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PRELIMINARY FINDINGS OF CRYPTIC DIVERSITY OF THE GIANT TIGER SHRIMP (*Penaeus monodon* Fabricius, 1798) IN INDONESIA INFERRED FROM COI MITOCHONDRIAL DNA

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This study investigated genetic diversity of the giant tiger shrimp (*Penaeus monodon*), an economically important penaeid species in Indonesia, using 558 base pairs of the mitochondrial *cytochrome c oxidase Subunit I* (COI) gene. A total of 10 samples were collected from three populations throughout Indonesia and three samples were taken from hatchery. The mitochondrial COI results found high levels of genetic differentiation. From Bayesian tree building method there were two clades on phylogenetic tree with high posterior probability value 1.00. COI mt-DNA analyses revealed that there were six haplotypes in which four haplotypes in clade A and two haplotypes in clade B. Divergences of COI between two clades showed an average 6.9% (range=6.7%-7.6%), while genetic distance within clade A 0.2% (range=0-0.5%) and within clade B 0.3% (range=0-1.1%). Results from this study suggest the occurrence of two cryptic species in the *Penaeus monodon* from Indonesia.

Keyword: Penaeus monodon, cryptic species, genetic diversity, COI.

INTRODUCTION

The effective fisheries management and conservation of genetic resources in exploited marine organisms can be applied if a better understanding of population structure and genetic

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diversity has been studied (EPIFANIO and NIELSEN, 2001; FEEDER *et al*., 2013). Polymerase chain reaction (PCR), sequencing, and the phylogenetic analysis of allelic variants, provide high-resolution genetic information useful for fisheries management and conservation (LIU and CORDES, 2004; YUE, 2013; PEREIRA *et al.*, 2008; MCCORMAC *et al.*, 2013). Many of the data for these studies have come from sequences of mitochondrial genes including COI mitochondrial sequence as a DNA Barcoding (WITT *et al*., 2006; HAJIBABAEI *et al*., 2007; JO *et al*., 2014; ARISURYANTI *et al*., 2018). Such information is valuable for genetic improvement programs, to further understand population genetic diversity and identify cryptic species, and to help ensure that correct taxonomic nomenclature is applied (SALTGIVER *et al.*, 2012; WHITE and LAST, 2012; WILSON and SING, 2013; RAJKUMAR *et al*., 2015).

Analysis on genetic diversity and population structure of marine biota have frequently revealed that organisms with low dispersal capacity would have high genetic distinction over large geographic scales (HAMNER *et al*., 2012; BARBOSA *et al*., 2013). The marine crustacean, *Penaeus monodon*, which is one of the most economically important cultured species in Southeast Asia, is considered to have low ability to migrate especially in the early larval stages (NGA, 2004; NIAMAIMANDI *et al*., 2010). A consequence of this limited migration is an increased likelihood of reproductive isolation between populations leading to genetic divergence, and over sufficiently long periods of time the possibility of speciation (FERGUSON, 2002). Indeed, this limited dispersal is thought to be an important factor in accounting for high diversity of the penaeid worldwide. Thus, even within the Indonesian archipelago, there is a possibility that *P. monodon* may consist of several cryptic species. Alternatively, the species may have high levels of genetic similarity among widely separated populations due to recent dispersal facilitated by humans due to translocation to new aquatic environments. It is also possible that both factors, cryptic speciation and translocation, have created complicated geographic patterns of genetic variation and diversity. Thus, the current taxonomy of *P. monodon* may not represent the true biodiversity of this "species" which could represent a complex of cryptic species. The previous study conducted by KHAMNAMTONG *et al*. (2009) in Thailand revealed that Thai *P. monodon* is genetically differentiated intraspecifically with mean COI sequence divergence 6.604%. However, no genetic identification study has be done for Indonesian *P. monodon* using COI mitochondrial gene as a DNA barcoding marker. This investigation can play an important role to identify different *P. monodon* stock as the first step for reestablishing an effective domestication and selective breeding program for *P. monodon* in Indonesia. Knowledge about the genetic identification through geographic differentiation of *P. monodon* in Indonesia is useful for the construction of an appropriate genetic-based stock enhancement program in this economically important species.

