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Reproductive biology and seasonal dynamics of the peanut worm *Antillesoma antillarum* (Phascolosomatiformes: Phascolosomatidae) in Toronipa, Southeast Sulawesi, Indonesia

BAHTIAR[1,♥], MUHAMMAD NUR FINDRA[2], AGUS KURNIA[1], YNGWY EZRA JIWANI[1]
[1]Department of Aquatic Resources Management, Faculty of Fisheries and Marine Sciences, Universitas Halu Oleo. Jl. H.E.A. Mokodompit, Kendari 93232, Southeast Sulawesi, Indonesia. Tel./fax.: +62-401-3190105, ♥email: bahtiarfpikuho@gmail.com
[2]Department of Aquatic Resources Management, Faculty of Fisheries and Marine Science, Universitas Khairun. Jl. Jusuf Abdulrahman Kampus II, Unkhair Gambesi, Ternate 97719, North Maluku, Indonesia

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Abstract. *Bahtiar, Findra MN, Kurnia MA, Jiwani YE. 2025. Reproductive biology and seasonal dynamics of the peanut worm* Antillesoma antillarum *(Phascolosomatiformes: Phascolosomatidae) in Toronipa, Southeast Sulawesi, Indonesia. Biodiversitas 26: 6458-6468. Antillesoma antillarum*, commonly known as the peanut worm, is a benthic invertebrate with important ecological and economic roles in coastal ecosystems. However, the lack of reproductive biological data may threaten its sustainability under increasing harvesting pressure. This study examined seasonal variations in reproductive traits sex ratio, gonadal Maturity Level (GML), Gonadosomatic Index (GSI), fecundity, and size at first maturity (Lm_{50}) based on 688 specimens collected over 11 months from the Toronipa Coast, Southeast Sulawesi, Indonesia. Females slightly outnumbered males (374 vs. 314), but the sex ratio did not significantly differ from 1:1 (χ^2: 5.23, p>0.05). Gonadal development followed four distinct maturity stages, with peak reproductive activity observed in November-December, when over 60% of individuals reached stages III-IV. GSI values followed a similar pattern, peaking at 6.42% before sharply declining post-spawning. The first maturity size (Lm_{50}) was estimated at 8.0 cm (R^2: 0.9946), and fecundity ranged from 920 to 4,500 eggs, with the highest egg counts in individuals measuring 8.0-8.5 cm in length. Although seawater temperature remained stable (30-33°C), allowing gonadal development to occur year-round, elevated sediment organic matter (>3.5%) negatively affected GSI (R: -0.1196), suggesting that sediment quality does not directly influence gonadal development. These findings provide critical baseline data for reproductive-based management, supporting the implementation of size limits (≥8 cm) and seasonal harvest closures to ensure the sustainability of A. antillarum populations in tropical intertidal zones.

Keywords: *Antillesoma antillarum,* gonadal development, Lm_{50}, peanut worm, reproductive biology

INTRODUCTION

Antillesoma antillarum, commonly known as the peanut worm, is a benthic invertebrate from the phylum Sipuncula that is broadly distributed across tropical coastal ecosystems, including Indonesian waters (Bahtiar et al. 2024). This species performs crucial ecological functions that sustain the structure and productivity of marine benthic environments. Through its bioturbation activities, *A. antillarum* mixes sediments, modifies substrate composition (Martins and Barros 2022), and enhances nutrient availability in benthic habitats (Lindqvist 2014; Janas et al. 2019; Fortune et al. 2023). These processes improve oxygen penetration and facilitate the decomposition of organic matter, which in turn supports a wide array of benthic organisms and boosts both primary and secondary productivity (Gammal et al. 2017). The presence of *A. antillarum* is often considered an ecological indicator of benthic health due to its role in maintaining sediment quality and nutrient cycling (Martins and Barros 2022). Despite its ecological significance, research on the species in tropical settings especially its population ecology remains sparse, limiting our understanding of its broader role in ecosystem functioning.

Beyond its ecological functions, *A. antillarum* holds economic relevance for coastal communities. In Indonesia and other tropical countries, the species is traditionally harvested for use as bait in artisanal fisheries, indirectly supporting livelihoods that depend on marine resources (Cintra et al. 2024). Additionally, recent scientific interest has focused on the species potential in pharmaceutical and nutritional industries due to its bioactive compounds (Li et al. 2017). Its tissue is rich in high-quality proteins and essential amino acids, suggesting its potential as an alternative food resource (Qi et al. 2021). However, increasing pressure from unregulated exploitation, particularly in regions where biological data is lacking poses a risk to wild populations (Bahtiar et al. 2024; Cintra et al. 2024). Without an adequate understanding of reproductive dynamics, including spawning cycles and fecundity, the sustainability of *A. antillarum* cannot be ensured. Hence, information on reproductive traits is vital not only for effective population management but also for the conservation of ecosystem processes where the species plays a foundational role (Khasanah et al. 2019; Bahtiar et al. 2022; Latuconsina et al. 2022).

