

Substrate Preference and Population Structure of Lingulid Shell Species on the North Coast of East Java

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Abstract

Lingulid shell (*Brachiopoda: Lingulata*) is a marine invertebrate that still exists. The mangrove profile on the north coast of East Java shows the potential to become a habitat for lingulid shell. Despite the significant potential, the lack of similar previous data on substrate profiles, population, and species distribution in East Java shows that the presence of lingulid shells has received less attention, suggesting the need for conservative efforts to conserve and sustainable uses of marine resource. Therefore, this study aimed to describe the habitat ecology of lingulid shell on the north coast of East Java based on regency or city, population structure, internal distribution pattern, and substrate profile, as well as identify species distribution. In addition, confirm the lingulid shell species by molecular identification based on cytochrome oxidase subunit I (COI) gene. Sampling was carried out using the purposive sampling method by digging the substrate in the plot area to a depth of 5-10 cm on the north coast of East Java to obtain lingulid frame substrate which was tested based on the fraction (size). The results showed that lingulid shell could be found in Surabaya City as well as other regencies including Pasuruan, Probolinggo, Situbondo, Bangkalan, Pamekasan, and Sumenep. The discovery results identified the *Lingula anatina* species based on morphological and molecular characteristics. The population density of lingulid shell in East Java was found to be 52.6 individuals.m⁻², while the internal distribution had no continuity. Furthermore, the presence and distribution of *Lingula anatina* had a preference for silt substrates.

Keywords: *Lingula*, marine invertebrate, molecular characters

Introduction

Lingulid shell (*Brachiopoda: Lingulata*) is among marine invertebrates with the most complete fossil record from the first appearance in the Cambrian period to sporadic distribution in the oceans (Zhang *et al.*, 2005; Koneva and Ushatinskaya, 2008; Skovsted *et al.*, 2016; Topper *et al.*, 2017). The class *Lingulata*, which comprised three orders in the newly revised Treatise, is now represented by only one living order, *Lingulida* (Zhang *et al.*, 2005). It is one of the *linguliformea* subphylum species recognized as one of the most primitive groups of *Brachiopods* (Goto *et al.*, 2022), and many scientists recognize *L. anatina* as a "living fossil" (Madison *et al.*, 2021). Despite consisting of several species, lingulid shell has more members of other

phyla. This leads to the classification as members of a small phylum, namely *Brachiopoda*. At a glance, the shape of lingulid shell has similarities to the bivalved members of *Mollusca*. Based on further examination, there is a fundamental difference compared to *Bivalvia* shell. It is observed that lingulids exhibit bilateral symmetry within each valve, whereas bivalves possess bilateral symmetry as a whole organism formed by paired left and right valves, although individual valves are often asymmetrical (Sundaram and Deshmukh, 2009; Samanta *et al.*, 2014).

Most coastal communities recognize lingulid shell by various names, including lantern, leaf, sea bean sprouts, or Tebalan. These species are often used by coastal communities as food for consumption. The majority of coastal communities

working as shellfish fishermen often find lingulid shell under the substrate in the intertidal zone of water, but their numbers are relatively small when compared to other benthic invertebrates (Lowery *et al.*, 2007; Samanta *et al.*, 2015). Similarly, Bitner (2010); Mitra and Pattanayak (2013); and Darmarini *et al.* (2017) found lingulid shell of *Lingula* sp. under the substrate at a depth of 5-10 cm in the mangrove intertidal zone.

Previous studies have reported the identification and distribution of lingulid shells across several areas. Mitra and Pattanayak (2013) reported habitat profiles and population studies of lingulid shellfish species *Lingula* sp. at the Subarnekha estuary, India. Bitner (2010) conducted a study of habitats and new species of lingulid shells in Caledonia. *Lingula anatina* has sporadic distribution with this species only establishing on some coastline (Fujii *et al.*, 2019; Karagozlu *et al.*, 2021). In Indonesia, Mudjiono and Suparman (1992) explored the habitat and distribution of lingulid shell in eastern area, including on Sulawesi Island, Ambon Regency and Balikpapan coastal area East Kalimantan, and coastal area of Rote Island (East Nusatenggara Province). This species is also distributed in Probolinggo, East Java (Ambarwati *et al.*, 2021) and on the Coast of Madura Island (Rakmawati and Ambarwati, 2020). Darmarini *et al.* (2017) also observed habitat and profiles of lingulid shell of the *Lingula* sp. on the mangrove ecosystem in Lubuk Damar, Aceh Tamiang, Aceh Province. However, there are no studies on substrate profiles, population, and species identification in East Java.

