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Critical Exploitation Status of the Mitre Squid, *Uroteuthis chinensis*, in the Karimata Strait Driven by an Extreme Size-at-Maturity to Size-at-Capture Discrepancy

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ABSTRACT

The mitre squid, Uroteuthis chinensis, is a commercially vital cephalopod in Southeast Asia, yet population-specific data essential for sustainable management are often lacking for key fishing grounds. This study provides the first comprehensive assessment of the reproductive biology and exploitation status of U. chinensis in the heavily fished Karimata Strait, Indonesia. A total of 1,329 specimens were collected monthly from April 2023 to March 2024 and were analyzed for sex ratio, gonad maturity, length at first maturity (Lm₅₀), and length at first capture (Lc_{50}). The results revealed a unique population structure, characterized by a persistent male-biased sex ratio (1.63:1; 62% males) and an exceptionally large size at maturity ($Lm_{50} = 28.9$ cm mantle length), nearly double that reported from adjacent regions. Crucially, the mean length at first capture (Lc₅₀) was only 18.1cm. The condition where Lc₅₀ is significantly smaller than L_{m50} provides unequivocal evidence of severe growth overfishing, indicating that the fishery predominantly harvests immature individuals before they can contribute to the spawning stock. These findings underscore the precarious status of the stock and highlight an urgent need for immediate management interventions, such as implementing a minimum legal size and gear modifications, to ensure the long-term sustainability of this critical fishery.

INTRODUCTION

Global capture fisheries are facing a crisis driven by intensive exploitation and climate change, leading to a drastic decline in commercial fish stocks (**Liu** et al., 2024). Amidst this situation, a paradigm shift is occurring, marked by the increasing role of cephalopods (squids, cuttlefish, and octopuses). Unlike finfish, the global catch of







cephalopods has steadily increased since the 1990s, now accounting for approximately 4% of the world's total fishery production (**Liu** *et al.*, **2024**). This rise represents a form of ecological succession: the overfishing of predatory fish has created an "ecological niche" that cephalopods have successfully filled, owing to their short life cycles, rapid growth, and high adaptability (**Liu** *et al.*, **2024**). One of the most prominent species is the squid *Uroteuthis chinensis*, which has become the most valuable fishery commodity in the Indo-Pacific and dominates catches in countless regions, such as the South China Sea (**Xu** *et al.*, **2020**). This phenomenon positions *U. chinensis* not only as a vital economic resource but also as an indicator species reflecting changes in marine ecosystems due to anthropogenic pressures.

For Indonesia, the world's second-largest fisheries producer with numerous fish stocks already fully or over-exploited (Napitupulu et al., 2022), the cephalopod fishery is a crucial component for sustaining coastal economies. One of the most important squid fishing grounds is Fisheries Management Area (FMA) 711, which includes the Karimata Strait and is a primary contributor to the national squid exports, with *U. chinensis* as its main target (Puspito, 2022). This species, with its "live fast, die young" life strategy (a life cycle of <200 days), possesses remarkable phenotypic plasticity that allows it to withstand fishing pressure (Liu et al., 2024). However, this adaptability can mask the impacts of exploitation. High fishing pressure tends to remove larger individuals, which indirectly favors individuals that mature earlier at smaller sizes (Fauziyah et al., 2020). Consequently, the population does not show clear signs of collapse but instead experiences "creeping degradation"—a gradual decline in average size and reproductive potential, a form of stock depletion that is difficult to detect without in-depth biological analysis.

To manage this resource sustainably, stock status assessment relies heavily on understanding its reproductive biology parameters. Two key parameters are the size at first maturity (Lm₅₀) and the size at first capture (Lc₅₀). Studies across various locations have shown extremely high variability in these parameters, affirming that data cannot be generalized between regions. The Lm₅₀ for *U. chinensis* has been reported to range from 83.5 to 149mm for males and from 112.5 to 151mm for females (Liu *et al.*, 2024). Similarly, the Lc₅₀ varies significantly depending on the fishing gear used, ranging from 94 mm to 139 mm (Fauziyah *et al.*, 2020). The use of fishing gear with small mesh sizes tends to result in a low Lc₅₀, increasing the risk of capturing juvenile individuals (Wang *et al.*, 2021).

The comparison between these two parameters serves as a fundamental diagnostic tool. A condition where the size at capture is smaller than the size at maturity (Lc₅₀ < Lm₅₀) is a classic indicator of growth overfishing—the capture of individuals before they have had a chance to reproduce and replace their generation. This phenomenon has been widely reported in various squid fisheries (**Fauziyah** *et al.*, **2020**) and is a primary management concern. This consistent finding suggests a systemic issue, yet its solution

must be based on biological data specific to each local stock. Therefore, this research is a crucial step in generating the local data needed to design targeted management strategies.