Despite its distribution across Indonesian coastal waters, scientific information on the reproductive biology of *A. antillarum* in the region is still highly limited compared to studies on other invertebrates, such as mollusks and crustaceans. While international research has explored sipunculan reproduction especially in temperate zones identifying patterns of gonadal development and environmental triggers (Maiorova and Adrianov 2005; Ying et al. 2009; Boyle and Rice 2014), such findings cannot be directly extrapolated to tropical populations, where environmental drivers are distinct. In Indonesia and in other tropical nations like Brazil and those in the Caribbean and Pacific regions, most studies have been limited to morphological identification and taxonomic classification (Quirós-Rodríguez et al. 2018; Silva-Morales et al. 2019; Franco 2023). There is a critical shortage of data on fundamental reproductive parameters such as sex ratio, gonad maturity level, Gonadosomatic Index (GSI), fecundity, and size at first maturity particularly in Southeast Sulawesi (Indonesia) populations (Bahtiar et al. 2024). Understanding these reproductive characteristics is essential for assessing the species' capacity for natural regeneration and for developing science-based strategies for conservation and sustainable use (Comizzoli et al. 2019; Wildt et al. 2002). This need becomes more urgent as anthropogenic disturbances in coastal zones increase and threaten benthic biodiversity (Deudero et al. 2015; Efendi and Suraya 2023).

The current study addresses these knowledge gaps by focusing on *A. antillarum* populations in Toronipa Coastal Waters, Southeast Sulawesi an area known for high biodiversity and growing anthropogenic pressures (Muchtar et al. 2019a; Wati et al. 2021). Previous studies in this region have revealed impacts of coastal development, pollution, and overharvesting on marine habitats (Muchtar et al. 2019b; Efendi and Suraya 2023), which likely influence benthic community dynamics, including those of *A. antillarum* (Cimon and Cusson 2018). This study aims to provide a comprehensive assessment of the reproductive biology of *A. antillarum* in this area. Specific objectives include determining sex ratio, Gonad Maturity Level (GML), Gonadosomatic Index (GSI), fecundity, and size at first gonadal maturity. Temporal variation in these parameters will also be evaluated to explore the influence of environmental factors on reproductive timing and energy investment. Findings from this research are expected to significantly contribute not only to the reproductive ecology of tropical sipunculans and to the development of evidence-based management policies and biodiversity monitoring programs that include lesser-known benthic invertebrates, instilling hope for the future of these species.

MATERIALS AND METHODS

Period and study area

This study was carried out over 11 months, from July 2023 to May 2024. Random sampling of *A. antillarum* was conducted in the intertidal zone (Figure 1) of Toronipa Beach, Konawe District, Southeast Sulawesi, Indonesia. The sampling area was located between the coordinates 3°53'39.65"S and 122°39'16.64"E to 3°53'40.78"S and 122°39'19.97"E. This place is located in an intertidal area with a sandy substrate, overgrown with the seagrass *Thalassia hemprichii*. Reproductive parameters were observed at the Laboratory of the Faculty of Fisheries and Marine Sciences, Universitas Halu Oleo, Kendari, Southeast Sulawesi, Indonesia.

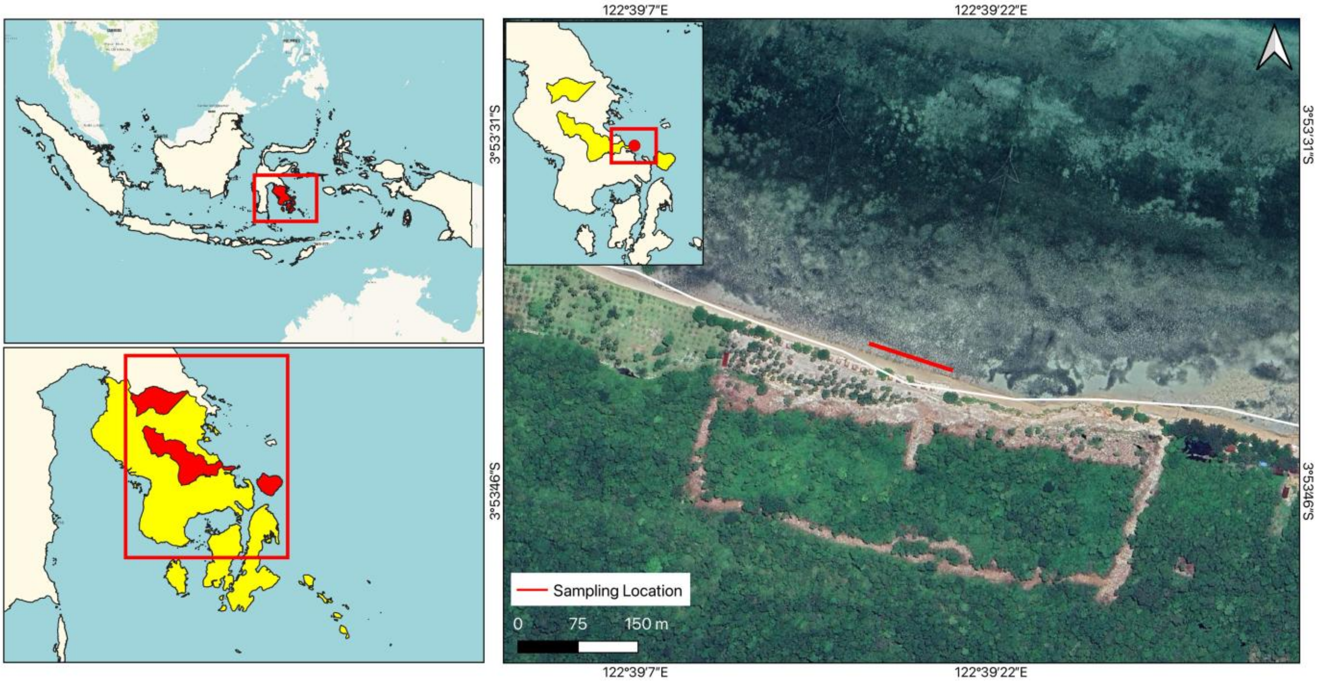

Figure 1. Sampling site of *Antillesoma antillarum* in Toronipa Beach, Konawe, Southeast Sulawesi, Indonesia