The existence of mangrove beaches in Indonesia can be found in all provinces, including the north coast of East Java. This distribution covers several areas including Tuban Lamongan, Gresik, Surabaya, and Sidoarjo. Others include Pasuruan, Probolinggo, Situbondo, Bangkalan, Sampang, Pamekasan, and Sumenep regencies. The mangrove profile on the north coast of East Java shows the potential to become a habitat for lingulid shell. This is because lingulids are fauna that consume mangroves. Mangrove debris is their primary food source (Darmarini *et al.*, 2017). Lingulids also utilize mangrove roots for burrowing and hiding from predators. Lingulids burrow in the substrate, which is located among the mangrove roots that are submerged in the substrate.

Despite their significant potential, the lack of similar previous data on substrate profiles, populations, and species distribution in East Java indicates that the presence of lingulid shellfish has received little attention. Most research conducted to date has focused on modern invertebrates, while research on ancient invertebrates (including lingulids) is very limited, especially in Indonesia.

Based on this, structured research on ancient invertebrates is needed as a form of conservation effort to preserve their rare existence. Therefore, this study aimed to explore the presence species, and internal distribution pattern of lingulid shells on the north coast of East Java. In this study, also confirmed lingulid shell species with molecular identification, based on cytochrome c oxidase subunit I (COI), and compared with GenBank data, as well as sequence data from previous studies (Collin *et al.*, 2019; Collin *et al.*, 2020a; 2020b; Ambarwati *et al.*, 2021)

Materials and Methods

Sampling was carried out on the north coast of East Java at all locations. These included waters of Bangkalan (S07°11.762'-E112°54.010'), Sampang (S07°12.575'-E113°04.198'), Pamekasan (S07°13.173'-E113°35.551'), Sumenep (S07°13.184'-E113°60.289'), Tuban (S06°53.202' - E112°03.161'), Lamongan (S06°52.165'-E112°21.077'), Gresik (S06°52.893'-E112°28.412'), Pasuruan (S07°13.581'-E112°47.406'), Probolinggo (S07°41.842'-E113°22.351'), and Situbondo (S07°43.559'-E113°41.229') regencies, including Surabaya. As shown in Figure 1, the selection of location points was carried out randomly.

Sampling was conducted during the lowest tide on the intertidal zone. The sampling was carried out by purposive sampling, namely by plotting technique. Lingulid shells samples were obtained by digging the substrate using a shovel 5-10 cm deep. The lingulid shell samples obtained were preserved with ethanol, prior to morphological and molecular identification. Furthermore, morphometric measurements and morphological identification (which includes the length of the shell to the length of the pedicle) were carried out based on the characteristics of shell and pedicle, as well as referring to previous studies (Liang *et al.*, 2023; Mitra and Pattanayak, 2013; Samanta *et al.*, 2014; 2015; Zhang *et al.*, 2020).

DNA isolation

Isolation of lingulid shell DNA was carried out using DNeasy Blood and Tissue Kits (QIAGEN). Subsequently, quantitative tests were immediately carried out using a UV NANO DROP 2000 spectrophotometer. The electrophoresis process, with a voltage source of 100 V, 200 MA, and separated DNA was used as a template to amplify the 657 bp fragment of the COI gene using the LCO1490 5' - GGT-CAA primer. -ATC-ATA-AAG-ATA-TTG-G-3' (F/forward) and HCO2198 5'-TAA-ACT-TCA-GGG-TGA-CCA-AAA-AAT-CA-3' (R/reverse) (Folmer *et al.*, 1994).

PCR amplification, and sequencing

PCR amplification was conducted in a thermal cycler under the circumstances of 1 min of initial denaturation at 94°C, 40 cycles of 45 s of denaturation at 94°C, annealing at 45°C for 45 s, and extension at 72°C for 1 min 30 s, and a final extension at 72°C for 10 min, PCR composition of for COI gene with total solution of 50 µL (according to the procedure of iNtRON Biotechnology) consisted of 2x PCR Master Mix Solution 25 µL, DNA template 1-2 µL, Primer F (10 pmol.µL⁻¹) 1 µL, Primer R (10 pmol.µL⁻¹) 1 µL, and double-distilled water (ddH₂O) 21-22 µL. The PCR products were visualized in 1% agarose gels discolored with ethidium bromide. Furthermore, the purified DNA products (Forward and Reverse) were sent to First Base Malaysia for sequencing. Subsequently, the DNA sequence analyzer used was 373XL DNA analyzer with BigDye v3.1, and each DNA specimen was sequenced for the COI barcode region's 657 bp.

Data analysis

Data Analysis Forward and Reverse sequencing were accomplished to obtain DNA sequences. Then, trimming process was achieved. MEGA6 software was manipulated to combine a pair of DNA sequences in order to generate a nucleotide base sequence from each sample. Basic Local Alignment Search Tool (BLAST) analysis was drive by using a nucleotide bases sequence. BLAST analysis was showed to examine the genetic species from each sample. It was obtained through alignment with data on the nucleotide base sequence from GenBank.

The observed population structure included density and internal distribution patterns of lingulid shell. Population density data shows the average number of lamp clam individuals per unit area, obtained using the following formula $D = x/m$, where D: Lingulids density (individuals.m⁻²), x: Number of individuals in the measured area, and m: Area of the Lingulids sampling quadrant (m²).