The study site, the Karimata Strait, was selected for its unique oceanographic and fishery characteristics. The strait is a dynamic ecological corridor connecting the South China Sea and the Java Sea, where its dynamics are controlled by the regional monsoon system (Yuliardi et al., 2025). During the southeast monsoon season (July-October), strong winds induce upwelling—the rising of cold, nutrient-rich water masses to the surface (Wyrtki, 1961; Yuliardi et al., 2025). This nutrient supply triggers a bloom in primary productivity that sustains a rich marine food web, making the Karimata Strait one of Indonesia's most productive fishing grounds (Susanto et al., 2001; Puspito, 2022). Nevertheless, a significant knowledge gap exists regarding the population biology of *U. chinensis* specific to this ecosystem. To address this gap, this study aimed to establish critical biological reference points for the *U. chinensis* population in the Karimata Strait by analyzing reproductive parameters and comparing Lm50 with Lc50 to evaluate the risk of growth overfishing. The results are expected to provide a robust scientific basis for sustainable fisheries management in FMA 711.

MATERIALS AND METHODS

1. Sampling

Sampling was conducted from April 2023 to March 2024 at the fish landing sites of fishers who capture squid in the Karimata Strait. The landing sites were Sungai Liat (Bangka Belitung) and Pekalongan (Central Java) (Fig. 1). Samples were randomly collected from the catches of commercial fishers. The fishing gear used in Sungai Liat was the squid net, whereas in Pekalongan, a mini purse seine was employed. These locations and gear types were selected because both are used to target *U. chinensis* in the Karimata Strait, and the sampled catches had not been sorted by size.

Data collection from the *U. chinensis* samples involved measuring the mantle length (ML) and dissecting individuals for sex determination and gonad maturity assessment. Mantle length measurements were taken fortnightly, while dissections for determining sex and maturity stage were performed monthly. The gonad maturity stage was classified according to the five-stage scale proposed by **Lipinski** (1979), where stages III and IV represent gonad-matured (adult) squid.

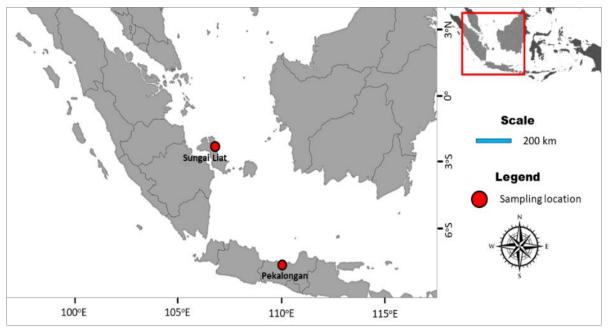


Fig. 1. Map of the study area showing the sampling locations. The red dots indicate the landing sites, Sungai Liat (Bangka Belitung) and Pekalongan (Central Java), where samples of *Uroteuthis chinensis* were collected from fisheries operating in the Karimata Strait.

2. Data analysis

Sex ratio analysis was performed by comparing the number of male and female individuals. The overall sex ratio for the entire sampling period and the monthly sex ratios were calculated. A Chi-square (χ^2) goodness-of-fit test was employed to determine if the observed ratios significantly deviated from the expected 1:1 ratio, with a significance level set at P<0.05. The overall sex ratio was visualized using a pie chart, while temporal variations in the monthly sex ratio were presented as a bar chart.

Estimation of length at first maturity (Lm₅₀) was obtained from the size proportion in 50% of squid that had matured gonads, calculated using the subsequent equation (**King**, 2007):

$$P = \frac{1}{1 + e^{-a(L - L_{m50})}}$$

Description: P = proportion of adult fish in length class L; L = mean length class; a = constant a.

The equation is converted to:

$$Ln[\frac{(1-P)}{P}] = aL_{m50} - aL$$

Information: The *intercept of* the equation is Lm₅₀ so the value of Lm₅₀ is:

 $Lm_{50} = intercept (a) / slope (a)$

Analyses for length at first capture (Lc₅₀) used the method of Beverton and Holt in **Sparre and Venema (1998)**:

$$SL = \frac{1}{1 + \exp(a - bL)}$$

Where the values of a (intercept) and b (slope) are calculated by linear regression estimation as follows:

$$\operatorname{Ln}(\frac{1}{SL_c} - 1) = a - bL$$

Where L = mean length value (cm) and $SLc_{50} =$ relative cumulative frequency of length. Lc_{50} can be calculated with the equation:

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

RESULTS

1. Sex ratio

Analysis of 1,329 specimens of *Uroteuthis chinensis* from the Karimata Strait revealed a significant skew in the overall sex ratio. The male-to-female ratio was 1.63:1 (62% males, 38% females) (Fig. 3), a value that deviates significantly from the expected 1:1 parity ($\chi^2 = 76.57$, df = 1, P < 0.001). This male-dominated pattern was not an isolated phenomenon but was observed consistently throughout the sampling year (April 2023–March 2024), indicating a persistent rather than seasonal trend. The year-round nature of this predominance suggests it is driven by underlying systematic factors rather than by behavioral aggregations associated with specific spawning peaks.



Fig. 2. A specimen of the mitre squid, *Uroteuthis chinensis*, collected from the Karimata Strait

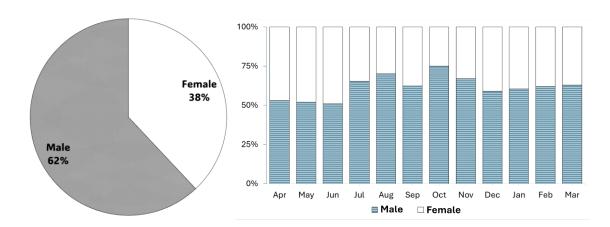


Fig. 3. Overall and monthly sex ratio of the squid *Uroteuthis chinensis* in Karimata Strait. The pie chart (left) shows the total proportion of males (62%) and females (38%) from all collected samples. The stacked bar chart (right) illustrates the monthly variation in the percentage of males and females. The total sample size was 1,329 (N = 1,329).

