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ORIGINAL PAPER

Assessing genetic diversity and connectivity of the dominant massive coral *Porites lutea* in the Gulf of Thailand

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Abstract. In light of recent coral reef ecosystems, there has been significantly degraded biodiversity in coral reef ecosystems by anthropogenic disturbance and global climate change. Studies on the genetic diversity and connectivity of coral populations are very important. However, there are very few studies of population genetics of corals in the Gulf of Thailand. In this study, we used four microsatellite loci to examine the genetic structure of the broadcast spawning coral *Porites lutea* populations. Our results revealed that *P. lutea* populations had relatively low genetic diversity. A significant genetic difference was detected among populations ($p < 0.001$). Population differentiation among study sites was examined using pairwise F_{ST} comparison. The highest F_{ST} values were observed between Ko Taiphlao and Ko Prong, while the lowest one was observed between Ko Samet and Ko Kula, Ko Samet and Ko Thong Lang. Principal coordinate analysis (PCoA) based on F_{ST} values showed that genetic connectivity was not influenced with the geographic location and distance between study sites. Genetic structure analyses also indicated closely knit genetic units within all study sites in the Gulf of Thailand. Our study provides important data of the connectivity and genetic diversity of *P. lutea* populations, and also supports coral reef conservation and restoration in Thailand.

Keywords: connectivity, genetic diversity, Gulf of Thailand, microsatellite, *Porites*

1. Introduction

Coral reefs have the highest biodiversity in marine ecosystems and provide high values of ecosystem services (McCook et al. 2009). Scleracitnian corals are major components of the coral reef ecosystems and build the reef structures. However, global warming has significantly reduced biodiversity and poses a critical threat to the health of corals. Coral reef ecosystems are vulnerable to both natural and anthropogenic disturbances, including elevated seawater temperatures, nutrient enrichment, destructive fishing and overexploitation, which have collectively led to the degradation of coral reefs worldwide. Furthermore, coral reefs are under increasing threat from the compounding impacts of global warming and ocean acidification. (Hoegh-Guldberg et al. 2007; Burke et al. 2011; Thomas et al. 2017). The elevation of sea surface temperature, primarily attributed to global warming, significantly impacts coral reef ecosystems. This phenomenon disrupts the delicate symbiotic relationships between coral hosts and their endosymbiotic dinoflagellates, ultimately leading to the widespread occurrence of coral bleaching (Chen et al., 2018). The potential for coral reefs to recover from disturbances significantly depends on the patterns and strength of population connectivity, primarily through the highly variable process of planulae dispersal. Consequently, population genetic studies provide valuable information that can be applied to the management of marine protected areas (Palumbi 2004; Ridgway et al. 2008; Underwood et al. 2009; Nakajima et al. 2012; van der Ven et al. 2021). Genetic diversity is a key driver of speciation and adaptation, signifying a population's genetic potential and adaptability. Higher genetic diversity enhances genetic potential (Barrett and Schluter, 2008; Hoegh-Guldberg and Bruno, 2010; Thomas et al. 2017; McManus et al. 2021). In Western Australia, coral populations at lower latitudes exhibited greater genetic potential compared to those at higher latitudes. Corals in higher latitudes were found to be more susceptible to the impacts of global climate change, particularly when contrasted with their tropical counterparts. These findings highlight the importance of considering latitude-dependent genetic diversity in conservation and climate resilience strategies (Ayre and Hughes, 2004; Miller and Ayre, 2010; Thomas et al., 2017).

The Gulf of Thailand is a shallow inlet of the South China Sea located in the western part of the Pacific Ocean. It is an important semi-enclosed tropical sea. It has a relatively shallow average depth of 45 m, with its deepest point reaching 80 m (Wattayakorn, 2006). In the Gulf of Thailand, the coral communities can be categorized into three groups based on variations in oceanographic conditions. These groups include the inner part of the Gulf of Thailand, the east and west coasts of the Gulf of Thailand (Yeemin et al., 2006). The distances separating the major reef groups were found to be within 500 km.