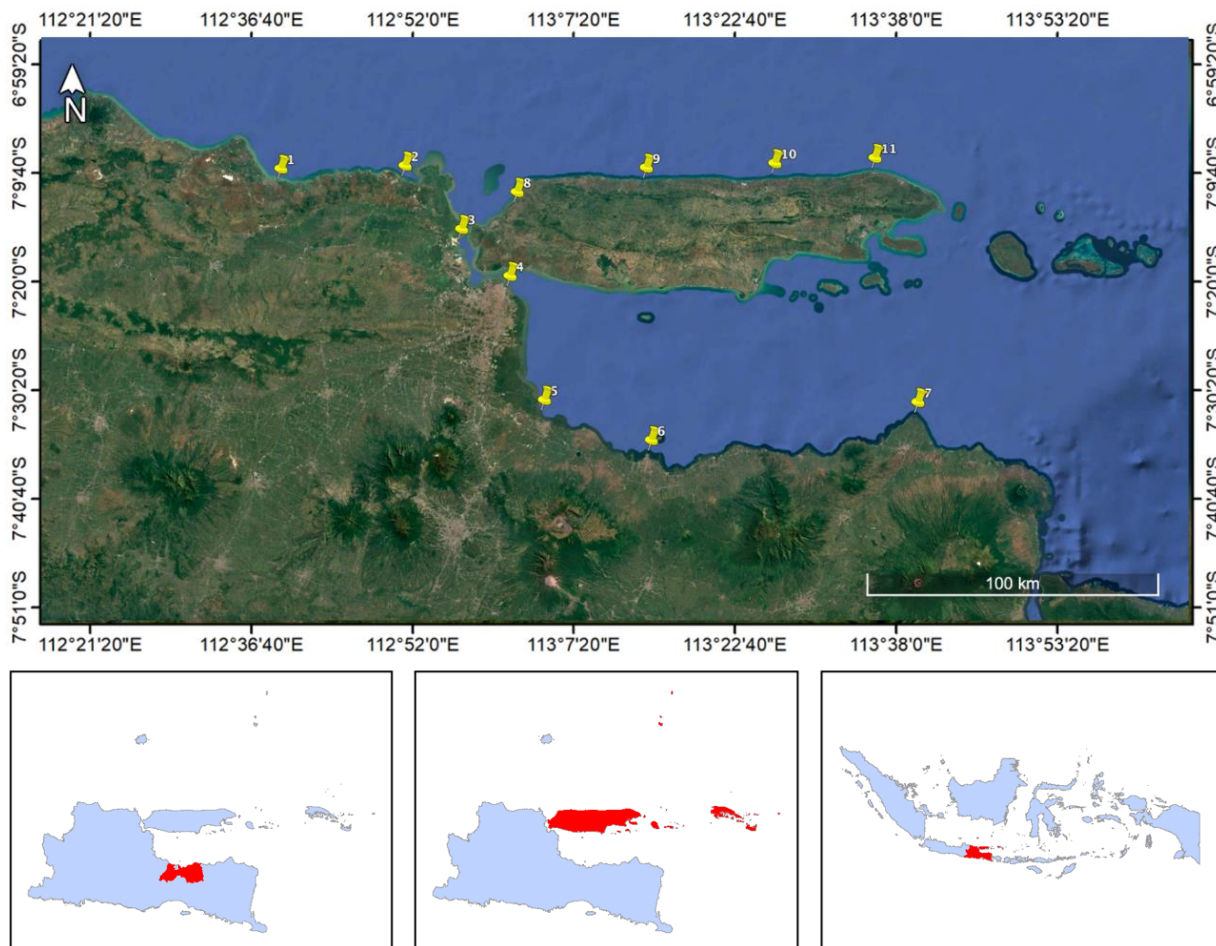


Figure 1. Location of sampling lingulid shell in north coast of East Java; 1) Tuban Regency; 2) Lamongan Regency; 3) Gresik Regency; 4) Surabaya Strait; 5) Pasuruan Regency; 6) Probolinggo Regency; 7) Situbondo Regency; 8) Bangkalan Regency; 9) Sampang Regency; 10) Pamekasan Regency; and 11) Sumenep Regency

The environmental parameters measured in this study were temperature, pH, and salinity. The substrate serving as the habitat of lingulids was analyzed for grain-size composition and classified into three main fractions—sand, gravel, and silt which are then categorized into certain types of sediment.

Results and Discussion

The lingulid shell (*Lingula* sp.) can be found in seven regencies and cities on the north coast of East Java, namely Surabaya, Pasuruan, Probolinggo, Situbondo, Bangkalan, Pamekasan, and Sumenep, with different morphometric variations (Table 1). However, lingulid shell was not found in Tuban Regency, Lamongan Regency, Gresik Regency, or Sampang Regency, probably due to the coastal structure, which was dominated by the presence of abundant coral rocks. The presence of coral would make it difficult for lingulid shell to burrow and dig into the substrate, thereby hindering the availability of habitat.

