = 0.8^{\,ln (M)}$$

where $L_\infty$ and K are the VBGF growth parameters, and T equals 29°C, which is the average temperature of habitat in Eastern Visayas and in tropical areas neighboring the Philippines (Kühlmann 2002; Gordon et al. 2011; Comiso et al. 2015; Beni and Wardiatno 2020; Ravelo et al. 2022).

Approximations of natural mortality were also determined using eight various empirical estimators of $M$ utilizing known input parameters $L_{\infty,}$ $K$, $t_{0,}$ $t_{max}$, annual habitat temperature, and user inputs from FISAT II (Table 1). Inverse variance-weighting (Hamel 2015) and method-weighting (Cope and Hamel 2022) generated mean approximations of $M$.

The fishing mortality $F$ was automatically determined using the estimates of $Z$ from FISAT II and the mean value $M$ via method-weighting. The exploitation rate was calculated according to Gulland (1969) as the ratio of total mortality due to fishing ($E = F/Z$).

c. Probabilities of capture

The probabilities of capture were estimated by extrapolation. The descending left side of the catch curve (lobsters that were "ought" to have been caught) was added to the curve with the ratio of the "expected" and "actual" catch. This information can be estimated using the equation:

$$P_i = ln (N_i/\Delta t)/ ln (N_{ai}/\Delta t),$$

where $P_i$ is the point of the probability of capture, $N_i$ is the number of observed catches or the size of the population, $N_{ai}$ is the number of available catches, and $\Delta t$ is the change in time. The values for $L_{25}$, $L_{50}$, and $L_{75}$ were computed using the software's logistic transformation routine.

d. Recruitment pattern

The recruitment patterns were predicted from growth parameter values and mortalities using the recruitment pattern routine. These were obtained through backward projection onto the length axis of a set of length-frequency data. In this prediction, the number of recruitment pulses per year and their relative strengths were also estimated.

e. Relative yield per recruit (Y'PR)

The theoretical yield per recruit prediction was estimated using the alternative Beverton and Holt's (1966) relative yield per recruit (Y'PR) model with the following equation:

$$(Y'/R) = EU^{M/K}\left\{1 - \frac{3U}{(1+m)} + \frac{3U^2}{(1+2m)} - \frac{3U^3}{(1+3m)}\right\}$$

where, $U = 1 – (L_c/L_\infty)$; $m = (1 – E)/(M/K) = (K/Z)$; and, $E = F/Z$. The traditional Beverton-Holt yield-per-recruit model assumes isometric growth ($b$ = 3.0) in fish (Ricker 1975). It should be noted that the $b$ coefficients for spiny lobsters in this study were estimated to be less than 3.0. The relative yield per recruit in FISAT II utilizes the above formula in estimating "relative" yield per recruit without the assumption of isometric growth ($b \neq 3$) (Pauly 1984). An isopleth graph was automatically generated using the Knife-edge Selection routine through inputs of $M/K$ and $L_c/L_\infty$ values.

The current exploitation ratio ($E$) was also plotted to express the present exploitation level of the spiny lobster species. The estimates for $E_{max}$, $E_{0.1}$, and $E_{0.5}$ were calculated using the first derivative of this function and were automatically generated in the FISAT II program. $E_{max}$ is the exploitation level that maximizes yield or biomass per recruit. $E_{0.1}$ refers to the level of exploitation where the increase in yield per recruit reaches a tenth of the marginal increase computed at a zero-exploitation rate. $E_{0.5}$ is the exploitation that will result in a 50% decrease in the unexploited biomass (Gayanilo et al. 2005).

Recommendations for minimum legal carapace length were formulated by estimating the annual growth of lobsters using the VBGF function (Pitcher 1993). The values for $t$ years were manipulated

Table 1. Empirical estimators used in determining the natural mortality of spiny lobsters in Eastern Visayas.

| Model name | Input requirements | Equation | Model empirically used by: |
|---|---|---|---|
| $Hoenig_{lm}$ | $t_{max}$ | $\log(M_{est}) = 1.717 - 1.01 \log(t_{max})$ | Then et al. 2015 |
| $Hoenig_{nls}$ | $t_{max}$ | $M_{est} = 4.899\ t_{max}^{-0.916}$ | Then et al. 2015 |
| One-parameter $A_{max}$ | $t_{max}$ | $M = 4.374/\ A_{max}$ | Hamel 2015 |
| One-parameter $K$ | $K$ | $M_{est} = 1.692K$ | Jensen 1996; updated by Then et al. 2015 |
| Two-parameter $K$ | $K$ | $M_{est} = 0.098 + 1.55K$ | Jensen 2001; updated by Then et al. 2015 |
| Revised $Pauly_{nls\text{-}T}$ | $K$, $L_\infty$ | $M_{est} = 4.118K^{0.73} L_\infty^{-0.33}$ | Pauly 1980; updated by Then et al. 2015 |
| Revised $Pauly_{nls}$ | $K$, $L_\infty$, $T$ | $M_{est} = 0.9766\, L_\infty^{-0.2775} K^{0.6551} T^{0.4641}$ | Pauly 1980; recalculated by Hamel 2015 |
| Zhang and Megrey ZM Model (revised Alverzon and Carney AC Model) | $K$, $t_{max}$, $t_0$ | $M_{est} = \frac{\beta K}{e^{K(t_{mb}-t_0)} - 1}$ where, $t_{mb} = 0.38t_{max}$ and $\beta$ is a parameter of length-weight relationship | Zhang and Megrey 2006; Alverson and Carney 1975 |

until the attainment of a carapace length value that would maximize the yield of the stock.

## 3. RESULTS

### 3.1 Relative abundance, size composition, and sex ratio

Six species and subspecies of spiny lobster were sampled in this study: *P. penicillatus* (66.15%), *P. ornatus* (20.99%), *P. versicolor* (2.87%), *P. femoristriga* (3.81%), *P. longipes longipes* (4.94%), and *P. longipes bispinosus* (1.24%). The largest landed lobsters belong to the species *Panulirus ornatus,* with a mean CL and body weight of 94.2 mm and 991.0 g for males and 105.9 mm and 1286.0 g for females (Table 2). On the other hand, the lowest average sizes of lobster catch belong to *P. penicillatus*, with a mean CL and body weight of 57.3 mm and 217g for males and 56.1 mm and 204 g for females, respectively. The mean CL of the other four spiny lobsters ranges from 56.6 to 76.9 mm, while the mean body weight ranges from 227 g to 464 g. The mean CL and BW significantly differ in males and females for the species *P. ornatus* ($p < 0.001$) with a medium effect size (Cohen's d equals -0.38 for CL and -0.36 for BW), and for *P. penicillatus*, however, with a negligible effect size (Cohen's d equals 0.07 for CL and 0.09 for BW).

The CL-frequency data for spiny lobsters were classified into 5 mm intervals (Figure 2). The highest percentage of juveniles and sub-adults, or individuals below size-at-sexual maturity, was observed for *P. penicillatus,* with a cumulative composition of 90%, and whose highest frequency was at 52.7mm (18.3%) mid-length. Following this were *P. versicolor* with 71% juvenile composition (modes at mid-lengths 67.5 mm and 72.5 mm), *P. l. bispinosus* with 61% (mode at 47.5 mm), *P. femoristriga* with 60% (modes at 47.5 mm and 52.5 mm), *P. l. longipes* with 51% (mode at 57.5 mm), and *P. ornatus* with 47% (mode at 122.5 mm).

A pooled proportion of 57.14% of spiny lobsters were male, while 42.86% were female. The pooled sex ratio for all spiny lobster species was 1:0.75 (male-to-female). Among the six spiny lobsters, *P.*

*penicillatus* had a sex ratio closest to 1:1 (1:0.80), while *P. versicolor* had the furthest with a ratio of 1:0.57. The sex ratio did not change significantly between months, quarters, and monsoon seasons when pooled and compared using a single-factor ANOVA ($p > 0.05$) (Figure 3).

### 3.2 Morphometric relationship and relative condition factor

Carapace length and body weight in all spiny lobster species had a significantly high degree of positive correlation, with an *R* value that ranged from 0.78 to 0.96 ($p < 0.001$) (Figure 4 and Table 3). Moreover, the growth behavior of all spiny lobsters, regardless of species and sex, showed negative allometric growth. The *b* coefficients ranged from 2.02 to 2.70, which deviated significantly from the isometric value of 3 using a Student t-test ($p < 0.001$). Moreover, the values of the relative condition factor ($K_n$) of spiny lobsters were > 1.0, with female *P. ornatus* being significantly highest (ANOVA, $p < 0.001$) (Table 3). No significant difference in $K_n$ was analyzed for the other species. Within each species, only *P. ornatus* showed a significant difference in $K_n$ between males and females (ANOVA, $p < 0.001$).