Massive coral P. lutea, a reef building coral species, plays a crucial ecological role by broadcasting its gametes. *P. lutea* significantly contributes to the formation and maintenance of coral reefs across the Indo-Pacific region. (Stat and Gates 2011; Tanzil et al. 2013; Veron 2000). *P. lutea* is known for its tolerance and adaptability to climate change and various forms of anthropogenic disturbance (Xu et al., 2017; Qin et al., 2019; Sutthacheep et al. 2018a; Luo et al., 2022). This coral species has demonstrated tolerance to climate change and various anthropogenic disturbances, including severe coral bleaching events in 1998 and 2010 (Sutthacheep et al., 2013). The scleractinian coral Porites complex are dominant corals generally found in coral reefs in the Gulf of Thailand. substantial genetic diversity and connectivity in P. lutea populations across the South China Sea were reported by using nuclear markers such as the internal transcribed spacer and beta-tubulin. Notably, their study did not reveal any discernible genetic structure or influential factors (Huang et al. 2018). Similarly, high genetic diversity in *P. lutea* was documented in populations near Sanya, Lembeh Strait (LB), and Indonesia (Tian et al. 2014; Niu et al. 2015). However, studies on population genetics of *P. lutea* are very limited. The objective of this study is to investigate population genetic patterns of the coral *P. lutea* at several geographic locations in the Gulf of Thailand.

2. Materials and Methods

2.1 Study sites and sample collection

P. lutea samples were collected from 16 locations throughout the Gulf of Thailand. Fragments of *P. lutea* were collected from a total of 120 colonies at three locations in Mu Ko Sichang Chonburi Province, one location in Mu Ko Samet, Rayong Province, four locations in Mu Ko Chang, Trat Province, four locations the Mu Ko Chumphon, Chumphon Province and four locations in Mu Ko Angthong, Surat Thani Province (Figure 1). A small fragment was taken from each colony. The coral fragments were preserved in 1.5 ml eppendorf tubes containing 100% ethanol and then were kept in the laboratory for DNA extraction. *P. lutea* were identified based on morphological characteristics. The collected samples of *P. lutea* were re-confrmed by ITS before DNA extraction (Huang et al. 2018).

2.2 Genomic DNA extraction, sequencing and microsatellite genotyping

The genomic DNA was extracted from coral tissue samples using DNeasy Blood and Tissue kit following the manufacturer’s protocol (Qiagen, Valencia, CA, USA). Four microsatellite loci for analysis the genetic structure of *P. lutea* populations in this study (Table 1). Primers Pl01, Pl02, Pl04, and P110 were from Basiita et al. (2016). A total volume of 10 µL contained 0.5 µL DNA template. The extracted DNA was amplified by PCR method, (Nakajima et al. 2012) using fluorescently labelled primers. The cycling protocol was modified as 94 ^{o}C for 1 minutes, followed by 40 cycles at 94 ^{o}C for 30 seconds, 53 ^{o}C for 30 seconds, 72 ^{o}C for 75 seconds and a final extension for 5 minutes. Fragments were analyzed using capillary electrophoresis, on an ABI 3100 XL sequencer (Applied Biosystems). Analysing genotype calling was conducted by using GeneMapper version 4.0 (Applied Biosystems).