Sample collection

Peanut worm identification was based on the presence of fecal pellets near burrows. Worms were excavated using a shovel inserted into the substrate to a depth of 20 cm. Each was counted as well as measured for total length and weight using a ruler and an analytical balance with accuracies of 0.5 mm and 0.0001 g, respectively. A total of 688 individuals (314 males and 374 females) were collected. Each was dissected longitudinally from the introvert to the anus to determine sex. Monthly, 60-72 individuals were examined for sex and gonad maturity stage. The gonads are located near the posterior end of the body; male gonads are finger-like and translucent white, whereas female gonads appear as brown grape-like clusters (Figure 2). Gonad maturity development was defined as the progression from inactive to mature to near-spawning stages. Observations were conducted microscopically, and gonad maturity stages of *A. antillarum* were determined following the description for the peanut worm *Siphonosoma australe australe* by Bahtiar et al. (2024) (Table 1). The gonadosomatic index and fecundity were determined gravimetrically by weighing the total gonad mass, followed by subsampling and counting oocytes under a microscope for fecundity estimation. Size at first gonadal maturity was determined by measuring the body length of male and female worms at maturity stages III and IV on a monthly basis. Water quality parameters were measured concurrently during the sampling process.

Data analysis

Sex ratio

Sex ratio was calculated as the proportion of males to females. A Chi-square (X^2) test was used to determine whether the observed ratio significantly deviated from the expected 1:1 ratio, with significance set at $P \leq 0.05$. Statistical analyses were performed using XLStat software (Bahtiar 2017, 2024), according to the following formula:

$$X = \frac{M}{F}$$

Where, X: Sex ratio, M: Number of male peanut worms, and F: Number of female peanut worms.

GML

GML was analyzed descriptively using a semi-quantitative method based on monthly observations, with data processing conducted using Microsoft Excel (Bahtiar et al. 2024). The classification follows development stages observed microscopically, adapted from *Sipunculus australe australe* (Table 1).

GSI

GSI was calculated by comparing both gonad and total body weight using the following formula (Tuwo and Conand 1992; Bahtiar et al. 2021, 2025):

$$GSI = \frac{Wg}{Wt} \times 100\%$$

Where, GSI: Gonadosomatic Index, Wg: Gonad weight, and Wt: Total weight (including gonads). Monthly differences in GSI were tested using the Mann-Whitney test, with $P<0.05$ indicating significant temporal variation.

Fecundity

Fecundity was estimated gravimetrically using the following formula (Hunter et al. 1989; Bahtiar et al. 2021, 2025):

$$N = n \times \frac{G}{g}$$

Where, N: Total fecundity (number of eggs), n: Number of eggs in the subsampled gonad, G: Total gonad weight (g), g: Weight of the subsampled gonad (g). The relationship between fecundity and body size was analyzed descriptively by examining the trend in the scatter plot generated using Microsoft Excel.

Size at first gonad maturity

Size at first gonadal maturity (length at 50% maturity) was estimated using non-linear regression analysis performed with SigmaPlot 12 software. This analysis models the probability of individuals reaching gonad maturity based on body length (Arocha and Barios 2009; Bahtiar et al. 2024), using the following logistic function:

$$Y = \frac{a}{1 + e\frac{-x+xo}{b}}$$

Where, Y: Probability of maturity (%), x: Individual body length (cm), x_0: Length at 50% maturity, a: Slope, and e: Base of the natural logarithm.

Relationship between gonadal development (GSI) and water quality

The relationship between gonadal development (GSI) and water quality (sediment organic matter; SOM) was analyzed using simple linear regression in Excel.

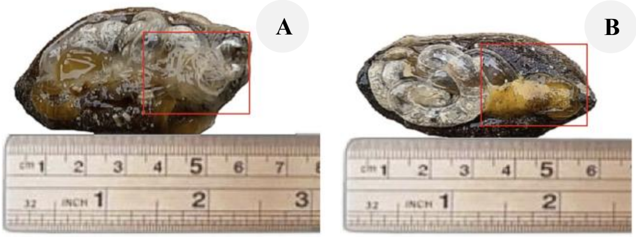

Figure 2. Visual differentiation of male and female *Antillesoma antillarum*. A. Panel shows a male specimen, B. Panel shows a female. Red boxes highlight the gonads of each sex for easier identification

Table 1. GML stages of *Antillesoma antillarum* refer to peanut worm *Siphonosoma australe australe* (Bahtiar et al. 2024)