### 3.3 Population parameters

#### 3.3.1 VBGF Growth parameters

The von Bertalanffy growth function (VBGF) and length frequency plots of spiny lobster species are shown in Figure 5. The results on various population parameters such as the length at infinity ($L_\infty$), growth coefficient (*K*), growth performance (*ø'*), values of instantaneous mortalities, *Z*, *F,* and *M* (total, fishing, and natural), exploitation rates, and various estimates of *M* are presented in Table 4.

The VBGF fitted to size intervals provided estimates for the asymptotic length $L_\infty$. A higher pooled estimate was observed for male spiny lobsters at 180.29 mm CL, compared to females at 169.76 mm CL. Most of the cohorts of spiny lobsters belong to sizes < 75 mm, except for *P. ornatus,* which has a wider spread of cohorts with CL > 125 mm. The highest average $L_\infty$ values were determined for *P. ornatus* at 270.5 mm CL, while the lowest were for *P. l. longipes* at 139.1 mm CL. The average $L_\infty$ estimated for *P. penicillatus* was at 183.8 mm CL, for *P. versicolor* it was at 152.3 mm CL, for *P. femoristriga* it was at 160.13 mm CL, and for *P. l. bispinosus* it was at 144.4 mm CL.

The growth rates *K* of spiny lobsters were pooled at 0.16 $y^{-1}$ ($K_{male}$ = 0.13 $y^{-1}$; $K_{female}$ = 0.18 $y^{-1}$). The pooled growth performance estimates, *ø',* for all spiny lobster species were 3.60 for males and 3.67 for females. The average maximum age $t_{max}$ for spiny lobsters was 23.6 years for males and 18.6 years for females. The highest $t_{max}$ was observed for male *P. ornatus* and male *P. l. bispinosus* with 30 yrs., while the lowest was observed for female *P. l. longipes* with 12 years.

#### 3.3.2 Mortality and exploitation rate

The linearized length-converted catch curve (Figure 6) was used to derive the values for total mortality (*Z*), natural mortality (*M*), fishing mortality (*F*), and exploitation rate (*E*).

Table 4 shows the values for *Z*, *M*, and *F*. The *Z* estimates for all species were $Z_{male}$ = 1.10 $y^{-1}$; $Z_{female}$ = 1.10 $y^{-1}$; and $Z_{pooled}$ = 1.0 $y^{-1}$. The pooled estimates of *M* using method-weighting and the resulting *F* were higher in females ($M_{female}$ = 0.31 $y^{-1}$; $F_{female}$ = 0.79 $y^{-1}$) than in male spiny lobsters ($M_{male}$ = 0.26 $y^{-1}$; $F_{male}$ = 0.64 $y^{-1}$). *P. l. longipes* had the highest average *M* estimate among the species, with 0.34 $y^{-1}$, ahead of *P. penicillatus* and *P. versicolor* with 0.33 $y^{-1}$, *P. femoristriga* with 0.31 $y^{-1}$, *P. ornatus* with 0.22 $y^{-1}$, and *P. l. bispinosus* with 0.19 $y^{-1}$. Moreover, *P. penicillatus* had the highest average *F* estimate of 1.15 $y^{-1}$, followed by *P. femoristriga* with 0.94 $y^{-1}$, *P. ornatus* with 0.86 $y^{-1}$, *P. l. longipes* with 0.56 $y^{-1}$, *P. l. bispinosus* with 0.43 $y^{-1}$, and *P. versicolor* with 0.37 $y^{-1}$. Moreover, the fishing mortality for all species, regardless of sex, was higher than their estimated *M* value, which translated to exploitation rates greater than 0.50.

The estimated exploitation levels are shown in Table 5. Exploitation rates were 0.70 and 0.69 for males and females, respectively. Among all species, *P. ornatus* had the highest pooled exploitation rate (0.79), while *P. versicolor* had the lowest value (0.53).

The exploitation levels as predicted using Beverton and Holt's yield-per-recruit analysis showed extremely higher current *E* values compared to $E_{max}$ for all species, except for *P. versicolor*. The current exploitation levels were 5.0–65.0% higher than the maximum exploitation level. The highest predicted $E_{max,}$ $E_{0.5}$, and $E_{0.1}$ were estimated for *P. ornatus* (pooled male and female: $E_{max}$ = 0.70; $E_{0.5}$ = 0.35; $E_{0.1}$ = 0.59), and the lowest for *P. penicillatus* (pooled male and female: $E_{max}$ = 0.47; $E_{0.5}$ = 0.29; $E_{0.1}$ = 0.38).

#### 3.3.3 Probability of capture

The size at first capture, $L_c$ or $L_{50}$, for *P.*

Table 2. Descriptive statistics, independent sample t-test and size effects of the carapace length and body weight of spiny lobsters in Eastern Visayas, Philippines.

| Species | Sex | N | Carapace length (mm) | | | | | | Body Weight (g) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Mean (± SD) | Min | Max | Welch's *t*-value | *p*-value | Cohen's d | Mean (± SD) | Min | Max | Welch's t-test | p-value | Cohen's d |
| *P. penicillatus* | M | 3316 | 57.3 ± 15.3 | 29 | 180 | 3.303 | <0.001 | 0.085 | 217.0 ± 200.3 | 20 | 3410 | 2.825 | <0.001 | 0.072 |
| | F | 2671 | 56.1 ± 13.5 | 30 | 167 | | | | 204.0 ± 158.8 | 20 | 1800 | | | |
| | Pooled | 5987 | 56.7 ± 14.6 | 29 | 180 | | | | 210.9 ± 183.0 | 20 | 3410 | | | |
| *P. ornatus* | M | 1163 | 94.2 ± 32.5 | 31 | 279 | -8.347 | <0.001 | -0.380 | 991.0 ± 834.6 | 10 | 4550 | -7.709 | <0.001 | -0.358 |
| | F | 737 | 105.9 ± 27.9 | 35 | 247 | | | | 1286.0 ± 808.9 | 50 | 3990 | | | |
| | Pooled | 1900 | 98.7 ± 31.3 | 31 | 279 | | | | 1105.7 ± 837.0 | 10 | 4550 | | | |
| *P. versicolor* | M | 165 | 72.6 ± 20.0 | 41 | 152 | -1.480 | 0.141 | -0.198 | 431.0 ± 326.6 | 70 | 1800 | -0.811 | 0.418 | -0.100 |
| | F | 95 | 76.9 ± 23.3 | 46 | 154 | | | | 464.0 ± 327.5 | 90 | 1810 | | | |
| | Pooled | 260 | 74.2 ± 21.3 | 41 | 154 | | | | 443.3 ± 326.8 | 70 | 1810 | | | |
| *P. femoristriga* | M | 214 | 59.1 ± 15.7 | 28 | 123 | -0.665 | 0.506 | -0.078 | 250.0 ± 190.4 | 30 | 1520 | -1.176 | 0.241 | -0.144 |
| | F | 131 | 60.5 ± 19.4 | 35 | 150 | | | | 283.0 ± 294.1 | 50 | 1940 | | | |
| | Pooled | 345 | 59.6 ± 17.2 | 28 | 150 | | | | 262.4 ± 235.4 | 30 | 1940 | | | |
| *P. l. longipes* | M | 250 | 63.1 ± 18.1 | 31 | 133 | -1.088 | 0.277 | -0.105 | 313.0 ± 253.6 | 60 | 1490 | -1.818 | 0.070 | -0.180 |
| | F | 197 | 65.2 ± 21.0 | 24 | 180 | | | | 368.0 ± 356.6 | 20 | 3480 | | | |
| | Pooled | 447 | 64.0 ± 19.4 | 24 | 180 | | | | 337.5 ± 304.2 | 20 | 3480 | | | |
| *P. l. bispinosus* | M | 64 | 56.2 ± 12.9 | 25 | 87 | -1.981 | 0.051 | -0.405 | 227.0 ± 127.8 | 50 | 550 | -1.790 | 0.078 | -0.373 |
| | F | 48 | 63.2 ± 21.7 | 37 | 133 | | | | 299.0 ± 254.6 | 60 | 1310 | | | |
| | Pooled | 112 | 59.2 ± 17.5 | 25 | 133 | | | | 257.9 ± 194.9 | 50 | 1310 | | | |