MATERIALS AND METHODS

Sampling collection for COI mitochondrial sequence

Tissue samples of *P. monodon* were collected or obtained from three populations (Ujung Batee-Aceh, Jepara, and Takalar-South Sulawesi) and one population taken from hatchery (Fig. 1). Sampling location, sample code, and sample size details are provided in Table 1. The tissue samples consisted of an average 50-100 mg of muscle tissue. Muscle tissue was dissected with a sterilized surgical scissor, placed into a 1.5 ml screw top cryogenic vial, and preserved in 99% ethanol in the field and stored at -20^{o}C in laboratory.

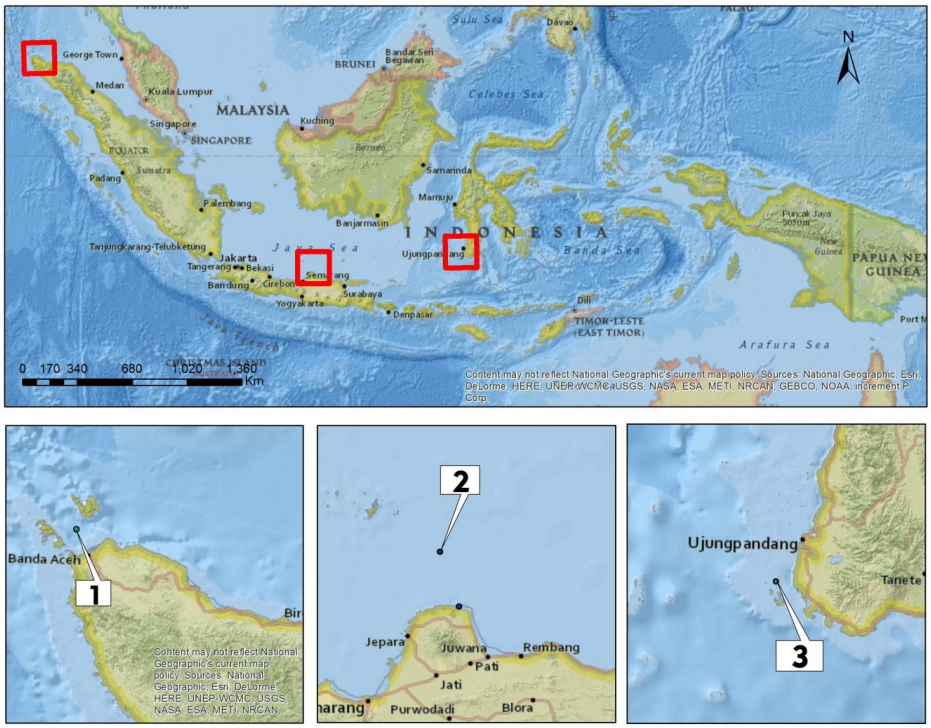

Figure 1. Map of sampling collection sites for *P. monodon* samples in (1) Ujung-Batee, Aceh Besar, Aceh; (2) Donorojo, Jepara, Central Java and (3) Galesong, Takalar, South Sulawesi

Table 1. Sample location, sample code, geographic reference and sample size of P. monodon

Location	Code	Latitude (S)	Longitude (E)	Sample number
Ujung-Batee, Aceh Besar, Aceh	ACH	05º39'01.93"	095º25'19.30"	3
Donorojo, Jepara, Central Java	JPR	06º24'31.34"	110º58'06.56"	3
Galesong, Takalar, South Sulawesi	TKL	05º19'39.75"	119º21'20.64"	4
Hatchery, Jepara, Central Java	DG9	06º24'31.34"	110º58'06.56"	3

DNA extraction, amplification and sequencing of cytochrome oxydase c subunit I (COI)