GML	Male characteristics	Female characteristics
I	The gonads appear as thin, translucent white rods that are easily detached from the body. The sperm cells are still in the early stage, forming tightly clustered morulae in a rounded shape.	The gonads are shaped similar to small, dense clusters of grape-like structures, yellowish-brown in color, and attached to the body wall. At this stage, the oocytes (egg cells) have an uneven surface and tend to clump together.
II	The gonads are still in the form of thin, translucent white rods. At this stage, the sperm cells develop from morula into spermatocytes, with an increase in cytoplasm observed, and densely packed clusters of spermatocytes start forming.	The gonads start to thicken and turn brown. The oocytes appear larger, the surface becomes smoother, the wrinkled structure disappears, and the vitelline membrane (protective layer of the egg) starts forming.
III	The gonads turn milky white and begin to thicken. Spermatocytes develop into spermatids that are prepared for release into the coelomic fluid, or body cavity. At this stage, the spermatids start to be released into the body fluid for further maturation.	The gonads are dark brown, large, and dense, while the oocytes develop in varying sizes. The follicles start to fill up completely, but there is no channel connecting the inside and outside of the cell membrane.
IV	The gonads appear creamy white and form thick, rod-like structures. At this stage, mature sperm are released into the coelomic fluid and move toward the nephridium (excretory organ), with clearly visible tails and clustered heads, indicating readiness for fertilization.	The gonads are grayish-brown in color and easily detached from the body. Clear egg distribution channels form, and the cell nuclei in the follicles are visible. The oocytes have enlarged, and the presence of an egg release canal suggests readiness for spawning.
Fertilization stage	-	Larvae were found in the nephridium canal and ready to be released (Figure 3).

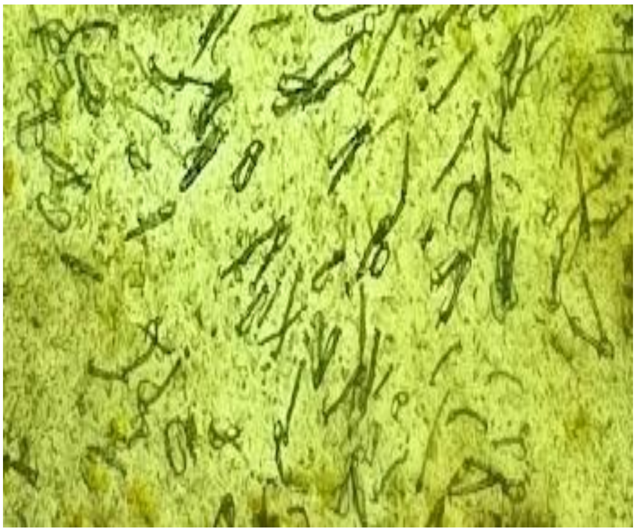

Figure 3. Larval development inside the nephridium of *Antillesoma antillarum*

RESULTS AND DISCUSSION

Results

Sex ratio

The sex ratio of *A. antillarum* during the study period showed a slightly higher number of females than males. Of the 688 individuals examined, 314 were males and 374 were females. Statistical evaluation using the Chi-square test indicated that the sex distribution between male and female worms did not differ significantly from a 1:1 ratio (X^2 test: $P \geq 0.05$). However, females were numerically more dominant (Figure 4).

Gonadal development (GML and GSI)

Gonadal development in the *A. antillarum* population exhibited a clear seasonal pattern, with all four GML stages (I-IV) present each month. During the early observation period (July-September), most individuals were at stages I and II. A similar pattern was observed in GSI, which had low values during this period. In October, the proportion of individuals at stages III and IV increased, accompanied by a significant rise in GSI values. The peak of gonadal development and GSI occurred in November-December, when most individuals reached stages III and IV, and GSI attained its highest values. Subsequently, in January-February, the majority of individuals reverted to stages I and II, along with a sharp decline in GSI values. During March-May, both gonadal development stages and GSI values increased again (Figure 5). The results of the Mann-Whitney test analysis for male peanut worms showed significant differences in GSI values across observation periods in certain months ($P<0.05$). Marked differences in GSI were observed between July and September, as well as between October and November. However, the GSI values in male peanut worms were relatively stable or showed no significant differences over time ($P>0.05$), such as the comparisons between August and September, and between October and December. In female peanut worms, significant differences across observation periods ($P<0.05$) were observed between July and September. Most of the other monthly comparisons showed no significant differences ($P>0.05$), particularly from October to March (Figure 5).

Fecundity

Fecundity is described as the relationship between body length (cm) and the number of eggs produced. Fecundity of *A. antillarum* increased proportionally with body length but tended to decline at larger sizes. Worms with a body length of approximately 2.4 cm produced fewer than 1,500-2,800 eggs. At maximum lengths of 9-14.5 cm, fecundity reached nearly 1,000-2,800 eggs. In the 8-8.5 cm length group, the average value was above 1,300-4,500 eggs (Figure 6).

First gonad maturity size

Non-linear regression analysis showed a highly significant relationship ($P \leq 0.0001$) with a coefficient of determination (R^2) of 99.46%, indicating that the model effectively described the relationship between body length and gonad maturity in *A. antillarum*. At a body length of 6.5 cm, only 20-30% of individuals had mature gonads. The estimated length at which 50% of individuals reached gonad maturity was approximately 8 cm. At lengths of 9 cm and above, more than 75% exhibited gonad maturity, while at lengths greater than 12 cm, nearly all individuals had developed mature gonads (Figure 7).

Relationship between gonadal development (GSI) and water quality

The results of the linear regression analysis indicated a weak relationship between GSI and SOM, as shown by the relatively low coefficient of determination (R^2: 0.1196) (Figure 8). However, a trend of decreasing GSI was observed with increasing SOM concentration. A significant decrease in GSI occurred when SOM exceeded 3.5%, particularly during the Januari-February period. Meanwhile, during periods of low SOM concentration, such as September-December, GSI values showed a significant increase. Although water temperature remained stable throughout the year (30-33°C), no direct correlation was found between temperature and GSI fluctuations (Figure 9).