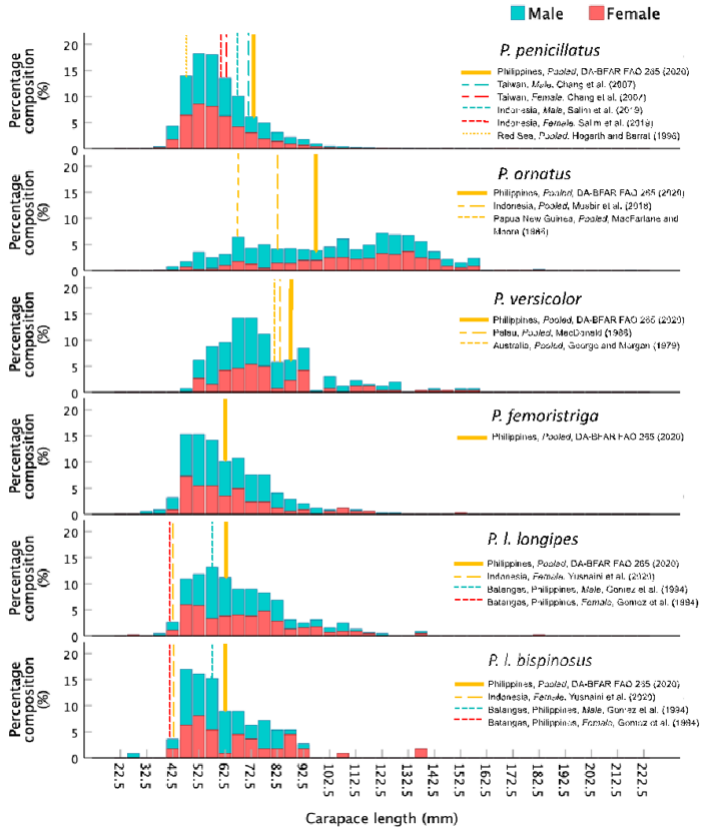


Figure 2. Carapace length frequency distribution of male and female spiny lobsters in Eastern Visayas. Note: Lines represent established size at sexual maturity of male and female spiny lobsters in various regions. Thickest yellow lines represent the minimum size in catching spiny lobsters in the Philippines and is based on size at initial sexual maturity according to Philippine Fisheries Administrative Order No. 265 (DA-BFAR 2020).

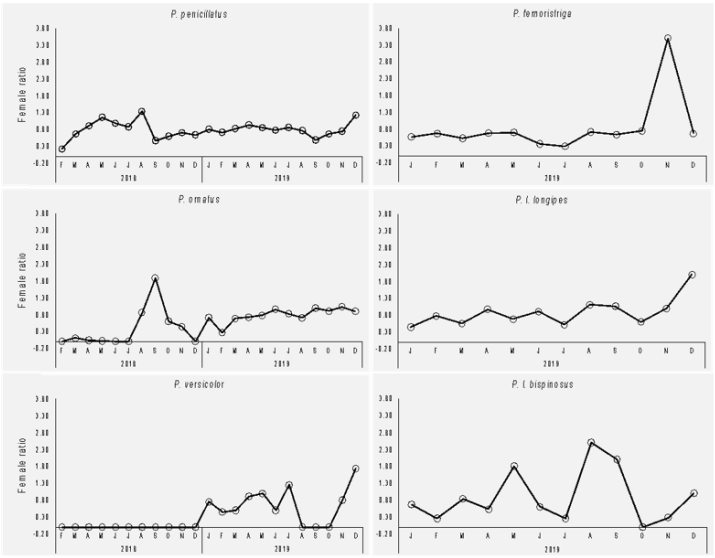


Figure 3. Monthly variation in female sex ratio of the six spiny lobsters relative to male ratio at 1.0. Note: No significant difference ($p > 0.05$) in monthly, quarterly, and monsoonal female ratios in all species. The colored range of months indicate the usual seasonal occurrence of Southwest monsoon (Habagat) in the Philippines, while the uncolored months indicate the Northeast monsoon (Amihan).

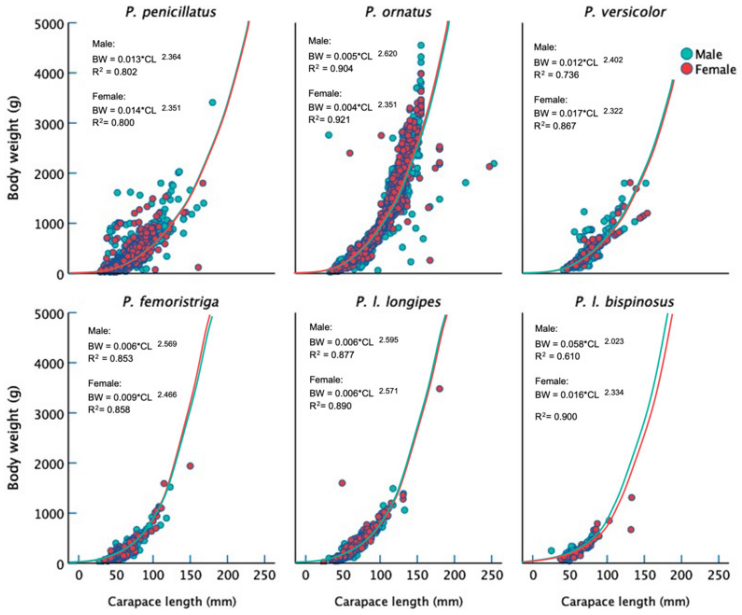


Figure 4. Length-weight (carapace length – body weight) relationship of male and female spiny lobsters in Eastern Visayas. Note: ANOVA of all regression lines have *p*-values <0.001.

Table 3. Regression parameters of the log-linear carapace length-weight relationship, body allometry and relative condition factor of the six spiny lobster species and subspecies in Eastern Visayas.

| Species | Sex | n | *a* | *b* | CI of *b* | *Adjusted R²* | *R* | *p*-value of regression | Allometry | $K_n$ (± SD) |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. penicillatus* | M | 3316 | 0.013 | 2.364 | 2.324 – 2.404 | 0.802 | 0.896 | <0.001 | – * | 1.035 ± 0.482[a] |
| | F | 2671 | 0.014 | 2.351 | 2.306 – 2.395 | 0.800 | 0.894 | <0.001 | – * | 1.024 ± 0.399[a] |
| *P. ornatus* | M | 1163 | 0.005 | 2.620 | 2.571 – 2.669 | 0.904 | 0.951 | <0.001 | – * | 1.107 ± 1.991[a*] |
| | F | 737 | 0.004 | 2.701 | 2.649 – 2.764 | 0.921 | 0.960 | <0.001 | – * | 4.802 ± 1.698[b*] |
| *P. versicolor* | M | 165 | 0.012 | 2.402 | 2.180 – 2.625 | 0.736 | 0.858 | <0.001 | – * | 1.090 ± 0.519[a] |
| | F | 95 | 0.017 | 2.322 | 2.134 – 2.509 | 0.867 | 0.931 | <0.001 | – * | 1.011 ± 0.265[a] |
| *P. femoristriga* | M | 214 | 0.006 | 2.569 | 2.425 – 2.714 | 0.853 | 0.923 | <0.001 | – * | 1.029 ± 0.281[a] |
| | F | 131 | 0.009 | 2.466 | 2.291 – 2.640 | 0.858 | 0.926 | <0.001 | – * | 1.064 ± 0.308[a] |
| *P. l. longipes* | M | 250 | 0.006 | 2.595 | 2.473 – 2.716 | 0.877 | 0.936 | <0.001 | – * | 0.961 ± 0.264[a] |
| | F | 197 | 0.006 | 2.571 | 2.444 – 2.698 | 0.890 | 0.944 | <0.001 | – * | 1.142 ± 0.814[a] |
| *P. l. bispinosus* | M | 64 | 0.058 | 2.023 | 1.613 – 2.434 | 0.610 | 0.781 | <0.001 | – * | 1.105 ± 0.733[a] |
| | F | 48 | 0.016 | 2.334 | 2.103 – 2.566 | 0.900 | 0.948 | <0.001 | – * | 1.006 ± 0.208[a] |

Note: **n** is sampled frequency; ***a*** and ***b*** are constants in $W = aL^b$; **CI of *b*** is the confidence interval of coefficient *b*; $\boldsymbol{R^2}$ is the adjusted coefficient of determination; ***R*** is the linear regression coefficient; **– *** means all species have negative allometric growth with significantly different *b* coefficient (p <0.001) when compared to the isometric growth $b = 3$ using student's t-test; $\boldsymbol{K_n}$ is the relative condition factor (Le Cren 1951) with standard deviation (**SD**); similar superscript letters of $K_n$ means no significant difference among all categories, while asterisk (*) in $K_n$ means a significant difference (p < 0.001) between male and female of the indicated species (*P. ornatus*).