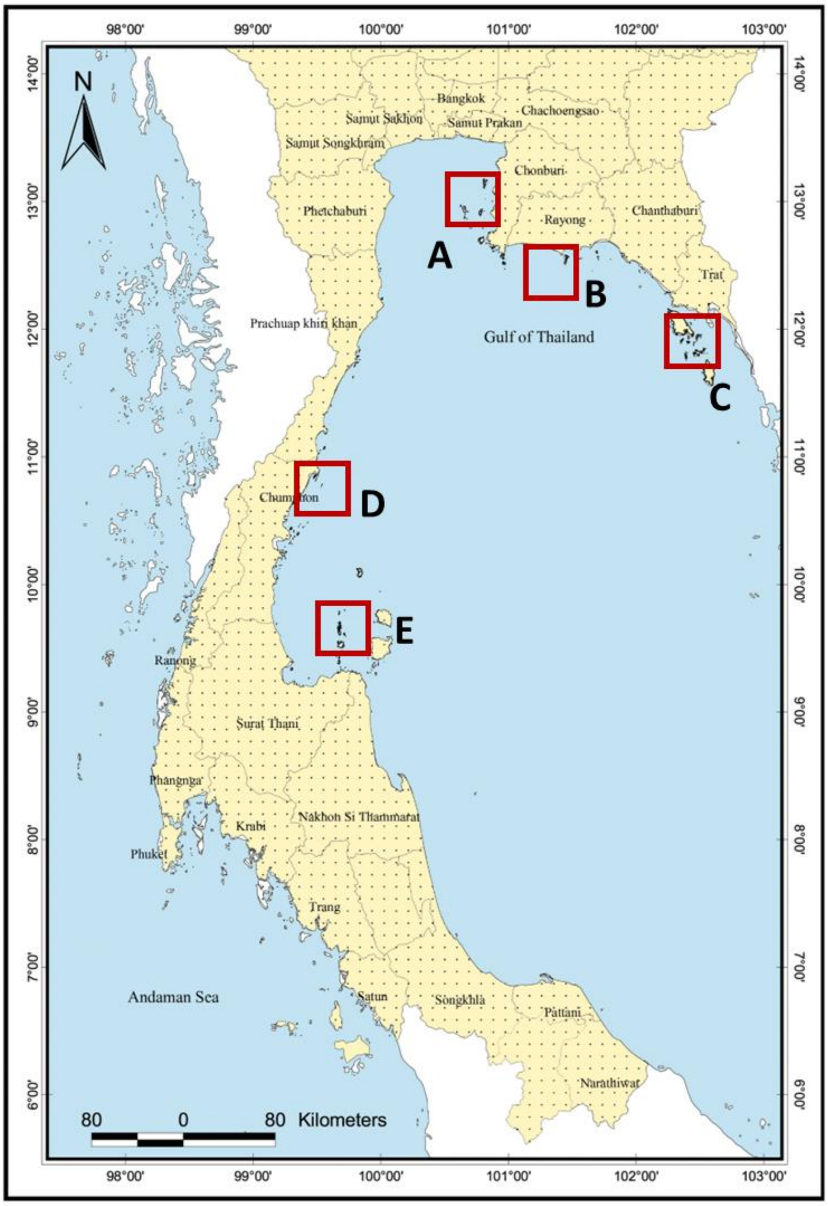

Figure 1. Map of the Gulf of Thailand showing sixteen study sites: (A) Mu Ko Sichang, (B) Mu Ko Samet, (C) Mu Ko Chang, (D) Mu Ko Chumphon, and (E) Mu Ko Angthong

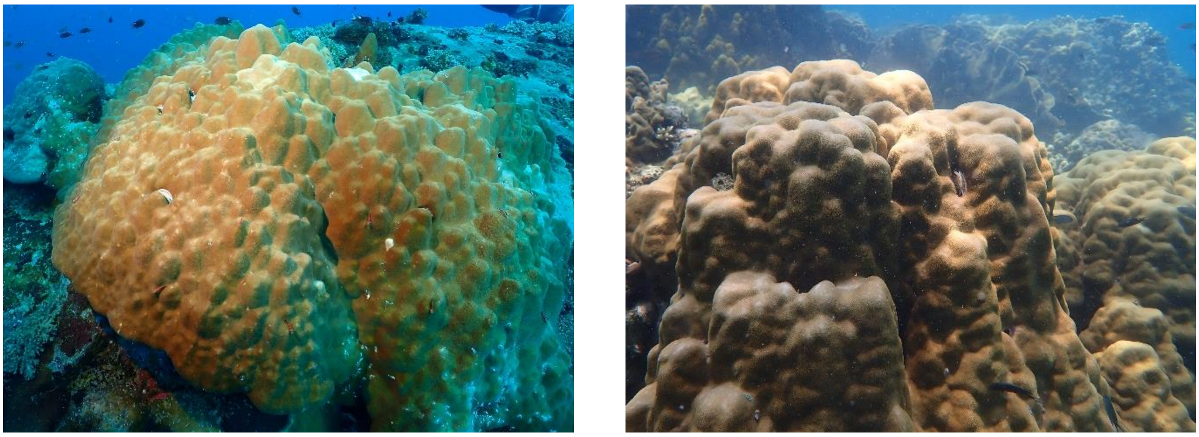

Figure 2. Underwater photographs showing the *Porites lutea* colonies at the study sites