Discussion

Sex ratio

Sex ratio is a fundamental parameter in reproductive biology studies, reflecting the proportion of male and female peanut worms in a population. In this study, among a total of 688 *A. antillarum* individuals collected over 11 months of observation along the Toronipa Coast, 314 were males and 374 were females. The Chi-square test results indicated a relatively balanced sex distribution in the population was relatively balanced, although there was a slight numerical dominance of females (Figure 4). This was evident from the relatively consistent monthly male-to-female ratio. The stability of environmental conditions, particularly the temperature in the Toronipa Coastal Waters (a tropical area), remained relatively constant throughout the seasons. This stability may regulate gene expression and population dynamics, thereby influencing the balance of sex ratios (Zapata-Restrepo et al. 2019; Zeng et al. 2024). A balanced sex ratio was also observed in *S. a. australe* peanut worms on Toronipa Beach (Bahtiar et al. 2024).

Environmental factors such as temperature and nutrient availability play an important role in sex determination, with higher temperatures tending to produce more male offspring, while lower temperatures favor females. This Environment-based Sex Determination (ESD) potentially also applies to *Antillesoma* (Mankiewicz et al. 2019). Poor habitat conditions and physiological stress, such as low oxygen levels, can alter hormone balance and increase the male ratio (Liew et al. 2012). Genetically, individual predisposition factors for a particular sex interact with environmental conditions, resulting in phenotypic variation that does not always reflect the genotypic ratio (Valdivieso et al. 2020; Hosseini et al. 2022). Population dynamics, including competition among individuals, also influence the sex ratio, with high competition tending to favor males due to greater access to habitat and mates (Golestaninasab et al. 2011; Wibowo et al. 2022).

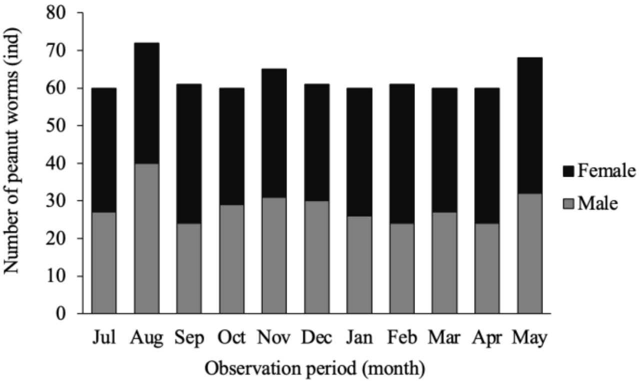

Figure 4. Sex ratio of male and female *Antillesoma antillarum*

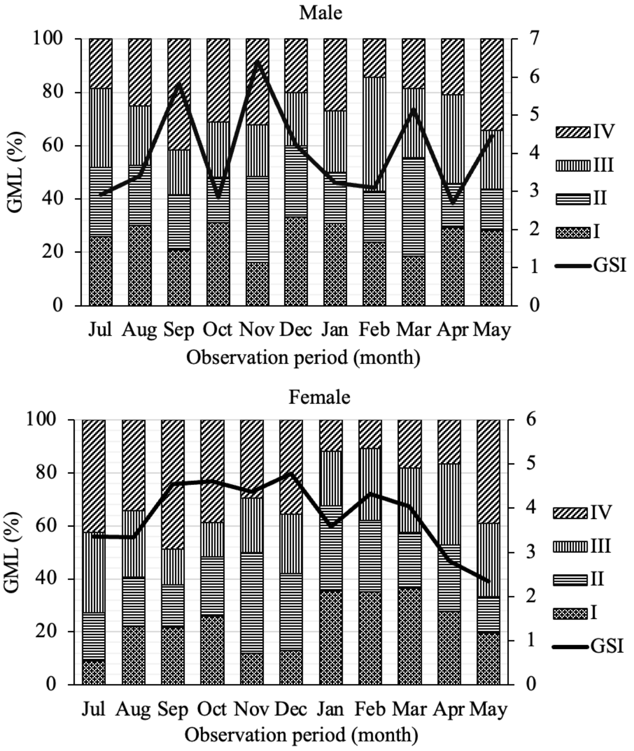

Figure 5. Seasonal variation in GML and GSI of *Antillesoma antillarum*. The left y-axis represents GML stages (I-IV), while the right y-axis shows GSI values

Reproductive biology of peanut worms, such as in *Phascolosoma esculenta*, shows a stable sex ratio pattern of about 1:1. This is a common phenomenon in marine taxa linked to an evolutionary strategy to increase mating opportunities and genetic diversity within populations. Although balanced sex ratios are often observed, evidence suggests that this ratio can fluctuate based on temporal and spatial variables (Liang et al. 2024).

Research on the sex determination mechanisms in Sipunculids reveals that molecular and genetic factors play important roles, allowing population organization to adapt to varying environmental pressures. The sex determination mechanisms in Sipunculids indicate that they may use environmental cues, including maternal conditions, to influence the sex ratio of their offspring (Dang et al. 2024). Therefore, further studies are needed to understand the complexity of sex determination within this group (Courteau and Lessard 2000).