Table 4. Estimated length at infinity ($L\infty$), growth coefficient ($K$), growth performance ($\phi'$), values of instantaneous mortality (total, fishing and natural), and various estimates of $M$ for spiny lobster species and subspecies in Eastern Visayas.

| Species | Sex | $L\infty$ | $K$ | $\phi'$ | $t_0$ | $t_{max}$ | $Z$ | CI of Z | $F$ | *Estimates of M* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | $M_{FISAT}$ | $M_1$ | $M_2$ | $M_3$ |
| *P. penicillatus* | M | 191.63 | 0.13 | 3.68 | -0.10 | 23.1 | 1.30 | 1.24 – 1.37 | 0.99 | 0.27 | 0.31 | 0.300 | 0.304 |
| | F | 175.88 | 0.19 | 3.77 | -0.26 | 15.8 | 1.66 | 1.56 – 1.75 | 1.32 | 0.30 | 0.34 | 0.270 | 0.363 |
| *P. ornatus* | M | 281.10 | 0.10 | 3.90 | -0.03 | 30.0 | 1.15 | 0.87 – 1.44 | 0.94 | 0.18 | 0.22 | 0.180 | 0.200 |
| | F | 259.88 | 0.11 | 3.87 | -0.06 | 27.3 | 1.01 | 0.83 – 1.19 | 0.78 | 0.18 | 0.231 | 0.180 | 0.217 |
| *P. versicolor* | M | 160.13 | 0.13 | 3.52 | -0.08 | 23.1 | 0.65 | 0.31 – 0.99 | 0.38 | 0.30 | 0.271 | 0.276 | 0.243 |
| | F | 144.38 | 0.20 | 3.62 | -0.26 | 15.0 | 0.74 | 0.41 – 1.07 | 0.36 | 0.22 | 0.384 | 0.310 | 0.378 |
| *P. femoristriga* | M | 160.13 | 0.16 | 3.61 | -0.17 | 18.8 | 0.89 | 0.73 – 1.04 | 0.62 | 0.25 | 0.273 | 0.250 | 0.267 |
| | F | 160.13 | 0.21 | 3.73 | -0.30 | 14.3 | 1.61 | 1.47 – 1.75 | 1.27 | 0.30 | 0.342 | 0.324 | 0.337 |
| *P. l. longipes* | M | 139.10 | 0.18 | 3.54 | -0.21 | 16.7 | 0.85 | 0.63 – 1.06 | 0.54 | 0.28 | 0.306 | 0.280 | 0.298 |
| | F | 139.15 | 0.25 | 3.68 | -0.36 | 12.0 | 0.95 | 0.72 – 1.18 | 0.58 | 0.36 | 0.366 | 0.360 | 0.367 |
| *P. l. bispinosus* | M | 149.63 | 0.10 | 3.35 | 0.05 | 30.0 | 0.59 | 0.37 – 0.80 | 0.41 | 0.18 | 0.185 | 0.180 | 0.176 |
| | F | 139.13 | 0.11 | 3.33 | 0.01 | 27.3 | 0.65 | 0.40 – 0.90 | 0.45 | 0.20 | 0.204 | 0.200 | 0.193 |

Note: $L\infty$ is length at infinity measured in millimeters (mm); $K$, $Z$, $F$ and $M$ estimates are measured in *per year* ($y^{-1}$); $t_{max}$ is measured in years (yr); Four estimates of $M$ are presented: (1) $M_{FISAT}$ is based on estimation using traditional model of Pauly (1980) in FISAT tool, (2) $M_1$ is the mean and (3) $M_2$ is the median of calculated natural mortality based in user input-weighting of various estimators in Natural Mortality Estimator Tool (Cope and Hamel 2022); 4) $M_3$ is the calculated natural mortality based on inverse variance-weighting of various estimators according to the method of Hamel (2015).

*ornatus* (124 mm CL) was three times larger than the pooled estimate for the other five species (43 mm CL) (Table 6). The pooled $L_c$ of male and female lobsters (*P. ornatus* excluded) were 42.6 mm and 43.4 mm CL, respectively. *P. ornatus* had a probability of capture starting with $L_{25\ male}$ = 107.9 mm and $L_{25\ female}$ = 103.22 mm, which were also two or three times larger than the $L_{25}$ of the other spiny lobster species. This size difference was also congruent with the values of $L_{75}$.

Moreover, the average sizes at first capture ($L_c$) for *P. penicillatus*, *P. femoristriga*, *P. l. longipes,* and *P. l. bispinosus* were only 22-27% of their respective $L_\infty$. On the other hand, the average $L_c$ estimates for *P. versicolor* and *P. ornatus* were 37% and 46% of their respective $L_\infty$.

### 3.3.4 Recruitment pattern

The recruitment peaks exhibited variations among spiny lobster species. Primary peaks for *P. penicillatus*, *P. ornatus,* and *P. versicolor* occurred during the first half of the year (February to July). The red lobster species *P. femoristriga*, *P. l. longipes,* and *P. l. bispinosus* had broader peaks spanning from June to September. On the other hand, recruitment was generally lowest from November to January across all species. In terms of variation in sex, a strong pulse of recruitment of male lobsters was observed to occur generally in June, while recruitment of females extends up to September.

Recruitment for both male and female *P. penicillatus* peaked during June (relative male recruitment = 17.3%; female recruitment = 16.6%, respectively). For *P. ornatus,* the highest recruitment for males occurred in June (16.0%) and July for females (18.7%). The peak for male *P. versicolor* recruitment was in May (18.2%), and for female recruitment in February (19.1%).

Male *P. femoristriga* had peak recruitment in August (14.3%), while female *P. femoristriga* had a peak in June (22.4%). For *P. l. longipes*, peak recruitment