Total DNA was extracted from preserved muscle tissue using Chelex 100. The COI mitochondrial gene was amplified using primers LCO1490: 5'-GGTCAAC AAATCATAAAGATATTG-3' and HCO2198: 5'-TAAACTTCAGGGTGACCAAAAAA

TCA-3' (COSTA *et al*., 2007). The KAPA2G Robust PCR kit (Kapa Biosystems) was used for the polymerase chain reaction (PCR). PCR amplifications were conducted in 25 μL reaction volumes containing 10-100 ng of genomic DNA, 0.2 mM of each dNTP, 1.5mM $MgCl_2$, 0.625U Tag Polymerase, 0.2 μM of each primer and 1x PCR reaction buffer. The thermal cycler profile consisted of a 5 min denaturation at 95ºC followed by 35 cycles of 60 s at 95ºC, 60 s at 56ºC, and 90 s at 72ºC. A final extension of 5 min at 72ºC was performed. Then, PCR products were visualized using 1.5% agarose gels and stained with SybrSafe and cleaned using ExoProStar^{TM} purification kit. Sequence reactions were performed in both directions using the Big Dye Terminator Ver. 3.1. sequencing kit (Applied Biosystems), 5-7 μL purified PCR product, and 0.8 μM of either primer per reaction. Sequence-reaction products were then loaded into an ABI 3500x1 Genetic Analyzer (Applied Biosystems). Amplicons were sequenced in both forward and reverse directions.

COI sequences were visualized and edited using SeqMan and Editseq Pro Program Lasergene DNASTAR software package (DNASTAR Inc., Madison, USA). Sequences were transferred to fasta format and aligned the opal (a multiple sequence alignment program) routine implemented by the MESQUITE 3.04 package (MADDISON and MADDISON, 2015) and ClustalW in MEGA5 (TAMURA *et al*., 2011). Subsequent inspection and editing of the alignments was done manually. Chromatograms were inspected for noisy and ambiguous base calling and translated to check stop codons. Noisy tails were trimmed. For each individual, sequencing reactions were performed using both forward and reverse primers, resulting in a consensus fragment of 558 bp in length. Therefore the data set used for phylogenetic analysis was composed only those sequences that consisted 558 bp after trimming. Diversity was estimated by number of haplotype, haplotype diversity, number of polymorphic sites, nucleotide diversity, and GC content using the software DnaSP 5.10.01 (LIBRADO and ROZAS, 2009). Kimura-2-parameter model were used to estimate intraspecific and interspecific genetic distance as it is the standard model of molecular evolution used in barcoding studies (HEBERT *et al*., 2003). Sequences of *P. monodon* (accession number KM508845, KC409381, KP976330, and KF714990) from GenBank (www.ncbi.nlm.nih.gov) were used for comparative purposes. In addition sequences of *P. semisulcatus* with accession number KT223765 and KF613002 taken from GenBank were used as an outgroup. Phylogenetic relationships were estimated by a Bayesian approach based on COI mitochondrial gene. The best-fit model of evolution was selected with jModelTest 0.1.1 (POSADA, 2008) under the Akaike information criterion (AIC) suggested by POSADA and BUCKLEY (2004). Bayesian inference was done using the software MrBayes 3.2 (RONQUIST *et al*., 2012) under the best-fit model. The analyses were run for 1,000,000 generations with a sampling frequency set to every 1000th generation. The analysis was done until the standard deviation of split frequencies was below 0.01. The analysis used a relative burn-in of 25% for diagnostics. Consensus trees were visualised in FigTree 1.4.0 (RAMBAUT, 2012). Principal Coordinat Analysis (PCA) based on genetic distance of COI mitochondrial gene was carried out in GenAlEx version 6.5 (PEAKALL and SMOUSE, 2012) in order to discriminate between haplotypes. Haplotype network were then analysed using software NETWORK ver. 4.510.