2. Gonad maturity

Based on the analysis of gonad maturity stages, the squid population as a whole, encompassing both males and females, exhibited a continuous year-round reproductive strategy (Fig. 4). This was evidenced by the presence of individuals from all four maturity stages (Immature, Developing, Mature, and Spawning) in every sampling month. Nevertheless, distinct peak spawning periods were observed, with a primary peak from May to September (particularly June-August) and a smaller, secondary peak

occurring from December to January. This spawning pattern indicates a high degree of temporal synchronization between the sexes, as males and females were ready to spawn during the same periods. Furthermore, the consistent monthly presence of immature and developing individuals, with a slight increase in February-March, signifies a continuous recruitment process of new individuals into the population.

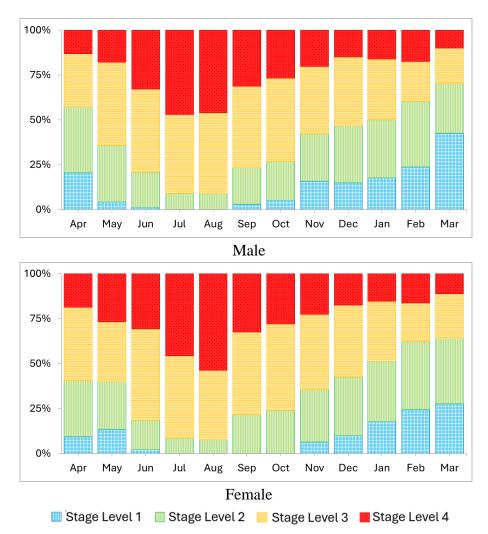


Fig. 4. Gonad maturity of *U. chinensis*, male squid (top) and female squid (bottom).

3. Length at first maturity (L_{m50}) and length at first capture (L_{C50})

The analysis revealed that the mantle length at which 50% of the population attains sexual maturity (Lm_{50}) was 28.9cm (Fig. 5). Meanwhile, the mantle length at which 95% of the population had sexually matured (Lm_{95}) was 34.5cm. The difference between Lm_{95} and Lm_{50} (i.e., 34.5cm - 28.9cm = 5.6cm) indicates variation in the maturation rate among individuals. This implies that the maturation process is not synchronous, with the remaining 45% of the population reaching gonad maturity within the mantle length range of 28.9 to 34.5cm.

The length at first capture (Lc₅₀) for the squid *Uroteuthis chinensis* in the Karimata Strait was 18.1cm. This Lc₅₀ value reflects the interaction between the size distribution of the population in the wild and the selectivity characteristics of the fishing gear employed. A key finding with serious implications for the sustainability of the *U. chinensis* fishery in the Karimata Strait is the comparison between the Lc₅₀ and the size at 50% maturity (Lm₅₀). With an Lc₅₀ of 18.1cm and an Lm₅₀ of 28.9cm, the Lc₅₀ is significantly lower than the Lm₅₀ (18.1cm < 28.9cm). This Lc₅₀ < Lm₅₀ condition directly indicates that the majority of squid captured by the fishery are immature and, therefore, have not had an opportunity to spawn and contribute to stock regeneration. This suggests a dominance of immature individuals in the catch, which will ultimately lead to overfishing.

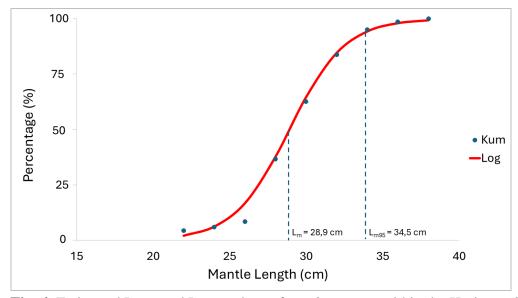


Fig. 4. Estimated Lm₅₀ and Lm₉₅ values of *U. chinensis* squid in the Karimata Strait

DISCUSSION

1. Sex ratio of the squid *Uroteuthis chinensis* in the Karimata Strait: An investigation of the factors causing male dominance

The highly male-biased sex ratio (approximately 1.63 males to 1 female) observed in the Karimata Strait shows a marked difference compared to several reports in the literature for *U. chinensis* or other closely related loliginid species. For example, **Arkhipkin** *et al.* (2015) reported a general sex ratio for *U. chinensis* of 1 male to 1.5 females, which means the male proportion was only about 40%. Another study by **Mulyono** *et al.* (2017) on *Loligo chinensis* (a probable synonym for *U. chinensis* or a very similar species) in the waters of Lamongan, East Java, found a sex ratio approaching equilibrium, at 1 male to 1.04 females (approximately 49% males). In contrast, other studies have reported that the proportion of male *U. chinensis* is higher than that of females (Jin *et al.*, 2019; Liu *et al.*, 2024). This substantial discrepancy between the data

from the Karimata Strait and these reports suggests the possibility of strong local factors or a systematic bias in the dominant fishing methods used in the Karimata Strait, which influences the sex composition of the catch.