2.3 Statistical analyses

The alleles numbers, allele frequencies, observed heterozygosity (*Ho*) and expected heterozygosity (*He*), number of private alleles, and inbreeding coefficient (F_{IS}) values were analyzed using the GenAlEx software (version 6.5) (Peakall and Smouse 2012). F_{IS} values were used to investigate the deviation from Hardy-Weinberg equilibrium (HWE) because of gaps between *Ho* and *He* under HWE showing proportion to the value of F_{IS}. F-statistics from analysis of molecular variance (AMOVA) was applied to test the significance of all estimates based on 999 random permutations in order to measure the proportion of genetic variation between locations. A low pairwise F_{ST} reveals a high extent of gene flow and vice versa. The levels of statistical significance for all pairwise tests were $P<0.05$. Pairwise geographic distances between locations were also analyzed by GenAlEx software to estimate the scale of populations (Nakajima et al. 2009). STRUCTURE analyses were conducted according to the assumptions with no prior population information. Each run consisted of 100,000 iterations with a burn-in of 100,000 for each value of K, from K = 1–10. For each K, the run was replicated ten times. The most likely value of K was analyzed using STRUCTURE HARVESTER (Earl and VonHoldt 2011.

Table 1. Details for four polymorphic microsatellite loci developed for *Porites lutea* as calculated from genotypes of 120 individuals

Locus	Primer sequence (5′-3′)	Repeat motif
Pl01	F: TCATTCAATACCTTCTCAAGATTCA R: TGGTATTTCATACATTATTTCCCTTG	$(AG)_{11}$
Pl02	F: GTCATCGTCATCACCATCCA R: GAGCCGAACAGATTTCAACC	$(ACC)_6$
Pl04	F: TTGCCCCATTCCAATAACTG R: GGAAAGACGAAATTAAATAGCCC	$(AAC)_7$
P110	F: CACCATAATCATGAGATTTACTATTGA R: GAATCAACCAATGGCAGTCC	$(AC)_9$

3. Results

A total of 120 complete multilocus genotypes of *P. lutea* were analyzed. In our study populations, mean *Ho* and *He* values for all loci across sites were in a range of 0.667 - 1.000 and 0.472 - 0.750, respectively. The total mean values were 0.862±0.026 and 0.644±0.020, respectively. Departures in population heterozygosity from HWE were indicated by mean FIS values, which ranged from -0.167 to -0.679 at all sites (Table 2)

Table 2. Population statistic (±SD) of *P. lutea* populations; H_o = observed heterozygosity (Mean±SD), H_e = expected heterozygosity (Mean ±SD); departures from Hardy–Weinberg equilibrium is expressed as F_{IS} (Mean ±SD)

Study site	Mean H_o	Mean H_e	Mean F_{IS}
Mu Ko Sichang			
Ko Khang Khao	0.875	0.734	-0.187
Ko Prong	0.667	0.472	-0.417
Ko Kham	1.000	0.639	-0.643
Ko Samet	0.857	0.705	-0.220
Mu Ko Chang			
Ko Bai Dang	0.833	0.528	-0.568
Ko Thong Lang	0.900	0.710	-0.264
Ko Thian	1.00	0.594	-0.679
Ko Yak Yai	0.833	0.639	-0.318
Mu Ko Chumphon			
Ko Ngam Yai	0.875	0.625	-0.414
Ko Lawa	0.875	0.719	-0.215
Ko Kula	0.875	0.609	-0.433
Ko Rang Kachiu	1.000	0.750	-0.335
Mu Ko Angthong			
Ko Taiphlao	0.667	0.528	-0.295
Ko Hindap	0.667	0.583	-0.167
Ko Sam Sao	1.000	0.750	-0.354
Ko Wua Kanthang	0.875	0.719	-0.217
Mean (±SD)	**0.862±0.026**	**0.644±0.020**	**-0.358±0.041**