RESULTS AND DISCUSSION

The optimal model of nucleotide sequence substitution for the COI matrix including the external group was the GTR model with gamma-distributed rate as inferred by the jModelTest 0.1.1 (POSADA, 2008) under the Akaike information criterion (AIC) suggested by POSADA and

BUCKLEY (2004). The Bayesian analyses of COI mitochondrial gene together with the sequence of *P. monodon* (accession number KM508845, KC409381, KP976330, and KF714990) taken from GenBank as comparative purposes and the sequence of *P. semisulcatus* with accession number KT223765 and KF613002 which was used as outgroups revealed that the *P. monodon* examined in this study could be classified into 2 genetic clades (designated as Clade A and B), with the reliability of the tree topology supported by posterior probabilities of 1.00 (Fig. 2). This finding defined a clear cryptic species of Indonesian *P. monodon* investigated in this study.

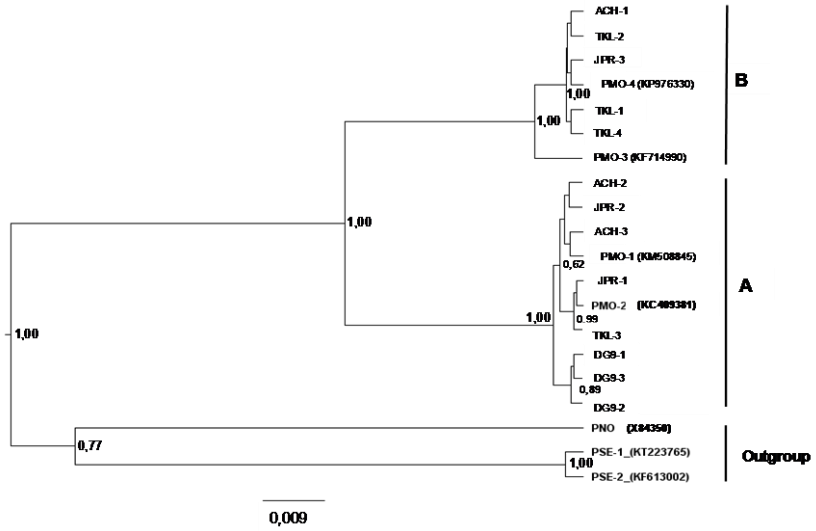

Figure 2. Bayesian tree inferred from COI mitochondrial gene sequences. Tree was produced from $1x10^6$ generations using GTR+G model. Number of each node represent posterior probabilities and scale correspond to substitution/site. Sample code with parentheses are taken from GenBank for comparative purposes

Levels of within-clade and between-clade divergences in the COI mitochondrial gene was estimated by calculating Kimura-2-parameter (K2P) genetic distances (Table 2). The mean K2P distance of COI within *P. monodon* was 3.70%. The average nucleotide sequence divergence within clade A and clade B is 0.2% (0-0.5%) and 0.3% (0-1.1%) respectively. In this study, the genetic divergence was observed between clade A and B varied from 6.70% to 7.60% (mean 6.90%).

Table 2. Mean percentage nucleotide sequence divergence of an 558-bp fragment of the COI mitochondrial gene among two identified clades of P. monodon in this study

	Clade A	Clade B
Clade A	0.2 (0-0.5)	
Clade B	6.9 (6.7-7.6)	0.3 (0-1.1)

In this study, COI mitochondrial sequence of *P. monodon* (PMO-3) taken from GenBank with accession number KF714990 was included as a reference. The 558-bp alignment contained 42 polymorphic site in positions with 37 parsimony-informative sites (Fig. 3) and amino acid sequence translations (invertebrae mitochondrial code) were unambiguous as there were no gaps or nonsense codons among the 16 sequences divided into 6 haplotypes (Table 3). From the Table 3, it can be seen that from four COI haplotypes were found in clade A from 10 individuals and two haplotypes were observed in clade B from six individuals. Most haplotypes within clade A only differed a few bp. Within clade B the level of divergence among haplotype was 6 bp. The haplotype diversities (h) within clade A and B were 0.778 and 0.286 respectively whereas the nucleotide diversities (π) were 0.00203 and 0.00307 respectively. Differentiation among haplotypes within and among clades is summarised by the Principal Coordinate Analysis (PCoA) (Figure 4).