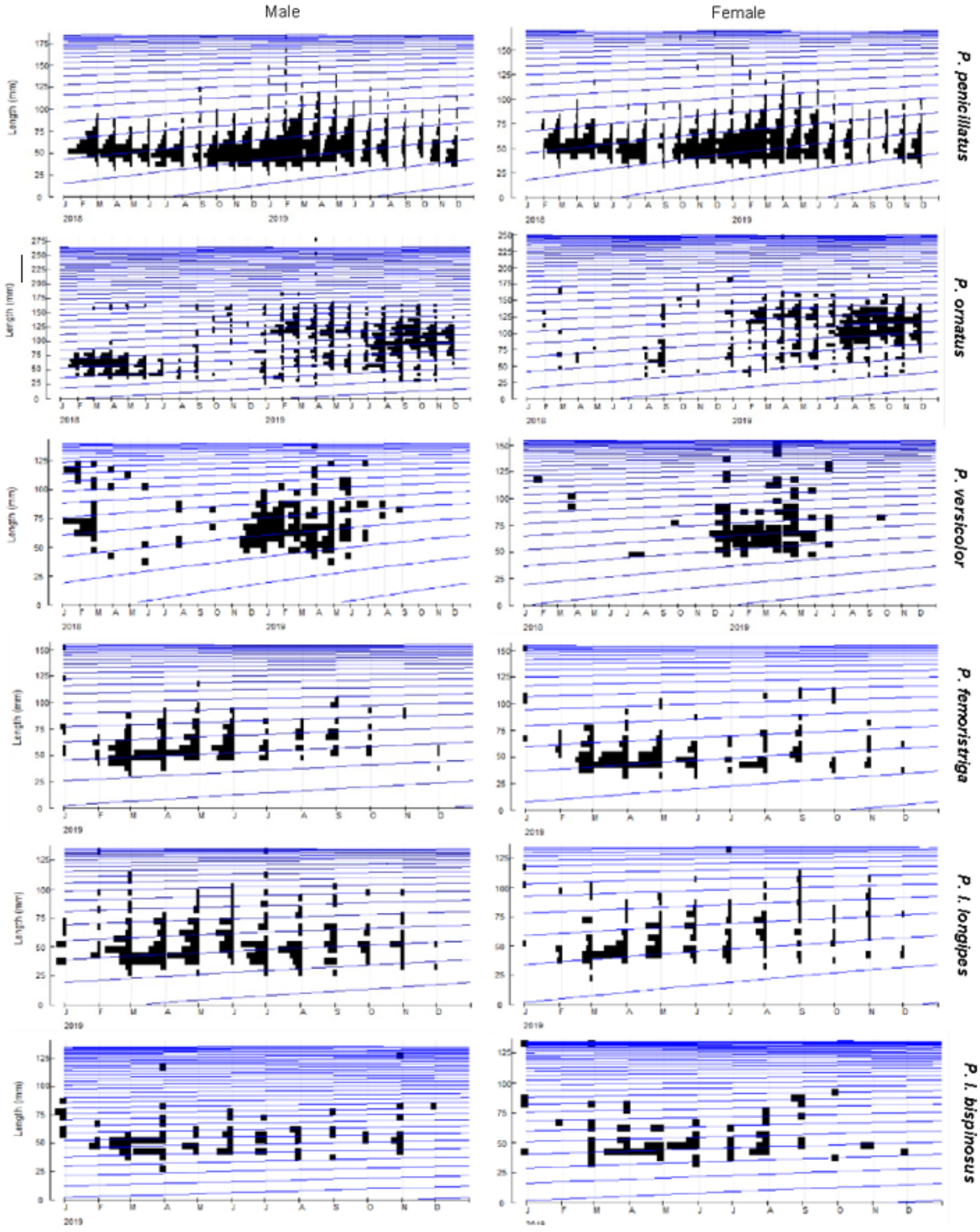


Figure 5. Plots of the von Bertalanffy growth function (VBGF) and length frequency for the six species and subspecies of spiny lobsters (male and female) caught in Eastern Visayas from 2018 to 2019.

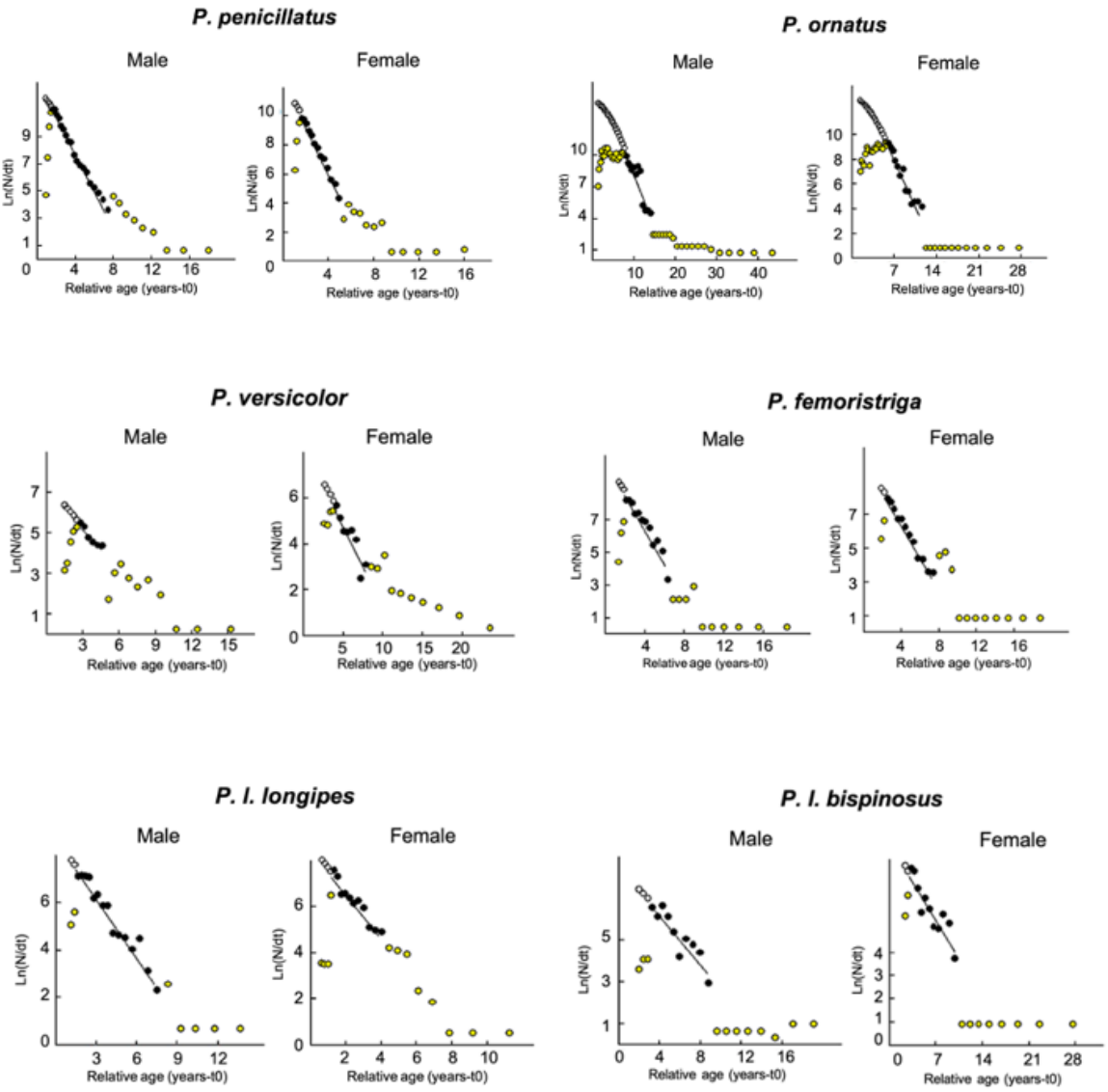


Figure 6. Linearized length-converted catch curve used to derive estimates of total (Z), natural (M), and fishing (F) mortalities, and exploitation rates (E) of spiny lobsters in Eastern Visayas.

occurred in June for males (14.6%) and September for females (22.3%). Lastly, male and female *P. l. bispinosus* recruitment peaked in June, with relative recruitment of 17.9% and 15.3%, respectively.

### 3.3.5 Relative yield-per-recruit analysis

Based on the previous analyses, the current *E* values of spiny lobsters were greater than 0.05, and the corresponding estimates of length at first capture were low. In this circumstance, the given *E* and $L_c/L_\infty$ point estimates did not produce the maximum sustainable yield for all species (Figure 8). The value proportion of MSY for *P. penicillatus*, *P. versicolor*, *P. femoristriga*, and *P. longipes* subspecies is shown in the orange area of the isopleth, with estimates ranging from 0.023 to 0.047. The theoretical values of relative Y'PR for these species ranged from 0.015 to 0.029. On the other hand, relative Y'PR values for *P. ornatus* ranged from 0.036 to 0.039 and were closer to the value proportion for MSY (0.040–0.047).

## 4. DISCUSSION

This study utilized size-structured methodologies included in the FISAT II tool package due to their capacity to fully leverage size composition data made available for spiny lobsters, produce outputs that can describe the population dynamics of the fishery, and provide information crucial for

Table 5. Predicted exploitation levels of male and female spiny lobsters in Eastern Visayas using Beverton and Holt's yield-per-recruit analysis, and exploitation rates based on the ratio of *F* and Z.

| Species | Sex | $L_c/L\infty$ | M/K | $E_{0.1}$ | $E_{0.5}$ | $E_{max}$ | E |
|---|---|---|---|---|---|---|---|
| *P. penicillatus* | Male | 0.20 | 2.38 | 0.36 | 0.28 | 0.46 | 0.76 |
| | Female | 0.24 | 1.79 | 0.40 | 0.29 | 0.48 | 0.79 |
| *P. ornatus* | Male | 0.46 | 2.20 | 0.56 | 0.34 | 0.67 | 0.81 |
| | Female | 0.46 | 2.10 | 0.61 | 0.35 | 0.73 | 0.77 |
| *P. versicolor* | Male | 0.33 | 2.08 | 0.51 | 0.32 | 0.59 | 0.58 |
| | Female | 0.41 | 1.92 | 0.51 | 0.32 | 0.61 | 0.48 |
| *P. femoristriga* | Male | 0.27 | 1.71 | 0.42 | 0.29 | 0.51 | 0.69 |
| | Female | 0.24 | 1.63 | 0.40 | 0.29 | 0.48 | 0.79 |
| *P. l. longipes* | Male | 0.27 | 1.70 | 0.42 | 0.29 | 0.50 | 0.64 |
| | Female | 0.27 | 1.46 | 0.42 | 0.30 | 0.50 | 0.61 |
| *P. l. bispinosus* | Male | 0.27 | 1.85 | 0.42 | 0.29 | 0.50 | 0.69 |
| | Female | 0.28 | 1.85 | 0.46 | 0.30 | 0.54 | 0.69 |