Several potential factors may contribute to this observed male-biased sex ratio:

1. Differences in Growth, Size, and Longevity

There is evidence that male *Uroteuthis chinensis* squid often attain a greater mantle length than females. Males are reported to grow up to 49cm in mantle length (ML), whereas females reach up to 31cm ML (**Arkhipkin** *et al.*, **2015**). Research in the South China Sea specifically indicates that male *U. chinensis* have a higher growth rate than females (**Liu** *et al.*, **2024**). Faster growth and larger size in males can lead to earlier recruitment into fishing grounds and higher selectivity by size-selective fishing gear. If males grow faster, they will reach a size vulnerable to the gear earlier than females from the same cohort. Furthermore, if the fishing gear has a minimum catch size or is more efficient at capturing larger individuals, a population with larger males will yield a higher catch of males. This can create an apparent male dominance in the catch even if the population sex ratio at earlier life stages is different.

It is possible that males have a longer lifespan or a longer period of availability to the fishery after reaching sexual maturity. The literature indicates that loliginid males may mature earlier and potentially live longer, with some very large male individuals presumably spawning in their second year, although direct evidence for multi-year spawning is still lacking (O'Dor, 1995). The size at maturity for *U. chinensis* is approximately 16cm ML for males and 14cm ML for females (Arkhipkin *et al.*, 2015). In the South China Sea, the mantle length at which 50% of males are mature (DML₅₀) varied among cohorts: the spring cohort was 116mm, the summer cohort 129mm, and the autumn cohort 149mm (Liu *et al.*, 2024). If males mature earlier and/or live longer as reproductively active individuals, they will be present in the mature, fishable stock for a longer duration, leading to their accumulation in samples over time.

Earlier maturity means males enter the "mature" segment of the population sooner. If they also have higher post-maturity survival than females (due to lower post-reproductive investment or other factors), the pool of mature males available for capture will be larger than the pool of mature females at any given time. This is exacerbated if males can participate in multiple mating events over a long period while females have a more concentrated reproductive window followed by mortality.

2. Reproductive strategy and post-spawning mortality

Most coleoid cephalopods, including loliginids, are considered semelparous, meaning they die after a single reproductive period (**Arkhipkin** *et al.*, **2015**). The phenomenon of extensive maternal care and subsequent death in female octopuses is well-documented (**Wang & Ragsdale, 2018**), and this relates to the general pattern of post-reproductive mortality in female cephalopods. A study on *Loligo opalescens*

showed a high daily mortality rate (0.45) on spawning grounds and a very short survival time (mean of 1.67 days) after spawning commenced (Macewicz et al., 2004). Even if not all oocytes are released, the residual oocytes in spent females (e.g., in Sepia officinalis) are often atretic (undergoing degeneration), indicating limited further reproductive potential (Salman et al., 2017). High and often rapid post-spawning mortality in females is a key driver of unbalanced sex ratios that favor males in adult populations, especially if sampling occurs on or near spawning grounds or if males survive longer after mating. Females invest immense energy in egg production and potentially in egg-laying site selection or care. This high investment leads to physiological exhaustion and programmed senescence (e.g., the "self-destruct system" described in octopuses) (Wang & Ragsdale, 2018). Males, while also investing in mating, may not experience such a rapid and universal post-reproductive decline, or may be capable of multiple matings. Consequently, females are quickly removed from the post-spawning population, leaving behind a higher proportion of males.

Female post-spawning mortality contrasts with potential male reproductive strategies. Males may mate multiple times and remain on or near the spawning grounds for extended periods (**Arkhipkin** et al., 2015). As previously mentioned, some males may survive longer (**O'Dor**, 1995). If males can mate repeatedly over a longer period than females are able to lay eggs, they will be overrepresented in samples taken from areas where reproductive activity occurs. Female reproduction is often a terminal investment. In contrast, male reproductive success can be maximized by mating with multiple females. This may select for males that can survive multiple mating encounters and remain reproductively viable for longer, leading to their persistence in the population.

3. Behavioral differences and mating system

Males often engage in various displays to attract females (Arkhipkin et al., 2015). Such conspicuous behaviors may make them more vulnerable to certain fishing gear (e.g., squid jigs, visual traps) or sampling methods. Spawning aggregations are common (Hanlon, 1998) and are often targeted by fisheries. If males arrive earlier, stay longer, or are more active/aggressive within these aggregations, they may be disproportionately captured. Sex-specific behaviors related to reproduction can directly affect catchability. Male squid often engage in competitive displays or territorial defense on spawning grounds. This behavior might make them more aggressive towards squid jigs (perceiving them as rivals or prey) or more visible to nets. Females may be more cryptic, focusing on laying eggs in safer locations, making them less available to the same gear.