Table 3. Haplotype of P. monodon based on COI mitochondrial gene region

Clade	Haplotype name	Number of samples	Individual code
A	HA1	4	ACH-2, ACH-3, JPR-2, PMO-1*
	HA2	3	DG9-1, DG-2, DG9-3
	HA3	2	JPR-1, PMO-2*
	HA4	1	TKL-3
B	HB1	5	ACH-1, JPR-3, TKL-1, TKL-2, TKL-4, PMO-4*
	HB2	1	PMO-3*

*samples taken from GenBank (www.ncbi.nlm.nih.gov)

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                 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 5 5 5
               5 5 7 0 1 2 4 4 4 5 6 7 7 8 2 3 3 3 4 6 7 9 0 2 3 5 5 7 8 2 3 5 7 8 8 9 9 9 3 3 5
             2 6 9 7 7 9 8 0 3 9 2 4 0 3 2 4 0 1 3 5 0 2 3 2 0 8 6 9 1 6 5 1 2 0 2 8 2 4 5 1 3 7
PMO-3(HB2)   C A C A C G A C G G A G T T A C G C A G C G C A C T A T C A T G G A T C C G T T A A
HB1          . T . . . . . T . . . G . . . . A . . . . . . . . . . . . A . . . . . . C . .
HA1          T T T G T A G T A A T A C C . A A T G . T T T G T C . C T T G A A G C T T A C C G .
HA2          T T T G T A G T A A T A C C . A A T G . T T T G T C . C T T G A A G . T T A C C G .
HA3          T T T G T A G T A A T A C C . A A T G . T T T G T C G C T T G A A G C T T A C C G .
HA4          T T T G T A G T A A T A C C . A A T G . T T T G T C G C T T G A A G C T T A C C G T
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Figure 3. Summary of nucleotide variations in the partial COI-mtDNA of *P. monodon* in this study. Only variable sites are shown. Haplotypes are named by letters referring to the lineage and number. Dots indicate identity with the *P. monodon* (PMO-3) sequence taken from GenBank with accession number KF714990 as a reference. Number above correspond to nucleotide base pair position.

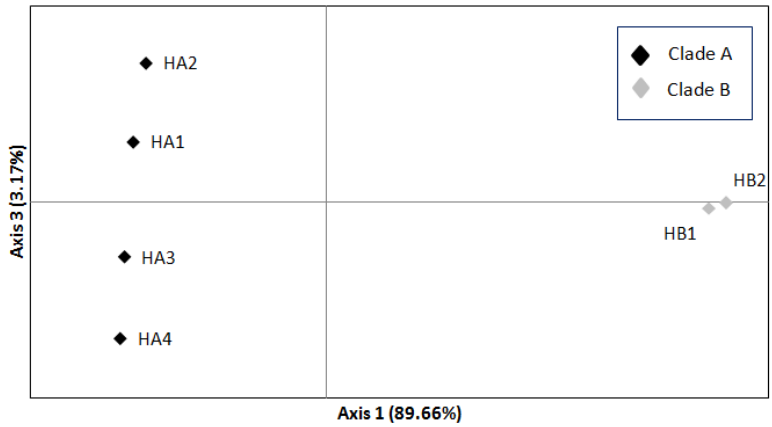

Figure 4. Principal Coordinates Analysis (PCoA) of pairwise genetic distances of six haplotypes of *P. monodon* based on COI mitochondrial sequences.

The research also showed that 558 bp from COI mitochondrial gene of Indonesian *P. monodon* was divided in two clusters which were separated by 33 mutation points (Figure 5). In this research, clade A was divided into four cluster by four mutation point whereas clade B was divided into two cluster by six mutation points.