The presence of mangroves in the coastal intertidal area is an important component in the encounter of lingulid shell. The existence of mangroves plays an important role in supporting the availability of the main food for lingulid shell (Darmarini *et al.*, 2017). In all locations where lingulid shell was discovered, mangroves were found along the intertidal zone. This differs from Tuban Regency, where there is no lingulid shell due to the presence of sea pine tree communities that are closer to the coastal intertidal area than the mangrove communities. The presence of sea pine trees influences food availability, as the main food of lingulid shell includes plankton, detritus, and fermentation of mangrove leaf litter (Samanta *et al.*, 2015; Darmarini *et al.*, 2017).

The morphological characters of *Lingula* from all locations were identified as follows; Shell length 24.50 ± 3.81 mm, width 18.09 ± 2.96 mm, thickness 7.68 ± 1.76 mm, pedicle length 8.78 ± 3.60 , and bilateral body symmetry (dorso-ventral), with shape following the shell. The structure is characterized by a slightly oval shape, glossy green to yellow, which is not symmetrical as the ventral part is longer than the dorsal. There are chaetae all over the shell margin, the anterior side is longer than the others, and the pedicle is cylindrical, slightly hard, thick, and transparent to white in consistency. Inside the pedicle, there is a liquid secretion and an attachment structure to the substrate at the end, which has the color of mud or sediment (Figure 2)..

The morphological features showed the species of *Lingula* which was observed in this study, namely *Lingula anatina* Lamarck 1801 (Mitra and Pattanayak, 2013; Samanta *et al.*, 2014; 2015). The results were supported by previous reports by Ambarwati *et al.* (2019; 2021). To confirm the molecular identification of the species, DNA barcoding was used, which was then analyzed using the MEGA application (Table 2). The similarity of the seven *Lingula* samples was categorized as very high, namely 97.42-99.69%. The high similarity between the study sample and *Lingula anatina* registered with Genbank was due to the high COI barcode sequence homology.

Population structure and habitat

The lingulid shell live in the aquatic substrate, characterized by a pedicle-like structure, which is firmly attached to the substrate at the bottom of the burrow and substrate mass. Communities around the coast recognize lingulid shell with various names, including Tebalan, sea sprouts, lanterns, and leaf shell.

During sampling, lingulid shell samples were in a position in the substrate, where the pedicle was at the bottom and shell at the top (Figure 3a). Emig *et al.* (2013), Zhang *et al.* (2005) stated that the lingulid shell burrows vertically in soft sediments, positioned at the top of the habitat burrow. This showed that the presence of lingulid shell could be determined by flat hole similar to the bivalvia habitat on substrate surface, as presented in Figure 3b. Another contributing factor was found to be the presence of sea anemone attached to the anterior shell of lingulid shells.

There are differences in population density of lingulid shell at each location in the northern waters of East Java. The highest value was found in Probolinggo regency with an average of 13.47 individuals.m⁻², while East Java had 52.6 individuals.m⁻² (Table 3). Additionally, population structure is significantly different from the population density value of the lingulid shell in Aceh Province. Agustina *et al.* (2019) reported that population density of lingulid shell in the Ujong Pancu and Syiah Kuala areas of Aceh Province were 2.08 individuals.m⁻² and 4.75 individuals.m⁻², respectively. The difference was due to variation in the number of individual encounters with lingulid shell because of several factors, including the coastal environmental profile, sampling period, reproductive season, community structure, and fishing activities (Agustina *et al.*, 2019; Ambarwati and Irawan, 2020; Chan *et al.*, 2022). The sampling period significantly influences lingulid shell because it is related to the reproductive period. During the

reproductive period, juvenile lingulids are abundant, which indirectly affects the low intensity of encounters. Juvenile lingulids live in deep, hard-to-reach substrate burrows and are fragile against sampling equipment. Furthermore, community structure also influences lingulid occurrence. Lingulids that coexist with abundant bivalves are limited in number due to food competition. Bivalves also often attach to lingulid shells to utilize the water

flow through their bodies. Meanwhile, the distribution pattern was closely related to larvae's ability to select areas for habitation Nybakken and Bertness, 2005). In this study, the geographic distribution pattern showed discontinuity because not all locations on the north coast of East Java had lingulid shells. Furthermore, calculations were carried out regarding the internal distribution pattern of lingulid shells in each regency or city.