The concept of sex ratio elasticity demonstrates how species can adjust their sex ratios in response to competition or environmental changes (West et al. 2005). This is important for population sustainability, given that this adaptive response can enhance ecosystem stability. In many species, a balanced sex ratio indicates good reproductive health, where both sexes can function effectively in reproduction. This balance can play a crucial role in population sustainability (Xu et al. 2024). A population with a balanced sex ratio has the best reproductive potential, enabling the maintenance or growth of the natural regeneration rate. Slight dominance of females may provide reproductive advantages, as more eggs are produced, thereby increasing the chances of successful fertilization and survival of the next generation (Mackintosh et al. 2020).

A balanced sex ratio is associated with ecosystem stability (Huang and Zhao 2024). Environmental factors such as temperature, food availability, and habitat conditions can influence sex ratio in marine invertebrates, including sipunculans (Du and Men 2024; Xu et al. 2024). In the context of this study, no significant shifts in sex ratio were observed throughout the year. This suggests that the *A. antillarum* population along the Toronipa Coast is relatively stable and not subjected to extreme environmental stress that could cause sex ratio imbalance.

Overall, studies on sex ratios in *Antillesoma* and the broader Sipuncula group reveal significant interactions between reproductive biology, environmental factors, and evolutionary strategies. Maintaining a balanced sex ratio appears to be a common strategy to optimize reproductive success, although various constraints and pressures within aquatic ecosystems influence this.

The results provide an important basis for population management, as maintaining a balanced sex ratio is a key indicator of population health that should be preserved to ensure the sustainability of resources and prevent extinction risks (Gaughwin et al. 2020). This expectation can be achieved by enhancing reproductive success, ensuring adequate mating opportunities, and preserving genetic diversity (Weerawansha et al. 2022; Chiba et al. 2023). In the context of fisheries, a balanced sex ratio can influence resource sustainability. Populations with well-maintained sex ratios tend to have greater resilience, including better resistance to overexploitation pressure, which often occurs in small-scale and traditional fisheries (Chiba et al. 2023; Gangal et al. 2024).

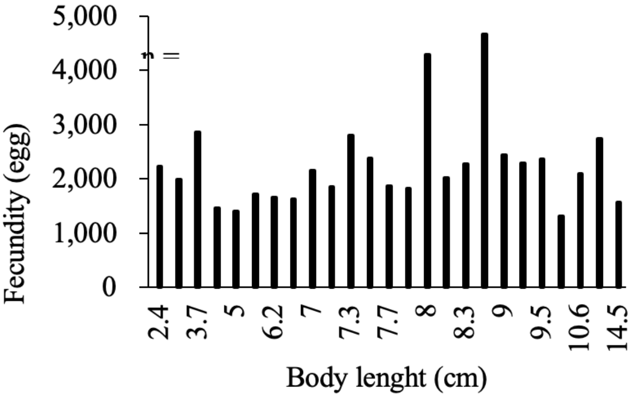

Figure 6. Fecundity of *Antillesoma antillarum*

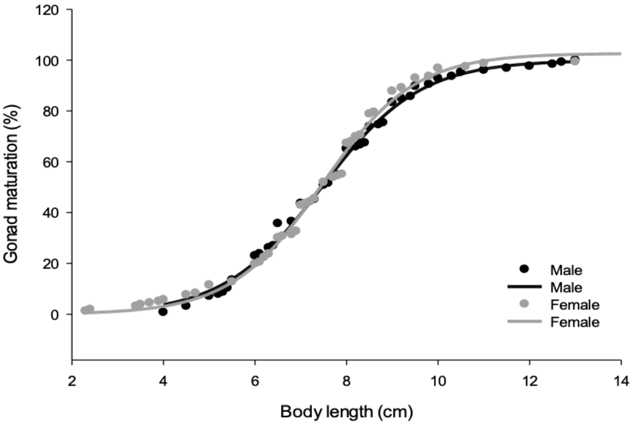

Figure 7. First gonad maturation size of *Antillesoma antillarum*

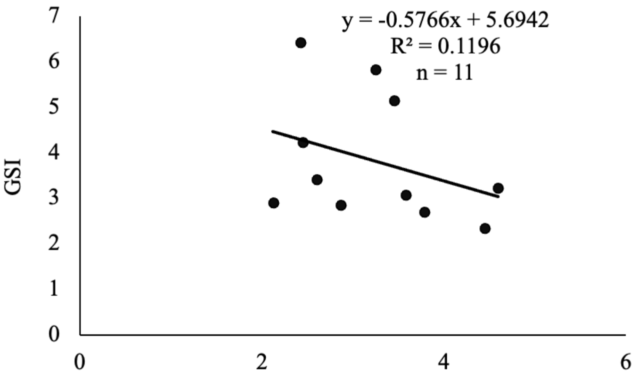

Figure 8. The linear relationship between GSI and SOM

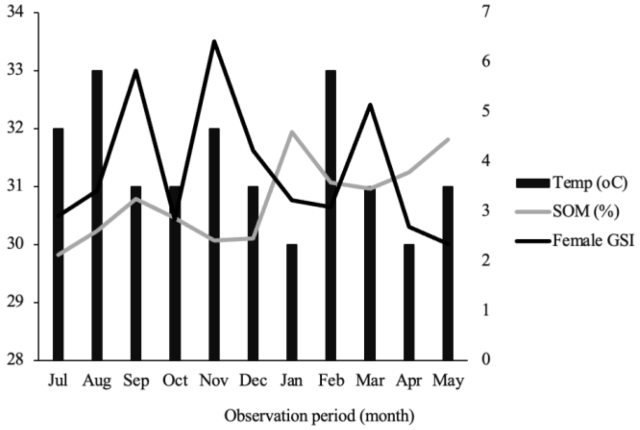

Figure 9. The relationship between the gonadosomatic index of *Antillesoma antillarum,* SOM, and water temperature