Studies such as those on *Illex coindetii* show that sex ratios can vary by depth and area, indicating potential spatial segregation of the sexes based on size, maturity, or reproductive stage (**Arkhipkin & Middleton, 2002**). Mature females may seek specific substrates or depths for egg-laying that differ from male aggregation areas. If

sampling in the Karimata Strait is concentrated in areas or at depths dominated by males (e.g., shallower mating grounds versus deeper egg-laying sites), this will yield a male-biased sample. The different sexes may have different habitat preferences or use different parts of the water column during various stages of their reproductive cycle. For instance, males might gather in one area for mating displays, while females move to another area for egg-laying. Fishing operations, if spatially limited or targeting specific features, may disproportionately sample from one of these sex-biased aggregations.

4. Environmental factors

Environmental conditions (e.g., temperature, food availability) can influence cephalopod life histories, including growth, maturation, and spawning (Liu et al., 2024). Although a direct link to sex ratio deviation in *U. chinensis* is not explicitly detailed in the reviewed literature, it is necessary to acknowledge that environmental pressures could differentially affect the survival or behavior of males and females. For example, research in the South China Sea demonstrated cohort-specific growth and maturation in *U. chinensis*, implying environmental influences during different seasons (Liu et al., 2024). While less direct, persistent environmental conditions in the Karimata Strait could favor male survival or behaviors that increase their catchability, or conversely, be detrimental to females. Environmental factors influence growth rates and size at maturity (as seen in cohort differences) (Liu et al., 2024). If these factors consistently favor faster male growth or earlier male maturity relative to females in a specific region, it could contribute to a higher proportion of catchable males over time. Extreme conditions could also lead to differential mortality, although this is more speculative without specific data.

5. Methodological considerations: Sampling bias and gear selectivity

This is a critical point. The observed sex ratio can be strongly influenced by the fishing gear used for sampling (Hanlon, 1998). Common gear types used for squid in Indonesia include squid jigs, lift nets (bouke ami), and trawls (Nugroho et al., 2024). Squid jigs often attract aggressive and actively feeding individuals. If males are more aggressive or feed more actively during certain periods (e.g., related to mating), jigs may yield more males. Trawls can be size-selective. Given that males grow larger, trawls may retain more males; studies on other species show complex interactions between depth, size, and sex for trawl catches (Arkhipkin & Middleton, 2002). Consistent male dominance across months may indicate a persistent gear bias if the same gear is used year-round. Different fishing gears do not sample the population randomly. Jigs rely on visual attraction and aggressive responses, potentially selecting for males if they are more visually oriented hunters or more aggressive during the mating season. Trawls select based on size and swimming ability/escape response; larger, faster-growing males may be more vulnerable. Lift nets may sample

aggregations, and if these aggregations are sex-biased due to behavior, the catch will reflect that.

If sampling is consistently conducted in locations or at times (e.g., day vs. night, specific seasons if behavior changes) where males are more abundant or active, this will produce a biased result (**Arkhipkin & Middleton, 2002**). The spatial and temporal strategy of sampling is as important as the gear itself. If sampling always occurs at a known male aggregation site for mating, or during peak times of male activity, the results will inevitably be male-biased, regardless of the overall population sex ratio across all habitats and times.

The data from the Karimata Strait (62% male, 38% female annually; consistent monthly male dominance) is most likely the result of a combination of the various factors discussed. It is unlikely that a single cause is responsible for the observed pattern. Instead, an interaction between the species' inherent biological traits (such as faster male growth and high post-spawning female mortality) and potential biases from the sampling methods appears to be the most plausible explanation. The consistency of male dominance throughout the year suggests that the underlying factors are persistent, rather than being solely related to a brief peak spawning season.

High post-spawning female mortality (**Arkhipkin** *et al.*, **2015**) combined with the potential for a longer reproductive lifespan or activity in males (**O'Dor**, **1995**) are strong biological candidates to explain the observed male dominance. The year-round spawning of *U. chinensis* (**Liu** *et al.*, **2024**), when combined with rapid female mortality after each spawning cycle, would cumulatively reduce the proportion of females in the fishable adult population. The consistent monthly male dominance reinforces the argument for persistent factors such as differential mortality or sustained behavioral differences linked to year-round spawning, rather than short-term spawning aggregation effects. The role of the fishing gear remains a crucial unknown variable. If, for example, squid jigging is the primary method, and males are consistently more aggressive or responsive to jigs, this could explain the persistent bias. Conversely, if bottom trawls are used and males reach larger sizes more quickly, this would also lead to a male bias.

If the observed sex ratio reflects the true adult spawning population, it could have ecological and fisheries management implications. Although the effective number of females may be low, male dominance could ensure a high fertilization rate if males are capable of mating with multiple females. However, if the number of females becomes severely limited, the overall reproductive potential of the stock could be compromised.

2. Monthly gonad maturity dynamics of the squid *Uroteuthis chinensis* in the Karimata Strait, Indonesia

The presence of all four gonad maturity stages in the combined, male, and female populations of *Uroteuthis chinensis* in the Karimata Strait throughout the year (April–March) clearly indicates that this species has a continuous spawning strategy (i.e., is a

year-round spawner). This aligns with numerous studies on *U. chinensis* and other loliginid species in various waters, which report the capacity for year-round reproduction. The study by **Liu** *et al.* (2024) in the South China Sea demonstrated a year-round spawning pattern for *U. chinensis*. Similarly, research in the waters of Lamongan, Indonesia, showed that *L. chinensis* (often considered a synonym or a very closely related species) was dominated by individuals with mature gonads (Gonad Maturity Stages III and IV) (**Mulyono** *et al.*, 2017).