Table 6. Probabilities of capture for male and female spiny lobster species in Eastern Visayas using logistic curve estimation.

| Spiny lobster species | Sex | $L_{25}$ | $L_{50}$ | $L_{75}$ |
|---|---|---|---|---|
| *P. penicillatus* | Male | 38.88 | 39.19 | 43.24 |
| | Female | 40.52 | 43.09 | 45.64 |
| *P. ornatus* | Male | 107.91 | 128.28 | 148.64 |
| | Female | 103.22 | 118.99 | 134.74 |
| *P. versicolor* | Male | 47.41 | 53.10 | 58.15 |
| | Female | 51.22 | 58.56 | 63.73 |
| *P. femoristriga* | Male | 40.01 | 43.88 | 47.95 |
| | Female | 35.07 | 38.90 | 42.90 |
| *P. l. longipes* | Male | 32.24 | 37.27 | 41.40 |
| | Female | 34.31 | 38.11 | 41.92 |
| *P. l. bispinosus* | Male | 35.73 | 39.69 | 43.54 |
| | Female | 34.58 | 38.40 | 42.48 |

management objectives such as the evaluation of catch level changes, exploitation levels that result in MSY, and size limits (Punt et al. 2013). Size-structured models were also used in contemporary assessments for spiny lobster fisheries in many countries like New Zealand, South Africa, Australia, and Southeast Asia (Pons et al. 2022; Holloway and Butterworth 2022; Hobday and Punt 2001; Punt et al. 2012; Tirtadanu et al. 2021), owing to their applicability to data-limited crustacean fisheries (Punt et al. 2013). However, it should be noted that the findings of this study are derived from methodologies that are continually being refined to investigate ecological dynamics and the management of capture fisheries (Keyl and Wolff 2008; Howell et al. 2021).

A limitation of this study is the absence of a direct assessment of gonadal maturity. Although size-at-maturity values from published studies and existing regulations were used as biological reference points, direct gonadal staging would provide stronger maturity ogives for Philippine spiny lobster stocks. Future studies should integrate reproductive biology, gonadal maturity staging, and size-at-maturity estimation to validate and refine the proposed minimum carapace lengths.

### 4.1 Relative abundance, size structure and sex ratio

Biostatistical data, such as species counts, sex, carapace length, and body weight, for the six species and subspecies of spiny lobsters in Eastern Visayas were among the important data collected in this study. These data generated valuable information on relative abundance, size composition, sex ratios, morphometric relationships, growth behavior, and

relative condition factors from catch observations.

The continued dominance of *P. penicillatus* and *P. ornatus* in the present catch suggests that these species have remained the principal targets of the Eastern Visayas lobster fishery since earlier assessments by Juinio and Gomez (1986) and Juinio-Meñez and Dantis (1996). However, exploitation patterns appear to have intensified and become more market-driven. Earlier, lobster fisheries were largely artisanal and locally traded, whereas current harvesting is increasingly shaped by the live lobster trade, in which even juveniles and sub-adults may be accepted by buying stations for direct sale or grow-out culture. This shift likely increases fishing pressure across a wider size range and reduces the selectivity expected from a fishery targeting only larger marketable adults.

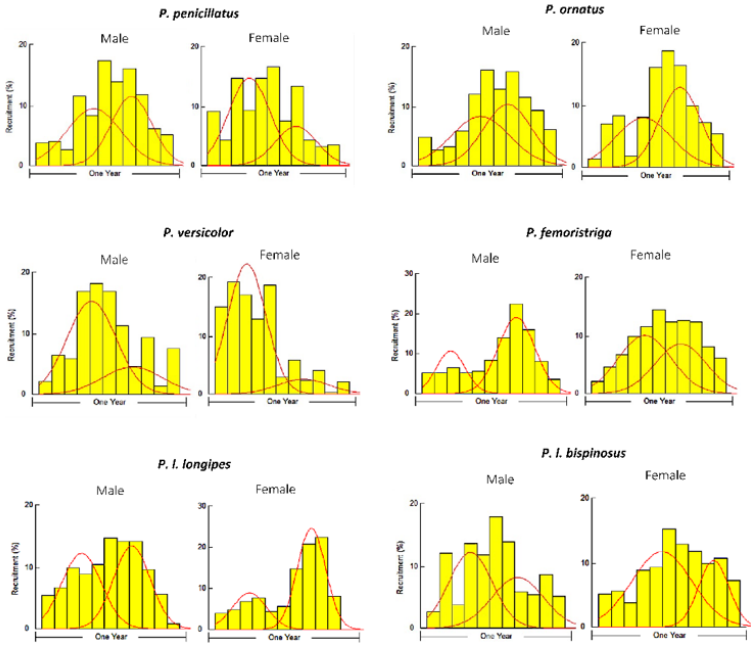


Figure 7. Recruitment pattern of spiny lobsters in Eastern Visayas, Philippines.

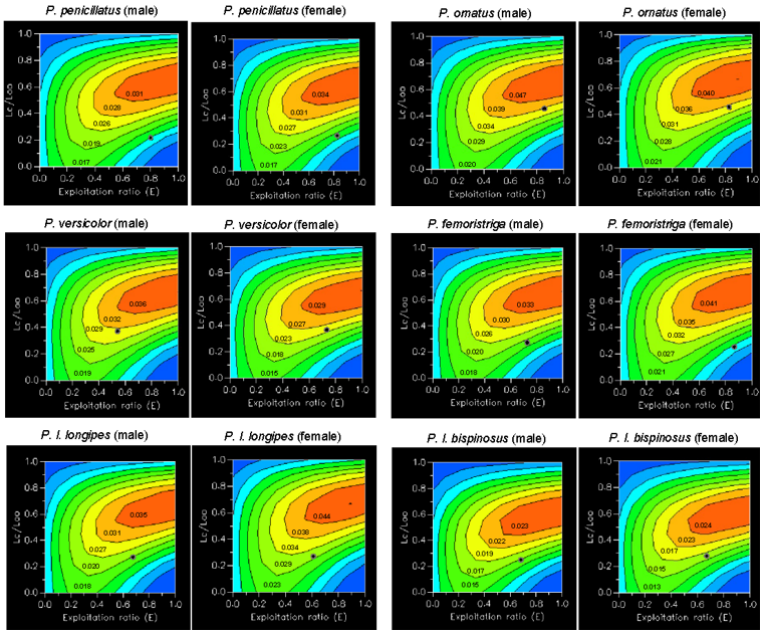


Figure 8. Relative yield-per-recruit (Y'PR) isopleth based on Beverton and Holt (1956) model for male and female spiny lobster species as a function of exploitation rate ($E$) and size at first capture ($L_c$) relative to length at infinity ($L\infty$). Note: The black dot represents Y'PR under current exploitation level and $L_c$.

The high proportion of immature individuals in the present study indicates that current fishing practices are less biologically sustainable because many lobsters are removed before reaching maturity. If this pattern continues, the fishery may experience declining spawning biomass, reduced recruitment potential, and progressive erosion of long-term yield.