Table 1. Morphometry of lingulid shells found on the north coast of East Java

Morphometry	Sampling Location						
	Bangkalan	Pamekasan	Sumenep	Surabaya	Pasuruan	Probolinggo	Situbondo
Pc (mm)	17.90-52.50 (33.56±8.43)	29.10-46.40 (38.42±5.30)	26.35-39.60 (36.03±3.81)	17.90-29.00 (24.50±3.81)	23.80-47.00 (37.50±6.71)	31.50-51.75 (43.75±3.70)	20.25-48.65 (36.18±7.47)
Lc (mm)	1.70-23.40 (15.66±3.82)	9.50-21.70 (18.09±2.96)	13.00-19.95 (16.69±2.40)	8.40-14.35 (12.03±1.99)	12.20-22.50 (17.66±2.72)	15.40-23.95 (19.70±1.72)	12.00-22.20 (17.42±2.80)
Tc (mm)	2.70-19.30 (6.87±2.79)	5.40-9.85 (7.80±1.16)	4.30-7.80 (7.01±1.05)	2.70-5.60 (4.40±0.80)	5.00-13.00 (8.00±2.07)	5.45-14.60 (8.80±1.24)	5.15-11.45 (7.68±1.76)
Pp (mm)	4.00-74.00 (35.97±15.14)	24.00-48.00 (38.75±6.82)	26.00-38.00 (33.56±9.88)	17.00-47.00 (29.43±7.64)	14.00-76.00 (50.06±15.89)	6.00-94.00 (63.71±16.63)	24.00-59.00 (43.79±11.98)
Pm (mm)	1.00-21.00 (7.93±4.50)	8.00-21.00 (16.67±4.10)	5.00-14.00 (8.78±3.60)	4.00-15.00 (6.79±2.83)	4.00-15.00 (9.12±3.49)	3.00-24.00 (11.50±4.94)	5.00-23.00 (11.40±4.83)
Ptotal (mm)	54.80-150.85 (99.99±26.23)	76.65-113.35 (119.72±15.23)	76.65-125.65 (102.07±13.62)	55.30-110.30 (77.15±14.79)	74.2-156.20 (122.35±22.84)	87.60-180.35 (147.46±20.40)	67.50-153.30 (116.47±25.96)

Description: Pc: shell length; Lc: shell width; Tc: shell thickness; Pp: pedicle length; Pm: Mud length; Ptotal: Total length

Tabel 2. The three highest compatibility values from identification with a representation of the similarity value

Sampling Location	Class	Genus	Species (3 highest)	Similarity (%)	Accession Number
Bangkalan	Lingulata	<i>Lingula</i>	<i>anatina</i>	99.69	MW454814.1
			<i>anatina</i>	99.69	MW454815.1
			<i>anatina</i>	99.69	MW454813.1
Pamekasan	Lingulata	<i>Lingula</i>	<i>anatina</i>	98.33	MW454814.1
			<i>anatina</i>	98.33	MW454815.1
			<i>anatina</i>	98.33	MW454813.1
Sumenep	Lingulata	<i>Lingula</i>	<i>anatina</i>	98.33	MW454814.1
			<i>anatina</i>	98.33	MW454815.1
			<i>anatina</i>	98.33	MW454813.1
Surabaya	Lingulata	<i>Lingula</i>	<i>anatina</i>	99.39	MW454814.1
			<i>anatina</i>	99.39	MW454815.1
			<i>anatina</i>	99.39	MW454813.1
Pasuruan	Lingulata	<i>Lingula</i>	<i>anatina</i>	99.54	MW454810.1
			<i>anatina</i>	98.92	MW454814.1
			<i>anatina</i>	98.92	MW454815.1
Probolinggo	Lingulata	<i>Lingula</i>	<i>anatina</i>	99.54	MW454810.1
			<i>anatina</i>	98.92	MW454814.1
			<i>anatina</i>	98.92	MW454815.1
Situbondo	Lingulata	<i>Lingula</i>	<i>anatina</i>	99.54	MW454810.1
			<i>anatina</i>	97.42	MW454814.1
			<i>anatina</i>	97.42	MW454815.1

Table 3. Population density of lingulid shells (*L. anatina*) found on the north coast of East Java

Location	Lingulid Shell Population Density (ind.m ⁻²)	
	Range	Mean
Bangkalan	4 - 32	13.20
Pamekasan	0 - 8	1.60
Sumenep	0 - 8	1.20
Probolinggo	0 - 32	13.47
Surabaya	0 - 8	1.87
Pasuruan	0 - 8	3.60
Situbondo	0 - 8	1.87
Total	0 - 32	52.6



Figure 2. Morphology of lingulid shells found in all research locations. A: Bangkalan Regency; B: Pamekasan Regency; C: Sumenep Regency; D: City of Surabaya; E: Pasuruan Regency; F: Probolinggo Regency; and G: Situbondo Regency; scale bar 30mm.



Figure 3. The position of the lingulid clam during sampling (in the substrate, i.e. the pedicle is at the bottom and the shell is at the top (habitat); and (b) the hole in the lingulid clam habitat.