Although spawning occurs year-round, the data from the Karimata Strait indicate the existence of peak periods of spawning activity. The primary peak appears to occur between May and September, with a possible secondary peak around December to January. These peaks are characterized by the highest proportions of individuals at Stage 4 (spawning/fully mature) and Stage 3 (mature). This spawning pattern with seasonal peaks is also commonly reported for *U. chinensis*. For example, in the waters of Thailand, peak spawning was reported to occur during March–June and August–November (Chotiyaputta, 1995). Variation in the timing of peak spawning among locations can be influenced by local environmental conditions such as sea surface temperature, food availability, and seasonal currents like monsoons (Hamad *et al.*, 2025). The waters of the Karimata Strait are heavily influenced by the monsoon system, which can modulate oceanographic conditions and trigger biological responses in marine organisms (Yuliardi *et al.*, 2025).

The monthly patterns of Gonad Maturity Stage in males and females show a high degree of synchrony. The increase in the proportion of mature and spawning individuals (Stages 3 and 4) occurs during the same periods for both sexes. This synchronization is crucial for reproductive success, ensuring the availability of male and female gametes at the optimal time for fertilization. The consistent monthly presence of immature (Stage 1) and developing (Stage 2) individuals of both sexes indicates continuous recruitment of young individuals into the observable population. This supports the relatively short life cycle and rapid growth that are characteristic of many cephalopod species (**Liu** *et al.*, 2024). The increased proportion of immature individuals in February–March may signify the entry of a new cohort resulting from spawning several months prior.

Understanding the gonad maturation patterns and spawning season of *U. chinensis* in the Karimata Strait is essential for designing effective fisheries management strategies. This information can be used to determine fishing closure periods (if required) to protect spawning aggregations or to regulate fishing effort to avoid excessively disrupting reproductive peaks. Given that spawning occurs year-round, management may need to focus on protecting spawning habitats or implementing minimum size limits to ensure individuals have the opportunity to reproduce at least once.

3. Gonad maturity and size at first maturity (Lm₅₀)

One of the most striking findings from the provided data is that the Lm₅₀ value of 28.9cm for *Uroteuthis chinensis* in the Karimata Strait is substantially larger than reports

from other studies conducted on the same or closely related species in different geographical regions. For comparison, **Arkhipkin** *et al.* (2015) report a size at maturity for male *U. chinensis* of approximately 16cm mantle length and for females of approximately 14cm mantle length. A more recent study by **Liu** *et al.* (2024) in the South China Sea found that the mantle length at 50% maturity (DML₅₀) for male *U. chinensis* ranged from 11.6 (for the spring cohort) to 14.9cm (for the autumn cohort). Research by **Mulyono** *et al.* (2017) in the waters of Lamongan, Indonesia, on *Loligo chinensis* showed a male Lm₅₀ of 12.47 cm and a female Lm₅₀ of 11.36 cm.

The difference between the Lm₅₀ in the Karimata Strait (28.9cm) and the values reported from other regions (generally ranging from 11–16cm) is highly significant, with the Lm₅₀ in Karimata being almost twice as large. This large disparity indicates that the *U. chinensis* population in the Karimata Strait likely possesses substantially different growth characteristics and maturation strategies compared to populations in other locations.

Several potential causes for this large difference in Lm₅₀ include:

- 1. Genetic Variation or the Presence of a Distinct Local Stock: The *U. chinensis* population in the Karimata Strait could constitute a genetically distinct stock unit, with unique growth rates and maturation strategies resulting from adaptation to local conditions (**Liu** *et al.*, 2024). Studies on the genetic structure of *U. chinensis* in Indonesian waters are still limited, but research suggests the potential for morphometric and genetic variation among populations in different regions, which may be influenced by oceanographic conditions (**Ervinia** *et al.*, 2024).
- 2. Specific Local Environmental Factors: Environmental conditions in the Karimata Strait, such as sea surface temperature (SST), food availability and quality, salinity, and current patterns, can significantly influence the growth rate and the age or size at which individuals reach gonad maturity (Yuliardi et al., 2025). The Karimata Strait is known to have oceanographic dynamics influenced by the monsoon system, which causes seasonal variations in these environmental parameters. These conditions could create a different growth and maturation regime compared to other regions that have more stable or different environmental conditions.
- 3. Long-term Fishing Pressure: Theoretically, high and persistent fishing pressure over a long period can result in selection for individuals that mature at smaller sizes and younger ages, as an adaptive response to ensure reproductive success before being caught. However, the high Lm₅₀ data from the Karimata Strait directly contradict this typical response. This suggests that if fishing pressure does play a role, its mechanism may be more complex, or that other, more dominant factors are driving maturation at a larger size.