The abundance of spiny lobsters in the catch is a function of their habitat preference, feeding behavior, breeding, and migration (Pitcher 1993; Radhakrishnan et al. 2019). *P. penicillatus* is considered to be the most extensively distributed spiny lobster species and exhibits the highest degree of habitat specificity. This species inhabits the upper slopes of coral reefs, utilizing coral boulder crevices as hiding spots during the daytime. During the night, they venture towards shallow reef crests and reef flats with depths less than 10 meters to forage on a diverse range of food sources, including mollusks and small crustaceans (George 1972; George 1974; Pitcher 1993; Radhakrishnan et al. 2019). On the other hand, *P. longipes* and *P. versicolor* are considered coral species and inhabit deeper waters with mild water movement (George 1972; Pitcher 1993). Unlike *P. penicillatus*, *P. longipes* also does not migrate up to the reef flats at night to feed (Pitcher 1993). *P. ornatus* is coined as a "continental species" inhabiting oceanic waters up to 200 m deep (George 1974). They are also highly migratory, traveling up to 600 km to breed (Moore and MacFarlane 1984). *P. ornatus* puerulus and juvenile fisheries on the eastern board of Samar Island also exist, but a high abundance of adults occurs in the northern area. This provides speculation that *P. ornatus* migrates towards the north as adults (Campo et al. 2023). Furthermore, the larval dispersal of *P. ornatus* has resulted in its widespread and abundant presence in the Philippines, owing to its interconnectivity with sources within the Southeast Asian archipelago (Dao et al. 2015).

The findings show a wide range of lobster sizes exploited in the Eastern Visayas region, from newly settled juveniles with a CL of 25 mm to the largest lobster with a CL of 279 mm. The analysis of the cumulative percentage of catch size composition indicates that a significant proportion, ranging from 47% to 90%, of the captured spiny lobsters were juveniles and sub-adults. These lobster catches had CL below the size at sexual maturity, as established under FAO No. 265 (DA-BFAR 2020), and as estimated in various studies on the reproductive biology of spiny lobsters (George and Morgan 1979; Moore and Macfarlane 1984; MacDonald 1988; Gomez et al. 1994; Hogarth and Barrat 1996; Chang et al. 2007; Ernawati et al. 2019; Salim et al. 2019; Yusnaini et al. 2020). The high frequency of juvenile and sub-adult captures can be attributed to their marketability and acceptability at local buying stations. However, it was observed that juvenile and sub-adult lobsters, particularly *P. ornatus*, were sometimes cultured in sea pens located in Northern Samar with the aim of attaining higher profits through improving lobster weight.

The male-biased sex ratio observed in this study may partly reflect sex-specific movement, reproductive behavior, and fishing selectivity. In spiny lobsters, reproductive females may shift habitat or move toward offshore or deeper areas during mating, egg extrusion, incubation, or larval release, reducing their availability to nearshore fishing grounds. Acoustic telemetry studies on *Panulirus argus* have documented daily movements, nomadic movements, and reproductive migrations, including rapid directional movements by reproductively active females (Bertelsen and Hornbeck 2009; Bertelsen 2013). Recent displacement and homing studies also indicate that juvenile and subadult spiny lobsters can show complex movement responses after relocation, emphasizing that local catch composition may be shaped by movement behavior as well as fishing location and gear selectivity (Childress et al. 2024). Although these studies were conducted on *P. argus,* they provide a useful ecological basis for interpreting sex-biased catches in other *Panulirus* fisheries. Local telemetry or mark–recapture studies are needed to confirm whether similar reproductive movements occur among Philippine spiny lobsters.

The absence of significant monthly, quarterly, or monsoonal variation in sex ratio does not necessarily contradict previous observations of seasonal spawning in Philippine spiny lobsters. The sex ratio in this study was derived from fishery-dependent landings and may therefore reflect catchability rather than the true population structure. Hookah diving may preferentially capture visible and accessible individuals in shallow reef habitats, while reproductive females may temporarily occupy deeper, less accessible, or offshore areas during egg-bearing and larval release. Market sorting may also affect the recorded sex composition if certain sizes, conditions, or species are preferentially retained by buyers. Environmental variability, including monsoon-driven changes in currents, turbidity, wave exposure, and habitat accessibility, may further influence both lobster movement and fishing operations. In addition, the multispecies nature of the catch may obscure species-specific reproductive seasonality, especially if spawning periods are asynchronous among *Panulirus* species. Thus, the observed male-biased but seasonally

stable sex ratio should be interpreted cautiously as a feature of the landed catch rather than direct evidence of reproductive periodicity.

### 4.2 Morphometric relationship and relative condition factor

Regression analysis for the morphometric relationship of lobster carapace length and body weight suggests a high degree of positive correlation ($R^2$ are close to 1.0). The *b* coefficient is a robust indicator of the relative health of lobster stock, where a value close to 3 indicates a good population health (Steinback et al. 2008; Fazhan et al 2021; Waiho et al. 2021). The *b* coefficients of all spiny lobster species in Eastern Visayas, regardless of sex, indicated negative allometry that significantly deviated from the ideal isometric value ($b = 3$). Negative allometry spiny lobsters was also observed in the neighboring Indonesian waters (Yonvitner et al. 2019; Beni et al. 2020; Muzammil and Kurniadi 2021; Situmorang et al. 2021).

Negative allometry in the present study indicates that body weight increased proportionally slower than carapace length, suggesting lower relative weight gain with increasing size rather than a direct shift toward a more elongated body form. This interpretation is consistent with lobster-specific studies reporting negative or hypoallometric carapace length–body weight relationships in *Panulirus ornatus*, *P. versicolor*, and *P. polyphagus* populations (Muzammil and Kurniadi 2021; Situmorang et al. 2021; Waiho et al. 2021).

Body allometry of crustacean populations depends on various factors such as individual health condition (Moutopoulos and Stergiou 2002; Datta et al. 2013), environmental conditions (Jones 2009; Vidya and Joseph 2012; Al Nahdi et al. 2016;), food supply (Chittleborough 1975, 1976); aggregation of lobster (Newman and Pollock 1974); and fishing pressure (Waiho et al. 2016). Even the selection of animal samples (Nazir and Khan 2017; Blasinaa et al. 2018) and preservation procedures (Shalloof and El-Far 2017; Olopade et al 2018; Mitu et al. 2019) also affect the determination of the regression coefficient. In this study, only biometric data from live and healthy lobster samples were analyzed since measurements from moribund and dead samples could affect the results of various analyses. The *b* coefficient can also vary seasonally and geographically among and within stock populations, across varying growth phases, age, sex, maturity, and ontogeny (Senevirathna et al. 2014; Azevedo et al. 2017; Hanif et al. 2020; Anderson et al. 2013).

This study revealed that spiny lobsters in Eastern Visayas had mean relative condition factors above 1.0 which were comparable to spiny lobsters in Indonesian waters, where $K_n$ values ranged from 0.96 (Fauzi et al. 2013) to 2.25 (Karisma et al. 2017). Individuals of a particular species with a relative condition factor ($K_n$) exceeding 1.0 are deemed to be in better condition than those same species with a $K_n$ value below 1.0 (Le Cren 1951). In this study, female *P. ornatus* had the highest relative condition factor (Kn = 4.8), suggesting comparatively higher body condition than the other groups.

In crustaceans, relative condition factor is commonly interpreted as the observed body weight relative to the expected weight for a given body size, with values near or above 1.0 indicating expected or relatively favorable body condition and values below 1.0 suggesting comparatively poorer condition. Similar interpretations have been applied in recent studies on decapod crustaceans, including lobsters, crabs, and shrimps (Paramo et al. 2024; Yusnaini et al. 2025; Picoy-Gonzales and Monteclaro 2023; Jumawan et al. 2026). In the present study, most species had mean Kn values close to or above 1.0, suggesting that landed individuals were generally within expected body condition for their size, although this should be interpreted cautiously because the sample consisted only of live, undamaged, and market-accepted individuals.

### 4.3 Population parameters

The population dynamics of spiny lobsters exhibit considerable complexity due to various internal and external factors such as genetics, environmental conditions, and life history traits (Foo and Wang 2013). They may vary across species and within species in different geographical and temporal contexts (Morgan 1980; Yellapu et al. 2017).

Growth parameters in spiny lobsters may be influenced by factors such as temperature and seasonality (Munro 1974; Pollock 1986; Forcucci et al. 1994), food availability (Barkai and Branch 1988; Edgar 1990; Melville-Smith and Goosen 1995; Simon et al. 2015) and population density (Chittleborough 1976; Barkai and Branch 1988; Pollock 1991; Jernakoff et al. 1994; Lozano-Alvarez 1996; Kittaka and Booth 2000). A perceptible difference between sexes also exists in spiny lobsters, based in several studies on morphometric characterization (Senevirathna et al. 2014; Waiho et al. 2021). Females may initially grow faster than males, however, then grow slowly as they

mature due to energy diversion for the production of eggs (Pitcher 1993).