The variance calculated by AMOVA was 0.023 (3%) for among regions and 0.868 (97%) within populations (total value: 0.890). A significant difference was detected among populations (*$P < 0.001$*) (Table 3).

Table 3. Hierarchical analysis of molecular variance (AMOVA) using GenAlEx software

Source	***df***	**Sum of squares**	**Est. Var.**	**% of the total variances**	***P***
Among populations	15	11.662	0.023	3%	<0.001
Among individuals within individuals	120	89.683	0.868	97%	<0.001
Total	135	101.346	0.890		

Population differentiation among locations was investigated using pairwise F_{ST} comparison (Table 4). Pairwise F_{ST} values across locations ranged from 0.013 to 0.211. The highest F_{ST} values were observed between Ko Taiphlao and Ko Prong, whereas the lowest value was found between Ko Samet and Ko Kula, Ko Samet and Ko Thong Lang.

Table 4. Pairwise F_{ST} values for all 16 populations of *P. lutea* in the Gulf of Thailand

Study site	Ko Samet	Ko Taiphlao	Ko Hindap	Ko Sam Sao	Ko Wua Kanthang	Ko Bai Dang	Ko Thong Lang	Ko Thian	Ko Yak Yai	Ko Ngam Yai	Ko Lawa	Ko Kula	Ko Rang Kachiu	Ko Khang Khao	Ko Prong	Ko Kham
Ko Samet	0.000															
Ko Taiphlao	0.082	0.000														
Ko Hindap	0.068	0.106	0.000													
Ko Sam Sao	0.043	0.171	0.119	0.000												
Ko Wua Kanthang	0.020	0.072	0.070	0.051	0.000											
Ko Bai Dang	0.081	0.049	0.036	0.160	0.079	0.000										
Ko Thong Lang	0.013	0.135	0.095	0.022	0.037	0.129	0.000									
Ko Thian	0.030	0.159	0.134	0.049	0.029	0.168	0.031	0.000								
Ko Yak Yai	0.031	0.170	0.117	0.043	0.070	0.151	0.024	0.062	0.000							
Ko Ngam Yai	0.061	0.015	0.059	0.135	0.050	0.024	0.105	0.133	0.138	0.000						
Ko Lawa	0.037	0.172	0.101	0.015	0.052	0.152	0.015	0.050	0.033	0.132	0.000					
Ko Kula	0.013	0.128	0.085	0.055	0.029	0.114	0.021	0.019	0.056	0.098	0.049	0.000				
Ko Rang Kachiu	0.031	0.132	0.095	0.033	0.051	0.107	0.025	0.075	0.029	0.096	0.036	0.057	0.000			
Ko Khang Khao	0.038	0.034	0.088	0.080	0.037	0.072	0.064	0.091	0.085	0.033	0.078	0.083	0.065	0.000		
Ko Prong	0.056	0.211	0.144	0.108	0.122	0.180	0.053	0.112	0.036	0.175	0.087	0.073	0.064	0.143	0.000	
Ko Kham	0.054	0.200	0.138	0.033	0.051	0.182	0.044	0.029	0.073	0.159	0.038	0.048	0.076	0.108	0.151	0.000

Principle coordinate analysis (PCoA) based on F_{ST} values showed that genetic connectivity was not correlated with the locations and distance between locations (Figure 3). According to plots of Delta K and LnP (D) from STRUCTURE analysis, with just three genetic clusters were detected as the optimal number (K = 3). Genetic structure analyses also indicated closely knit genetic units within all locations in the Gulf of Thailand (Figure 4)