4. Length at first capture (Lc₅₀) and its relationship with gonad maturity

The results of the Lm50 and Lc50 analysis indicate that the majority of the squid individuals captured by the fishery in the Karimata Strait are gonadally immature. Consequently, these individuals have not had the opportunity to spawn and contribute to stock regeneration. A study by **Pramulati** *et al.* (2023) explicitly states that if Lc50 is lower than Lm50, this indicates a dominance of juvenile fish (immature and unspawned individuals) in the catch, which will ultimately lead to a state of overexploitation (overfishing). The relationship Lc50 < Lm50 is a classic indicator of the occurrence of *growth overfishing* (**Diekert, 2011**). *Growth overfishing* is defined as a condition in which a fishery resource is exploited before the individuals in the population have reached their optimum size or weight and, more importantly, before they have had a chance to realize their full growth and reproductive potential (**Diekert, 2011**; **Quaas** *et al.*, **2013**). The data from the Karimata Strait, with an Lc50 = 18.1cm that is far below the Lm50 = 28.9cm, strongly aligns with this definition. This means that the fishery is harvesting squid at a juvenile stage, thereby reducing the potential total yield per recruit and significantly threatening the stock's ability to renew itself through reproduction.

With an Lm₅₀ of 28.9cm, the difference between Lm₅₀ and Lc₅₀ is 10.8cm (28.9 -18.1cm). This means that, on average, squid in the Karimata Strait are captured at a size that is 10.8cm smaller than the size at which 50% of them reach gonad maturity. This represents a very large size deficit. Furthermore, with an Lm95 (the size at which 95% of the population is mature) of 34.5cm, the squid captured at the Lc₅₀ of 18.1cm are extremely far from the size at which nearly all of the population have the opportunity to mature and reproduce. Thus, nearly the entire catch around the Lc50 of 18.1cm consists of juvenile individuals. Severe growth overfishing, as indicated by the data from the Karimata Strait, not only impacts the current spawning stock biomass (SSB) but also has the potential to trigger recruitment overfishing in the long term (Majeed et al., 2025). Recruitment overfishing occurs when the number of adult individuals that successfully spawn continuously declines due to the intensive harvesting of young individuals, such that the number of new recruits (young individuals entering the population) also becomes threatened. This can create a worsening cycle of stock decline that is difficult to reverse. A case study by Majeed et al. (2025) on the fish Otolithes ruber explicitly links the condition of Lc₅₀ < Lm₅₀ to the occurrence of growth overfishing, a significant decline in the Spawning Potential Ratio (SPR), and ultimately, recruitment overfishing and a drastic stock decline (Majeed et al., 2025). A similar situation is very likely occurring or is already underway in the *U. chinensis* population in the Karimata Strait.

5. Reproductive status and fisheries implications

The integration of the analyzed data presents a concerning overview of the reproductive status and exploitation condition of the squid stock *Uroteuthis chinensis* in the Karimata Strait. Three prominent findings are:

- 1. Male Dominance in the Catch: A significant sex ratio bias exists, with the male proportion reaching 62% in the annual catch and consistent male dominance observed in the monthly data.
- 2. Relatively Large Size at Maturity: The length at first maturity ($Lm_{50} = 28.9$ cm and $Lm_{95} = 34.5$ cm) for the population in the Karimata Strait was recorded to be much higher than reports from other regions for the same species.
- 3. Capture of a Majority of Immature Individuals: The mean length at capture (Lc50 = 18.1 cm) is well below the Lm50 and Lm95 values, indicating that the majority of the exploited squid are juvenile individuals that have not yet participated in reproduction.

The combination of capturing very young individuals (Lc₅₀ < Lm₅₀) and the presence of a male bias in the catch creates a dual pressure on the reproductive potential of the *U. chinensis* stock in the Karimata Strait. Not only is the total number of potential spawners drastically reduced due to capture before maturity but the sex structure of the remaining potential spawning population may also be disrupted. The majority of the captured individuals are juveniles, and of this juvenile group, the majority are males. This means a large number of young males are removed from the population before they reach maturity and have the opportunity to fertilize females. If this trend continues long-term, females that successfully reach maturity may face a shortage of mature and reproductively competent male partners. Although males of some cephalopod species are known to be capable of fertilizing multiple females, a significant reduction in the number of available adult males could reduce overall fertilization efficiency and, ultimately, decrease the overall reproductive success of the population.

The capture of squid at sizes well below the Lm₅₀ directly and significantly reduces the number of individuals that can contribute to the spawning stock biomass (SSB). This becomes particularly crucial for cephalopod species that are generally semelparous, i.e., they spawn only once in their life cycle and then die. For a semelparous organism, each individual has only one opportunity to reproduce and pass on its genes. If that individual is caught before maturing and spawning, its genetic and reproductive contribution to the next generation is lost entirely. A sustained reduction in SSB due to the exploitation of juvenile individuals will negatively impact recruitment levels in subsequent generations. The fewer adults that successfully spawn, the fewer eggs are produced and the lower the potential for new larvae or juveniles to enter the population. This can trigger a long-term spiral of stock decline, as has been documented in various other fishery case studies experiencing Lc₅₀ < Lm₅₀ and severe *growth overfishing* (Majeed *et al.*, 2025).