Spatial and temporal variation in population parameters within species of spiny lobster also exists (León et al. 2014; Yellapu et al. 2017; McLeay et al. 2019). The asymptotic length and growth coefficients for different spiny lobster species vary across Southeast Asia, Australia, and Pacific regions. The estimated asymptotic lengths of *P. penicillatus* and *P. ornatus* in Eastern Visayas, Philippines, were relatively larger compared to neighboring waters in Indonesia, based on various studies. The current estimates of growth coefficients only slightly deviate from the values generated in the northern Philippines (Arellano 1988). Using size-frequency data, the highest growth rate for *P. penicillatus* was observed in Labangka Tidal Waters, Indonesia, with 0.75 $yr^{-1}$ (Asrial et al. 2020); for *P. ornatus* in Australia, with 0.44 $yr^{-1}$ (Skewes et al. 1997); and for *P. versicolor* in Bumbang Bay, Indonesia, with 0.49 $yr^{-1}$ (Yonvitner et al. 2019). Prior to this work, there has been no assessment of the growth parameters for *P. versicolor*, *P. femoristriga*, and the two subspecies of *P. longipes* in the Philippines.

A composite estimation using various estimators of natural mortality for spiny lobsters was conducted to show uncertainty in the calculation made from the conventional Pauly equation. The average natural mortality using various estimators ranged from 0.185 to 0.384 $y^{-1}$. The standard deviation (SD) of *M* of spiny lobsters varies from 1.0 to 12.0% of the estimated average *M*, with an outlier SD of 28% for female *P. versicolor*.

This study revealed higher estimates of fishing mortality *F* compared to natural mortality *M* for all spiny lobster species. Estimated values of *F* (0.36–1.32 $y^{-1}$) were two to five times larger than *M*, which implies the major role of exploitative fishing in the total mortality of spiny lobster stocks in Eastern Visayas.

The instantaneous *F* and *Z* ratio, which translates to the current exploitation rates of spiny lobsters, were greater than 0.5, a threshold that indicates overexploitation of stocks (Gayanilo et al. 2005). In addition, all spiny lobster species in Eastern Visayas, except for *P. versicolor*, had current exploitation levels that were beyond the predicted maximum exploitation level using Beverton and Holt's Y'PR analysis. It can also be noted that *P. ornatus* and *P. penicillatus* had the highest exploitation rates among the different lobster species, while *P. penicillatus* had the highest breach beyond the estimated maximum exploitation level (0.31).

The high exploitation rates and low size at first capture indicate that the fishery is experiencing growth overfishing, where lobsters are harvested before they can contribute fully to biomass accumulation and reproduction. In the long term, persistent removal of juveniles and sub-adults may reduce spawning-stock biomass and weaken recruitment by limiting the number of mature individuals contributing larvae to the population. This is particularly concerning for spiny lobsters because recruitment depends on the survival of planktonic larvae, successful settlement of pueruli, and the persistence of suitable nursery habitats. When fishing pressure removes a large proportion of individuals before maturity, the fishery becomes increasingly dependent on annual recruitment pulses rather than a stable adult breeding population. Such dependence may heighten vulnerability to environmental variability, habitat degradation, and market-driven fishing pressure, ultimately compromising stock resilience and long-term yield.

The analysis for recruitment revealed that there exist variations in the relative recruitment patterns of the six spiny lobster species in Eastern Visayas (Figure 7). A notable surge in recruitment was generally observed for male lobsters during the months of June to July and for female lobsters from June to September. This implies that the post-larval stage of spiny lobster begins to settle at least a month prior to this period of strong recruitment. This was evident in the observed peak season for puerulus larvae in Eastern Samar from the months of February to May. Recruitment in the spiny lobster fishery reflects the number of puerulus larvae that settled in the nearby nursery habitat and survived to grow into juveniles and later into adults of catchable size (Butler and Herrnkind 1992). The lobster stocks in this study were theoretically considered recruits upon reaching the catchable size range of 37–58 mm for the species *P. penicillatus*, *P. versicolor*, *P. femoristriga,* and the two subspecies of *P. longipes*. For *P. ornatus*, the catchable size range was 119–128 mm. This also suggests that newly recruited spiny lobsters were the major contributors to fishers' catch in the area.

The capture probabilities for spiny lobsters in Eastern Visayas show overexploitation of undersized lobster species, except for *P. ornatus*. A proportion of 47–90% of the catches were lobster juveniles and sub-adults measuring less than 77.5 mm, which is the average CL for spiny lobster sexual maturity. Moreover, the average size at first capture ($L_c$) for all spiny lobster species studied was < 50% of their respective $L_\infty$, signifying that lobsters are harvested even before they

become fully mature. Given the high abundance of undersized catches, an assertion can be made that the spiny lobster population in Eastern Visayas waters is experiencing growth overfishing.

The artisanal nature of the fishery in Eastern Visayas and the marketability of all lobster sizes motivate gatherers to become unselective in fishing. Field observations during sampling indicated that live juvenile and sub-adult lobsters, particularly *P. ornatus*, were accepted by local buyers and, in some cases, retained for grow-out culture because of their high market value. Similar collection of wild lobster fry and juveniles for aquaculture has been reported in Davao Oriental (Macusi et al. 2019). *P. ornatus*, the most expensive among the species, is usually caught live in large sizes due to its high price of up to Php 6,000/kg, while cage-grown lobsters are usually sold at 80–90% of the price of live-caught lobsters. However, because hookah diving is a major method for catching spiny lobsters, it also provides an opportunity to reinforce selective fishing practices, such as releasing berried lobsters and catching only individuals above the prescribed size limits.

The relative yield per recruit (Y'PR) analysis, among other parameters, could help fishery managers diagnose the potential for growth overfishing (Pitcher 1993). The results of this study suggest that the size at first capture (Lc) should be increased for species that are being overfished, especially *P. penicillatus*, *P. versicolor*, *P. femoristriga*, and the two subspecies of *P. longipes*. This will allow lobster growth and eventually maximize the yield of the fishery over time. Ideally, the model also recommends a reduction in the exploitation rates of lobsters. Exploitation rates and fishing mortalities can be significantly reduced through the establishment of minimum size limits. However, abruptly introducing a minimum CL size for each lobster species will have significant negative impact on the fishery's economy, as most fishers rely heavily on catching undersized lobsters. To mitigate this scenario, Pitcher (1993) suggested that the minimum size be increased gradually each year, based on the VBGF growth rates. This would make it easier for the fishery to reach its full potential over time. The findings about the relative YPR of spiny lobsters in this study, however, should be understood as hypothetical or speculative only. It should be noted that the purpose of Y'PR is to offer comparative measurements of spiny lobster yield at different levels of exploitation rates and fishing mortalities.

## 5. CONCLUSION

This study provides evidence that spiny lobster fisheries in Eastern Visayas are under strong fishing pressure, as indicated by high exploitation rates, low size at first capture, and the substantial proportion of juveniles and sub-adults in the landed catch. These patterns suggest that current harvest practices may reduce spawning biomass, weaken recruitment potential, and compromise the long-term productivity of the fishery.

Management should prioritize the phased implementation and strict enforcement of species-specific minimum legal carapace lengths, particularly for *P. penicillatus* and *P. ornatus*, which were the most abundant and heavily exploited species. Regulations should also strengthen the protection of berried females, pueruli, juveniles, and sub-adults, and extend monitoring to landing sites, buying stations, holding facilities, transport routes, and grow-out operations where undersized lobsters may enter the trade.

Future research should integrate gonadal maturity assessment, recruitment monitoring, fishing-effort data, habitat mapping, and species-specific stock assessment to refine biological reference points and support adaptive management. Together, size-based harvest controls, improved monitoring of the live lobster trade, regulation of selective fishing practices, and protection of settlement and nursery habitats can help sustain the ecological and economic value of Philippine spiny lobster fisheries.

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## 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, analysis, curation and visualization. **Cabacaba**

**NS**: Conceptualization, Writing – original draft preparation Methodology, Supervision, Writing – Reviewing and Editing.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## ETHICS STATEMENT

Spiny lobster specimens used in this study were obtained from routine commercial landings and buying stations during fishery monitoring activities. No live experimental manipulations, laboratory animal trials, or destructive procedures were conducted as part of this study. As the study involved fishery-dependent sampling of commercially harvested animals and did not include experimental animal procedures, formal animal ethics committee approval was not required under institutional practice. All sampling and handling followed applicable institutional and national guidelines for fisheries research and the ethical use of aquatic organisms.

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