Seasonal reproductive cycle

The seasonal reproductive cycle of *A. antillarum* in the coastal waters of Toronipa exhibited a highly regular and synchronized pattern between gonadal development (Gonad Maturity Level, GML) and the Gonadosomatic Index (GSI). The GML parameter represents the stages of gonad development in individuals within a population and plays a crucial role in estimating spawning stock biomass and peak reproductive timing (Follesa et al. 2019). GSI, which is defined as the ratio between gonad weight and total body weight (Wang et al. 2009). In this study, the dynamics of GML and GSI in *A. antillarum* demonstrated a clear seasonal pattern.

Based on microscopic classification, the gonadal maturation cycle is divided into four stages (I-IV), as described in Table 1 (Bahtiar et al. 2024). At the beginning of the observation period (July-September), most individuals were in stages I and II, indicating immature gonads. This corresponded with the low GSI values during this period, reflecting the absence of significant gonadal maturation. Over time, from October onward, the proportion of individuals in stages III and IV increased rapidly, marking the onset of widespread gonadal maturation. Peak gonadal maturity was recorded in November-December, with the proportion of individuals in stages III and IV reaching its highest level, indicating the main spawning period, with GSI values also reaching their peak.

The sharp decline in GSI values during January-February, which coincided with the reduced proportion of individuals with mature gonads, indicates the release of gametes during the spawning period. Interestingly, although most individuals returned to stages I and II after the peak spawning period, mature gonads (stages III-IV) continued to be observed throughout the year. This suggests the potential for continuous spawning, a phenomenon also recorded in related species such as *S. a. australe* (Bahtiar et al. 2024), *Sipunculus nudus* (Guo 2002), and *P. esculenta* (Wang et al. 2009).

However, this phenomenon of continuous spawning may be linked to broader environmental factors such as habitat quality and nutrient cycles. Continuous spawning in *A. antillarum* may be associated with stable habitat quality, encompassing physical and chemical water conditions as well as nutrient availability that supports gonadal development throughout the year. Previous studies have shown that gonadal maturation in marine invertebrates is strongly influenced by the availability of Polyunsaturated Fatty Acids (PUFAs), particularly omega-3 fatty acids, which play a key role in gonadal maturation and egg quality (Stabili et al. 2018; Angilè et al. 2020).

Meanwhile, the results of the correlation analysis between GSI and Sediment Organic Matter (SOM) in this study showed a weak relationship (R^2: 0.11), indicating that although there was a tendency for GSI to decrease with increasing SOM, the relationship was not strong enough to serve as a major determinant in the reproductive dynamics of *A. antillarum*. Therefore, although sediment organic matter may affect habitat quality, other factors, such as water temperature and biological factors, may have a greater impact on the reproductive cycle of this species.

One important factor influencing the reproductive cycle of *A. antillarum* is the stability of water temperature, which remained within the range of 30-33°C throughout the year. Studies on other marine invertebrates have shown that stable water temperature can support gonadal maturation and extend the spawning season (Crisóstomo et al. 2023). In addition, reproductive adjustments to environmental factors can be explained through the adaptive strategy of *A. antillarum*, which exhibits year-round spawning, although with lower intensity after the peak spawning in November-December. Research on other benthic invertebrates, such as *Scrobicularia plana*, has revealed a latitude-dependent spawning pattern, with populations in southern areas showing more frequent spawning throughout the year (Raleigh and Keegan 2006). This reproductive strategy may serve as an adaptation to varying environmental conditions in tropical regions, where spawning can occur year-round, though with variable intensity depending on external factors (Anajjar et al. 2008). Climate variability may also influence spawning patterns through changes in temperature, rainfall, and habitat quality. As global climate change progresses, more extreme temperature fluctuations or alterations in sediment quality could impact the reproductive cycles of various benthic species (Piqué-Fandiño et al. 2022).

More reproduction-based management recommendations (Eero et al. 2019; Tuohy et al. 2023) include establishing closed seasons during peak spawning periods (November-December) and prohibiting harvesting in the subsequent months (January-February). This aims to minimize disturbance to the natural regeneration of the population and ensure optimal spawning success (Tsuji and Shibata 2020; Ta et al. 2023). Reproduction-based management can also help address exploitation pressures (Schmidt et al. 2015) faced by *A. antillarum* populations in the coastal waters of Toronipa.

Fecundity

Fecundity is a key parameter that describes the number of eggs produced by a female peanut worm during a single reproductive cycle (Llodra 2002). The results show a proportional pattern between the body length of *A. antillarum* and the number of eggs produced. However, increased fecundity is not often accompanied by an increase in body size. The highest fecundity was observed at the productive size range of 8-8.5 cm, reaching up to 4,500 eggs (Figure 7).