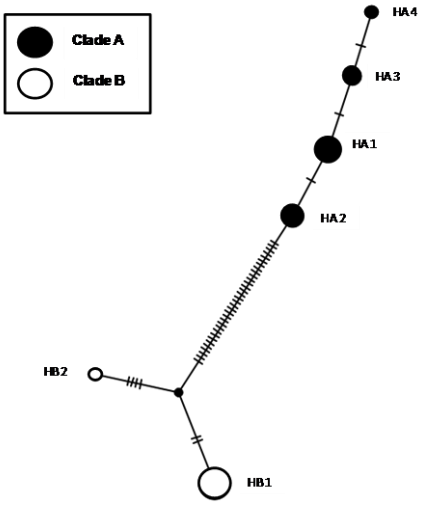

Figure 5. Median joining network from 558 bp COI sequence. Size of circles corresponds to the number of sequences found for each haplotype.

Using DNA-barcoding this research found evidence of cryptic species in the Indonesian *P. monodon*. This is due to if the criterion used by ZEMLAK *et al*. (2009) is adopted, who considered that nucleotide sequence divergences exceeded 3.5% could be used as a rule of thumb for discriminating species, then the recognition of clade A and clade B as species would be more than justified given the average divergence level of 6.90%. While the conclusions based on COI distances for separate species status for clade A and clade B is somewhat inconclusive, the finding that variation within clades is much less than between clades (Figure 4) and that the clades remain distinct over significant geographic space, which includes a zone of geographic overlap, provide support for speciation of *P. monodon* in Indonesia.

These research findings revealed that the genetic divergence between the two clades was not based on geographic distribution. This means all of the population that the *P. monodon* was collected for this study have this cryptic species. This result was different with Thailand *P. monodon* investigated by KHAMNAMTONG *et al*. (2009). They reported that the three cryptic of Thailand *P. monodon* was based on geographic population. Their analysis revealed significant population divergences between Thailand *P. monodon* from different coastal regions.

Cryptic species of Indonesian *P. monodon* should be treated as a separate management unit because it may display unique populations. A genetic-based stock enhancement program have to be implemented to protect stocks from overexploitation or introgression from alien gene pools and to maintain the genetic diversity of Indonesian *P. monodon.* In terms of aquaculture, the establishment of appropriate domesticated stocks of *P. monodon* will require samples from different geographic locations as the founder stocks for genetic improvement of the commercially important traits through selective breeding programs. This will in turn lead to the sustainable aquaculture of *P. monodon* in Indonesia.

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PRELIMINARNI NALAZI RAZNOLIKOSTI DŽINOVSKIH TIGRASTIH ŠKAMPA (*Penaeus monodon Fabricius*, 1798) U INDONEZIJI NA OSNOVU *COI* MITOHONDRIJALNE DNK

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Izvod

U radu je istraživana genetička raznovrsnost džinovskih tigrastih škampa (Penaeus monodon), ekonomski važne vrste *Penaeida* u Indoneziji, korišćenjem 558 baznih parova mitohondrijske *cytochrome c oxidase Subunit I* (COI). Ukupno je prikupljeno 10 uzoraka iz tri populacije širom Indonezije, a tri uzorka su uzeta iz mrestilišta. Rezultati mitohondrijskih COI pokazali su visok nivo genetičke diferencijacije. Na osnovu *Bayesovog* metoda izdvojene su dve grane na filogenetskom stablu sa visokom vrednošću posteriorne verovatnoće od 1.00. Analize COI mt-DNA su otkrile da je bilo šest haplotipova u kojima su četiri haplotipa u grani A i dva haplotipa u grani B. Divergencije COI između dve grane bila je u proseku 6,9% (opseg = 6,7% -7,6%), dok je genetička udaljenost unutar klase A bila 0,2% (raspon = 0-0,5%), a unutar klase B 0,3% (raspon = 0-1,1%). Rezultati ovog rada ukazuju na pojavu dve kriptične vrste *Penaeus monodon* iz Indonezije.

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