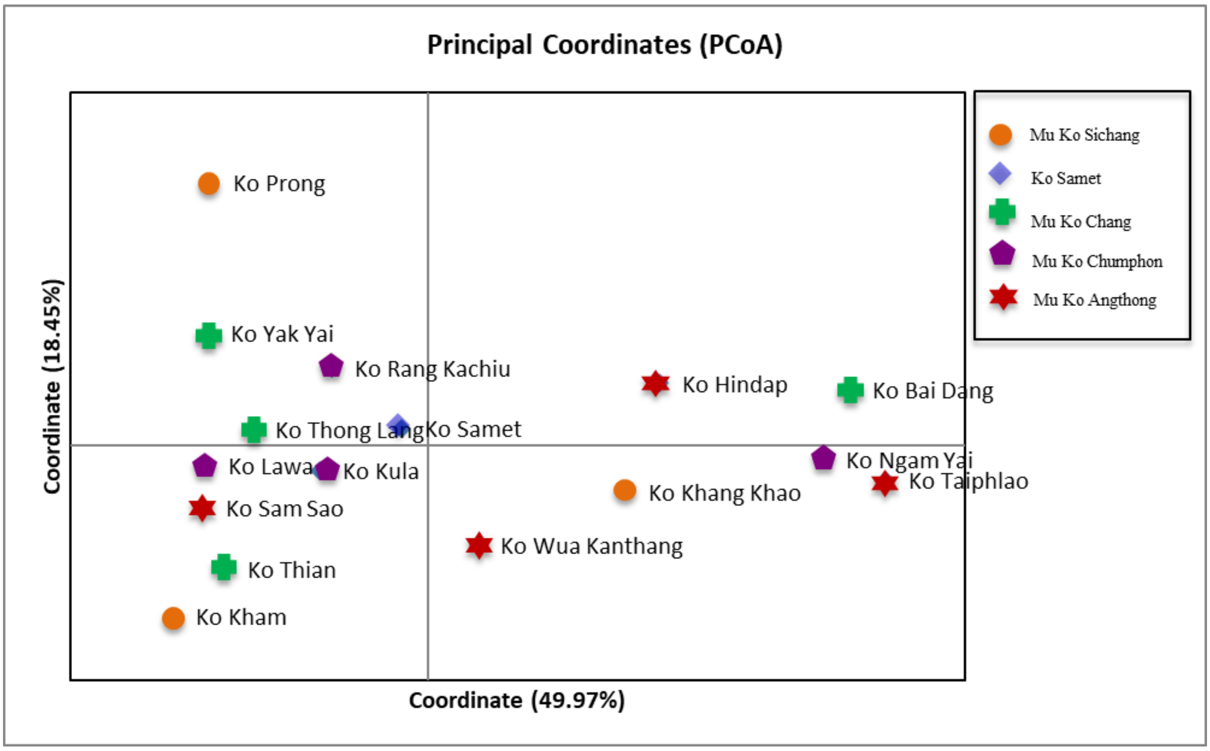

Figure 3. Principal coordinate analysis (PCoA) of *P. lutea* from the Gulf of Thailand