Table 4. Internal distribution pattern of *L. anatina*

lingulid Shells	Location	Poisson		Cofirm Variant/Mean			Category
		Xcount	Xtable	Varian (S ²)	Mean (\bar{X})	S ² / \bar{X}	
<i>L. anatina</i>	Bangkalan	26.10	18.48	4.01	3.30	1.22	Group
	Pamekasan	1.31	6.635	0.40	0.40	1	Random
	Sumenep	0.02	6.635	0.30	0.30	1	Random
	Probolinggo	12.69	18.48	3.37	3.37	1	Random
	Surabaya	1.10	6.635	0.47	0.47	1	Random
	Pasuruan	16.58	13.28	0.92	0.90	1.02	Group
	Situbondo	1.12	6.635	0.47	0.47	1	Random

Descriptions: $\alpha = 0,01$; $db = n-2$

Table 5. Measurement results of environmental parameters and test results of substrate composition

Location	Environmental Parameters		Substrate Composition (%)				Category
	Temp (°C)	Salinity (‰)	pH	Sand	Silt	Gravel	
Bangkalan	32	35	6.8	4.22	95.78	0	Silt
Pamekasan	32	36	6.8	11.80	88.08	0.12	Silt
Sumenep	32	36	6.8	12.16	87.70	0.14	Silt
Probolinggo	32	34	6.4	80.19	28.72	1.09	Silty sand
Surabaya	31	35	6.4	11.50	88.38	0.12	Silt
Pasuruan	31	33	6.4	22.90	74.98	2.11	Sandy silt
Situbondo	32	35	6.2	61.80	34.15	4.05	Silty sand

The results showed that lingulid shell found during the study had two types of internal distribution patterns, namely clustered and random (Table 4). The random internal distribution pattern indicated uniform habitat, consistent with reports by Garcia-Charton and Perez-Ruzafa (2001) and Indarjo and Muslim (1997), which found similar patterns in substrate size and nutrition. Furthermore, random internal distribution pattern showed that there was no tendency for organisms to live together (Riniatsih and Kushartono, 2009). The clustered internal distribution pattern was caused by the preference of lingulid shell to live in the most suitable habitat, both according to the physic-chemical factors of the waters and the availability of food. This is often caused by the collection of individuals as a strategy in responding to changes in weather, seasons, habitat, and reproductive processes (Odum and Barrett, 2005; Slavevska-Stamenković *et al.*, 2012).

The results also showed that the distribution pattern of lamp shells in East Java differed from that observed in Ujong Pancu and Syah Kuala, Aceh. According to Agustina *et al.* (2019), the distribution pattern of lamp shells in Aceh was regular. The variation in reports could be attributed to environmental (substrate) and nutritional factors. Prasojo *et al.* (2012) stated that the even

distribution of physical and chemical properties in habitat, along with the availability of food, were the factors determining whether the animals live in groups, randomly, or normally.

By collecting the ecological data of lingulid shells, environmental parameter data were considered an important supporting factor including temperature, salinity, pH, and substrate composition. In this study, salinity and pH of the sampling locations were in the range of 33-35‰ and 6.2-6.8, respectively, while substrate fraction consisted of silt, sand, sandy silt, and silty sand, as shown in Table 5. However, lingulid shell in East Java are most often found in habitats that have a silt substrate fraction due to the presence of organic matter, which serves as a high source of food. Furthermore, silt substrate provides a wider living space because of the smaller particle size compared to other fractions.

Conclusion

The results of the identification of lingulid shell based on morphological and molecular characteristics showed *Lingula anatina* species. The population density in East Java was 52.6 individuals.m⁻², with discontinuous internal distribution

pattern, while the presence and distribution of *Lingula anatina* had a preference for silt substrates. Further research is needed on the comprehensive profile of lingulid shells to ensure the conservation of this ancient shellfish species.