The pattern of *A. antillarum* is similar to that of other invertebrates, where fecundity increases with size up to a certain point, after which the rate declines, indicating signs of senescence or the presence of an optimal size threshold for reproduction (Swiney et al. 2012). Only 26% of fecundity variation is explained by body size (Levitan 1991). Understanding the relationship between fecundity and body size is important for establishing a minimum catch size that ensures individuals have the opportunity to reproduce at least once before being harvested (Wardiatno et al. 2015). The reproductive potential of *A. antillarum* peaks at a productive body size of around 8 cm, which produces a higher number of eggs and enhances the chances of successful reproduction and population regeneration in the wild (Poulin and Leung 2011). From a management perspective, peanut worms of a specific size (8 cm) contribute significantly to the population's egg stock. Therefore, protecting individuals of this size is crucial for ensuring population regeneration and sustainable resource management without threatening population survival.

Size at first gonadal maturity

Non-linear regression analysis showed that peanut worms began gonadal maturation at a size of 2.3 cm, at which oocytes were detected in *A. antillarum*. The gonadal maturity at a length of 8 cm was 50% (Lm_{50}). At 9 cm and above, more than 75% were mature, and nearly all individuals measuring over 12 cm were sexually mature. Oocytes were detected in females of other peanut worm species, such as *Aspidosiphon muelleri* (Ferrero-Vicente et al. 2014), *S. australe australe* (Bahtiar et al. 2024), *S. nudus* (Ainnoun et al. 2019), and *Siphonosoma cumanense* (Rice 1988), starting at 4-5 mm, 12.4-13.5 cm, 15 cm, and 20 cm, respectively (Figure 8).

The size at first gonadal maturity (Lm_{50}) in *A. antillarum* is estimated to be around 8 cm, at which 50% of individuals reach gonadal maturity. This size is crucial for establishing effective minimum catch size regulations. Protecting individuals that have not yet reached first maturity can enhance the chances of natural regeneration and reduce the negative impacts of overfishing on the population (Lassis et al. 2023). A maturity size greater than 8 cm indicates that smaller individuals should be protected to ensure future reproductive sustainability.

Implementing minimum catch size regulations that align with the Lm_{50} can contribute to population sustainability (Takar and Gurjar 2020). Protecting individuals smaller than 8 cm will allow them to reproduce before being harvested, thus supporting long-term population recovery and sustainability (Dias et al. 2022).

The reproductive performance of marine invertebrates is strongly influenced by environmental variables, particularly temperature and sediment quality (Miller et al. 2015). In *A. antillarum*, the analysis of the relationship between the Gonadosomatic Index (GSI), water temperature, and Sediment Organic Matter (SOM) revealed important ecological patterns in its seasonal cycle (Yamahira 2004). The GSI values showed clear temporal variation-lowest between July and September, increasing significantly in October, and peaking between November and December. Following this peak, GSI declined sharply in January-February and showed an increasing trend again from March to May. These findings have practical implications for the management and conservation of marine ecosystems, highlighting the importance of considering environmental variables in such efforts.

Interestingly, these seasonal GSI fluctuations did not correlate directly with water temperature, which remained relatively stable within a tropical range of 30-33°C throughout the study period. For instance, a high GSI in November (6.42%) occurred at 32°C, the same temperature recorded in July when GSI was much lower (2.91%). This suggests that water temperature does not directly regulate gonad development in *A. antillarum*, although a stable tropical temperature does provide favorable conditions for reproductive activity (Zeh et al. 2015).

In contrast, although the statistical relationship between GSI and SOM is weak (R^2: 0.1196) (Figure 8), a trend was observed between GSI and sediment organic matter content. Periods with high SOM concentrations (e.g., January-February, >3.5%) coincided with significant decreases in GSI (Figure 9), indicating that increased accumulation of organic matter may negatively affect reproductive activity. This may result from the formation of anaerobic conditions or the release of toxic compounds such as hydrogen sulfide or ammonia from decomposing organic material, which can impair the physiology of benthic organisms, including gonad development (Völkel and Grieshaber 1992). Conversely, low SOM levels during the peak gonad maturation period (September-December) correlated with higher GSI values (Kandratavicius et al. 2024). This pattern contrasts with other species, such as *S. australe* (Bahtiar et al. 2024) and *Tenualosa ilisha* (Ahammad et al. 2021), in which temperature and organic matter content were found to support gonad maturation and spawning. Therefore, further research is needed to explore in greater depth the relationship between habitat quality, nutrient availability, and the reproductive cycle of *A. antillarum*. Given these findings, it is urgent and crucial to adopt an integrated management approach, considering catch size, seasonal timing, and sediment quality, which is crucial for the conservation and sustainable use (Breuyn et al. 2023; Rodrigues-Barreras et al. 2018), including that of *A. antillarum* resources.

This study provides the first reproductive biology assessment of *A. antillarum* in Toronipa, Southeast Sulawesi. The species exhibited year-round gametogenesis with a clear spawning peak from November to December, coinciding with the onset of the rainy season. Size at first maturity (Lm_{50}) was estimated at 8 cm, and maximum fecundity occurred in individuals of 8.0-8.5 cm length, while sex ratio remained balanced. Environmental factors such as salinity, oxygen, and organic matter showed only minor influence on reproductive activity. These findings indicate that management of *A. antillarum* should prioritize protecting individuals below 8 cm and enforcing closed seasons during peak spawning (November-February). Such measures, combined with community-based monitoring, are essential to ensure sustainable exploitation of this ecologically and economically valuable sipunculan in Southeast Sulawesi.

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