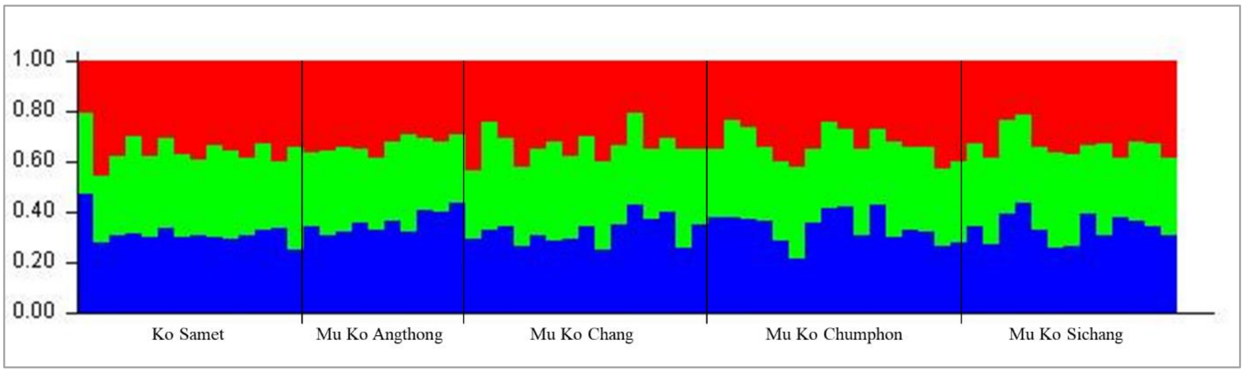

Figure 4. Cluster analysis of Porites lutea in the Gulf of Thailand performed using STRUCTURE (optimal K=3). The y-axis shows the membership probability of each location in distinct population clusters (different colors). Sampling locations are showed along the x-axis

4. Discussion

In this study, we analyzed a dataset encompassing 120 coral fragments of *P. lutea*, all gathered from the Gulf of Thailand. Our examination of these genotypes consistently revealed F_{ST} values at each location, indicating an excess of heterozygosity when compared to the expected Hardy-Weinberg Equilibrium (HWE). Our results are different from previous research conducted by Niu et al. (2015), who reported high genetic diversity within P. lutea populations in Lembeh Strait (LB), Indonesia, using ITS nuclear markers. It is noteworthy that LB, located within the Coral Triangle, serves as a pivotal center for global coral populations, accommodating over 75% of reef-dwelling species worldwide (Dubinsky and Stambler 2011). Our results suggest that the reproduction mode of *P. lutea* is largely by sexual propagation with abundant gene diversity. The genetic diversity of *P. lutea* populations was relatively high at Mu Ko Chumphon, Mu Ko Chang and Mu Ko Samet but decreased in the Mu Ko Sichang and Mu Ko Angthong. The adaptability of marine organisms is largely controlled by reproduction patterns and genetic diversity (Bernhardt and Leslie, 2013; Wu et al., 2021). Our findings suggest that low genetic diversity may hinder the adaptability of *P. lutea* in the Gulf of Thailand. Previous studies showed high genetic diversity values for two broadcast spawning coral species, *Montastraea cavernosa* and *Pavona gigantea*, found in the Western Atlantic and Mexican Pacific, respectively (Saavedra-Sotelo et al. 2011; Goodbody and Gvringley et al. 2012). Our results suggest the increased vulnerability of *P. lutea* populations in Mu Ko Sichang and Mu Ko Angthong areas to the effects of climate change and human activities. Such vulnerability may be influenced by a variety of factors, including local environmental conditions and human interactions, highlighting the necessity for targeted conservation efforts within this specific region.

The genetic connectivity of *P. lutea* is similar to that of *Pocillopora damicornis*, which was reported to be low genetic connectivity in the Gulf of Thailand (Sutthacheep, 2018b). These two coral species have different reproductive strategies. *P. damicornis*, being a brooder coral, retains embryos internally, limiting larval dispersal, while *P. lutea* reproduces through broadcast spawning, allowing for more extensive gamete dispersion in ocean currents. Moreover, the local hydrodynamics in the Gulf of Thailand, as indicated by Sojisuporn's study in 2010, wherein tides can converge or flow towards each other, further contribute to the patterns in genetic connectivity. These findings highlight the intricate interplay between reproductive biology, oceanic conditions, and genetic connectivity among coral populations. Larvae produced through sexual reproduction often play a crucial role as long-distance colonizers, contributing to gene flow between geographically distant populations (Adjeroud and Tsuchiya 1999; Adjeroud et al. 2014; Edmunds et al. 2018).

Knowledge of population genetics studies on scleractinian corals in the Gulf of Thailand is currently limited, and the majority of research in this area is still in its initial phases. Nevertheless, detailed studies are highly required for studying population genetics in scleractinian corals in the Gulf of Thailand. Such research can provide valuable insights into the genetic diversity, connectivity of other coral species which are very important scientific information for protection and restoration of coral reefs in Thai waters.

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