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References

- Agustina, S., Octavina, C., Sarong, A., Nurhaliza, A., Dewiyanti, I. & Iqbal, T.H. 2019. The Density and Distribution of *Lingula* sp. in Aceh Northern Shore. *IOP Conf. Ser. Earth Environ. Sci.*, 348(1): 012058. <https://doi.org/10.1088/1755-1315/348/1/012058>
- Ambarwati, R., Rahayu, D.A., Rachmadiarti, F., & Khaleyla, F. 2021. DNA Barcoding of Lingulid Shells (*Brachiopoda: Lingula anatina*) from Probolinggo, East Java, Indonesia. *Biodiversitas*, 22(4): 1764–1774. <https://doi.org/10.13057/biodiv/d220421>
- Ambarwati, R. & Irawan, B. 2020. The Population of *Solen* sp. (*Bivalvia: Solenidae*) from Pamekasan, Indonesia. *Ecol. Environ. Conserv.*, 26: 199–204.
- Ambarwati, R., Rahayu, D.A. & Faizah, U. 2019. The Potency and Food Safety of Lingulid Shells (*Brachiopoda: Lingula* sp.) as Food Resources. *J. Phys. Conf. Ser.* 2019;141 7(1): 012039. <https://doi.org/10.1088/1742-6596/1417/1/012039>
- Bitner, M.A. 2010. Biodiversity of Shallow-Water Brachiopods from New Caledonia, SW Pacific, with Description of a New Species. *Sci. Mar.*, 74(4): 643–657. <https://doi.org/10.3989/scimar.2010.74n4643>
- Chan, B.K., Tsao, Y.F., Wangkulangkul, K., Amjud, K. & Sukparangsi, W. 2022. Biogeography and Biodiversity of The Intertidal Barnacle *Tetraclita* Species in the Gulf of Thailand and Andaman Sea: Influences of Oceanographic Currents and Pleistocene Glaciations. *Front. Mar. Sci.* 2021; 8:774041. <https://doi.org/10.3389/fmars.2021.774041>
- Collin, R., Venera-Pontón, D.E., Driskell, A.C., Macdonald, K.S. & Boyle, M.J. 2019. Planktotrophic Brachiopod Larvae from the Pacific and Caribbean of Panama. *Diversity*, 11(2):2. <https://doi.org/10.3390/d11010002>
- Collin, R., Venera-Pontón, D.E., Driskell, A.C., Macdonald, K.S., Geyer, L.B., Lessios, H.A. & Boyle, M.J. 2020a. DNA Barcoding of Echinopluteus Larvae Uncovers Cryptic Diversity in Neotropical Echinoids. *Invertebr. Biol.*, 139(2): e12292. <https://doi.org/10.1111/ivb.12292>
- Collin, R., Venera-Pontón, D.E., Paulay, G. & Boyle, M.J. 2020b. World travelers: DNA Barcoding Unmasks the Origin of Cloning Asteroid Larvae from the Caribbean. *Biol. Bull.*, 239(2): 73–79. <https://doi.org/10.1086/710582>
- Darmarini, A.S., Wardiatno, Y., Prartono, T. & Soewardi, K. 2017. Short Communication: New Record of Primitive Brachiopod *Lingula* sp. in Mangrove Ecosystem of Lubuk Damar, Aceh Tamiang, Indonesia. *Biodiversitas*, 18(4): 1438–1444. <https://doi.org/10.13057/biodiv/d180420>
- Emig, C.C., Bitner, M.A. & Alvarez, F. 2013. Phylum Brachiopoda. *Zootaxa*, 3703(1): 75–78. <https://doi.org/10.11646/zootaxa.3703.1.14>
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. 1994. DNA Primers for Amplification of Mitochondrial Cytochrome C Oxidase Subunit I from Diverse Metazoan Invertebrates. *Mol. Mar. Biol. Biotechnol.*, 3(5): 294–299.
- Fujii, R., Ueno, R. & Yamamoto, T. 2019. Breeding Season and Life History of *Lingula anatina* After Settlement in Amami-Oshima Island, Kagoshima, Japan. *Plankton Benthos Res.*, 14(1): 45–51. <https://doi.org/10.3800/pbr.14.45>
- García-Charton, J.A. & Pérez-Ruzafa, Á. 2001. Spatial Pattern and Habitat Structure of a Mediterranean Rocky Reef Fish Local Assemblage. *Mar. Biol.*, 138(5): 917–934. <https://doi.org/10.1007/s002270000524>
- Goto, R., Takano, T., Seike, K., Yamashita, M., Paulay, G., Ku'ulei, S.R., Hunter, C.L., Tongkerd, P., Sato, S.I., Hong, J.S. & Endo, K. 2022. Stasis and Diversity in Living Fossils: Species Delimitation and evolution of Lingulid Brachiopods. *Mol. Phylogenet. Evol.*, 175: 107460. <https://doi.org/10.1016/j.ympev.2022.107460>