The Karimata Strait has dynamic oceanographic characteristics, heavily influenced by regional monsoon patterns that cause seasonal variations in environmental parameters such as sea surface temperature (SST) and salinity (Yuliardi et al., 2025). Changes in SST and other environmental parameters are known to affect various aspects of squid biology, including spatial and temporal distribution, spawning time, growth rate, and

fecundity (**Liu** *et al.*, **2024**). If the peak fishing season for squid in the Karimata Strait coincides with the period when squid form spawning aggregations (which may be triggered by optimal seasonal environmental conditions), and the fishing gear used predominantly captures individuals below the size at maturity (Lc₅₀ = 18.1cm, while Lm₅₀ = 28.9cm), then the negative impact on the stock will be greatly magnified and damaging. Squid often form dense aggregations during spawning periods, which makes them an easy and attractive target for fishing activities due to the potential for high catch per unit effort (CPUE) (**Hanlon**, **1998**). Fishing effort that is concentrated on spawning aggregations composed largely of immature individuals is a worst-case scenario for the sustainability of the resource. This is because the fishery not only removes individuals from the population but also effectively eliminates a large amount of potential reproductive biomass just before they have the chance to spawn and contribute to the next generation. This impact is far more detrimental than simply catching juvenile individuals randomly from a dispersed population outside of the spawning season.

6. Management recommendations

Based on the critical findings of this analysis, and by referencing the principles of sustainable fisheries management as well as recommended management practices in similar cases of *growth overfishing* (Majeed *et al.*, 2025), the following management recommendations are proposed for the *U. chinensis* fishery in the Karimata Strait:

- 1. Increase the Length at First Capture (Lc₅₀) to Meet or Exceed Lm₅₀:
 - Gear Regulation: Implement and enforce regulations on more selective fishing gear specifications to reduce the capture of small (juvenile) squid individuals. This may include establishing a minimum mesh size (for net-based gear such as lift nets) or larger minimum hook/jig sizes (for hook-and-line gear). Specific research on the selectivity of the various dominant gear types used in the Karimata Strait is urgently needed as a scientific basis for these regulations (**Prihantoko & Saputra, 2025**).
 - Establishment of a Minimum Landing Size (MLS): Establish and strictly enforce a minimum size of squid that can be landed. Ideally, the MLS should be set at or above the Lm₅₀ value (i.e., >28.9 cm mantle length) to ensure that the majority of captured individuals have had an opportunity to spawn.
- 2. Fishing Effort Reduction: Implement measures to reduce the overall fishing pressure on the *U. chinensis* stock. This can be achieved through various mechanisms, such as limiting the number of fishing fleets, limiting the number of fishing days, or establishing a Total Allowable Catch (TAC), if sufficient data are available for its estimation.
- 3. Spatial and Temporal Protection of Spawning Areas and Seasons:
 - o Conduct further research to accurately identify the primary spawning grounds and the peak spawning seasons for *U. chinensis* in the waters of the Karimata Strait.

- Once identified, implement spatial closures or temporal (seasonal) closures in these areas and at these times to protect spawning aggregations and provide squid an opportunity to reproduce without disturbance.
- 4. Development of a Continuous Research and Monitoring Program: Establish and implement a routine and systematic biological and fisheries monitoring program. This program should include the collection of catch length-frequency data, gonad maturity analysis (with data segregated by sex), standardized catch per unit effort (CPUE) data, and other relevant data such as gear types used and the distribution of fishing grounds (Majeed *et al.*, 2025).
- 5. Collaborative Approach and Awareness Enhancement:
 - Actively involve fishers, fishery business operators, and other stakeholders in the entire planning and implementation process of management actions. This participatory approach is essential to increase the acceptance, compliance, and effectiveness of any policies implemented.
 - Conduct outreach and awareness-raising programs on the importance of sustaining the squid resource and the negative impacts of harvesting juvenile individuals.

Given the very high observed Lm_{50} value for the U. chinensis population in the Karimata Strait (28.9cm), achieving the ideal target of $Lc_{50} \ge Lm_{50}$ may require quite drastic changes to current fishing practices and could potentially face socio-economic challenges from the fishing community. Therefore, an adaptive and phased management approach may be more realistic to implement. This could begin with setting a more achievable intermediate Lc_{50} target in the short term, which is gradually increased towards the Lm_{50} , combined with the immediate implementation of other protective measures such as spawning area/season closures and a general reduction in fishing effort. Effective and transparent communication with all stakeholders regarding the scientific basis, objectives, and long-term benefits of these management actions will be key to the success of efforts to sustain the U. chinensis squid resource in the Karimata Strait.

CONCLUSION

This study of *Uroteuthis chinensis* in the Karimata Strait concludes that the squid stock is at high risk due to severe growth overfishing. This conclusion is based on the primary evidence of a significant disparity between an exceptionally large size at maturity (Lm50) of 28.9cm and a much smaller mean size at capture (Lc50) of 18.1cm. This condition leads to the exploitation of the majority of the squid before they have an opportunity to reproduce. The population also exhibits unique characteristics, including year-round spawning and a male-biased sex ratio. Based on these findings, urgent management interventions are recommended, particularly through gear regulation and the establishment of a minimum legal catch size (above 28.9cm) to protect juvenile

individuals. These measures must be supported by further research and stakeholder collaboration to ensure the sustainability of the fishery.

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