- Indarjo, A. & Muslim. 1997. *Tingkat Fluktuasi Bioavailable Phosphat Sedimen dan Terlarut Kehidupan Makrobenthos dan Karang di Perairan Teluk Awur Jepara*. Lemlit UNDIP.
- Karagozlu, M.Z., Dot, D., Kim, J.I., Choi, T.J., Kim, S.G. & Kim, C.B. 2021. An Investigation of The Variations in Complete Mitochondrial Genomes of *Lingula anatina* in the Western Pacific Region. *Biology*, 10(5): 367. <https://doi.org/10.3390/biology10050367>
- Koneva, S.P. & Ushatinskaya, G.T. 2008. New Upper Cambrian Lingulata (Brachiopoda) from the Agyrek Mountains (Northeastern Central Kazakhstan). *Paleontol. J.*, 42(2): 139–148. <https://doi.org/10.1007/s11492-008-2004-9>
- Liang, Y., Strotz, L.C., Topper, T.P., Holmer, L.E., Budd, G.E., Chen, Y., Fang, R., Hu, Y. & Zhang, Z. 2023. Evolutionary contingency in Lingulid Brachiopods Across Mass Extinctions. *Curr. Biol.*, 33(8): 1–8. <https://doi.org/10.1016/j.cub.2023.02.038>
- Lowery, J.L., Paynter Jr, K.T., Thomas, J. & Nygard, J. 2007. The Importance of Habitat Created by Molluscan Shellfish to Managed Species Along the Atlantic Coast of the United States. Atlantic States Marine Fisheries Commission, Washington, DC.
- Madison, A.A., Kuzmina, T.V. & Temereva, E.N. 2021. Analysis of The Juvenile Shell of *Lingula anatina* (Brachiopoda: Linguliformea) Provides Insight into the Evolution of Life Cycles of Fossil Brachiopods. *Paleobiology*, 47(1): 134–148. <https://doi.org/10.1017/pab.2020.51>
- Mitra, S. & Pattanayak, J. 2013. Studies on *Lingula anatina* (Brachiopoda: Inarticulata) in Subarnarekha Estuary. *Rec. Zool. Surv. India*, 113(3): 49–53. <https://doi.org/10.26515/rzsi/v113/i3/2013/12179>
- Mudjiono & Suparman, M. 1992. Sekilas Tentang Kerang Lentera Filum Brachiopoda. *Oseana*, XVII:159–166.
- Nybakken, M.D. & Bertness, J.W. 2005. *Marine Biology: An Ecological Approach*, 6th ed. Pearson Education, Inc., San Francisco.
- Odum, E.P. & Barrett, G.W. 2005. *Fundamentals of Ecology*, 5th ed. Thomson Brooks/Cole. 598 p.
- Prasojo, S.A., Irwani & Suryono, C.A. 2012. Distribusi dan Kelas Ukuran Panjang Kerang Darah (*Anadara granosa*) di Perairan Pesisir Kecamatan Genuk, Kota Semarang. *J. Mar. Res.*, 1(1): 137–145.
- Rakmawati, R. & Ambarwati, R. 2020. Komunitas Bivalvia yang berasosiasi dengan Kerang Lentera (Brachiopoda: Lingulata) di Zona Intertidal Selat Madura. *J. Ris. Biol. Apl.*, 2(1): 36–41. <https://doi.org/10.26740/jrba.v2n1.p36-41>
- Riniatsih, I. & Kushartono, E.W. 2009. Substrat Dasar dan Parameter Oseanografi sebagai Penentu Keberadaan Gastropoda dan Bivalvia di Pantai Sluke Kabupaten Rembang. *Ilmu Kelautan Indonesian Journal of Marine Science.*, 14(1): 50–59.
- Samanta, S., Choudhury, A. & Chakraborty, S.K. 2014. Lipids and Fatty Acid Fractions in *Lingula anatina* (Brachiopoda): An Intertidal Benthic Fauna in the West Bengal-Orissa Coast, India. *J. Coast. Life Med.*, 2(5): 382–388.
- Samanta, S., Choudhury, A. & Chakraborty, S.K. 2015. Eco-Biology of a Precambrian Intertidal Benthic Brachiopod *Lingula anatina* from The Confluence of Subarnarekha Estuary with Bay of Bengal, India. *J. Mar. Biol. Assoc. India*, 57(1): 41–46. <https://doi.org/10.6024/jmbai.2015.57.1.1836-06>
- Skovsted, C.B., Pan, B., Topper, T.P., Betts, M.J., Li, G. & Brock, G.A. 2016. The Operculum and Mode of Life of The Lower Cambrian Hyolith Cupithea from South Australia and North China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 443: 123–130. <https://doi.org/10.1016/j.palaeo.2015.11.044>
- Slavevska-Stamenković, V., Paunović, M. & Smiljkov, S. 2012. Factors Affecting Distribution Pattern of Dominant Macroinvertebrates in Mantovo Reservoir (Republic of Macedonia). *Biologia*, 67(6): 1129–1142. <https://doi.org/10.2478/s11756-012-0102-1>
- Topper, T.P., Strotz, L.C., Skovsted, C.B. & Holmer, L.E. 2017. Do Brachiopods Show Substrate-Related Phenotypic Variation? A Case Study from the Burgess Shale. *Paleontol.*, 60(2): 269–279. <https://doi.org/10.1111/pala.12281>
- Zhang, Z., Shu, D., Han, J. & Liu, J. 2005. Morpho-Anatomical Differences of the Early Cambrian Chengjiang and Recent Lingulids and Their Implications. *Acta Zool.*, 86(4): 277–288. <https://doi.org/10.1111/j.1463-6395.2005.00205.x>

Zhang, Z., Holmer, L.E., Liang, Y., Chen, Y. & Duan, X.
2020. The Oldest 'Lingulellotreta' (Lingulata,
Brachiopoda) from China and Its Phylogenetic

Significance. *J. Syst. Palaeontol.*, 18(11): 945–
973. <https://doi.org/10.1080/14772019.2019.1698669>