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ORIGINAL PAPER

First evidence of genetic connectivity of the brooder coral *Pocillopora damicornis* in the Gulf of Thailand

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Abstract. Although the population genetics of corals have been intensively studied, the knowledge of population boundaries, source-sink dynamics, and highly variable population genetic structures in scleractinian corals in Thailand is considerably limited. In this study, we aim to examine population genetic patterns for the coral *Pocillopora damicornis* from several locations in the Gulf of Thailand. The samples were extracted and genotyped using six microsatellite loci to analyze the genetic structure of *P. damicornis* populations. Based on the analyses, a total of 214 complete multilocus genotypes from 241 coral fragments of *P. damicornis* were yielded with the mean H_o and H_e values for all loci across sites of 0.810±0.060 (±SD) and 0.630±0.038 (±SD), respectively. A significant difference was detected among populations ($p < 0.001$). The highest F_{ST} values were found between Ko Khang Khao samples (the Inner Gulf of Thailand) and Ao Thien, Ko Tao samples (the Western Gulf of Thailand), whereas the lowest value was found between Ko Thalu (northwest, the Western Gulf of Thailand) samples and Ko Klung Badan (the Inner Gulf of Thailand) samples. Principle coordinate analysis (PCA) based on FST values revealed that genetic connectivity was not associated with the geographic location and distance between sites. The results from this study are useful for further exploring the connectivity and genetic diversity of *Pocillopora* populations, and will also support coral reef conservation in Thailand.

Keywords: population genetics, Pocillopora, connectivity, microsatellite, Gulf of Thailand

1. Introduction

Coral reefs are the highest biological diversity of marine ecosystems and are of ecological significance and economic value (McCook et al. 2009). Reef-building corals play an important role in the structure and maintenance of coral reef ecosystems and make the structure of coral reefs. However, coral reefs are currently numerous threats and deteriorating worldwide due to natural or anthropogenic disturbances, such as elevated seawater temperatures, nutrient enrichment, and destructive and overfishing, have degraded coral reefs around the world and are also under threat from global warming and ocean acidification (Hoegh-Guldberg et al. 2007; Wilkinson et al. 2010; Burke et al. 2011), which has brought about conservation and restoration efforts. Marine sessile organisms are typically distributed across a network of habitats in which geographically separated locals, including corals have limited adult movement, so the relatively short, pelagic larval phase represents the primary opportunity for dispersal. (Hanski 1998). Coral recovery depends on the successful recruitment of new coral colonies from surviving populations. The ability of coral reefs to recover from disturbances is highly influenced by the pattern and strength of connectivity among populations through the dispersal of planulae, which is highly variable. Hence, population genetic studies provide important information that can be applied for managing marine protected areas (Palumbi 2004; Cowen et al. 2007; Ridgway et al. 2008; Underwood et al. 2009; Nakajima et al. 2012).

The scleractinian coral *Pocillopora damicornis* is encountered on fringing reefs and found on tropical Indo-Pacific coral reefs (Veron 2000). *P. damicornis* has shown to be very sensitive to many natural disturbances, including coral bleaching (Yeemin et al. 1998; Marshall and Baird 2000; McClanahan et al. 2008; Pengsakun et al. 2012a), low salinity (Pengsakun 2013) and diseases (Ben-Haim and Rosenberg 2002, Luna et al. 2007). According to the monitoring on coral communities in Thai waters, almost of *P. damicornis* colonies were bleached and died due to the 2010 coral bleaching event (Yeemin et al., 2010). Fortunately, this coral species can potentially colonize on an available substrate and it is a dominant coral recruit on settle plates, based on the recruit settlement experiments conducted in the Gulf of Thailand (Pengsakun et al., 2012b).

Studies on population genetics among larvae-brooding of *Pocillopora* spp. have been studied French Polynesia (Magalon et al. 2004), Raja Ampat, Indonesia (Starger et al. 2008), Kane‘ohe Bay (Gorospe and Karl 2013) and Okinawa Island, Japan (Nakajima et al., 2017). In the Indo-West Pacific, the populations of *P. damicornis* mainly have different levels of local inbreeding and clonality (Ayre et al., 1997; Adjeroud and Tsuchiya 1999; Sherman et al., 2006; Whitaker 2006; Souter et al., 2009). A recent study has revealed that the levels of population genetic structure are significantly different, indicating the limitation of gene flow among the regions in the Indo-West Pacific as well as within regions in the tropical Eastern Pacific (Combosch and Vollmer 2011). However, knowledge of population boundaries, source-sink dynamics, and highly variable population genetic structures in scleractinian corals is considerably limited (van Oppen 2006; Hellberg 2007; Jones et al. 2009; Souter et al. 2009).

The Gulf of Thailand is a semi-enclosed tropical sea, located in the South China Sea. The Gulf is quite shallow with mean depth of only 45 m. The deepest part is only 80 m deep. (Wattayakorn, 2006). In the Gulf of Thailand, three group of the coral communities can be classified based on the difference of oceanographic conditions, consisting of the inner part of the Gulf of Thailand, the east and west coasts of the Gulf of Thailand (Yeemin et al., 2006). The distances between major reef groups were less than 500 km. This study aims to examine population genetic patterns for the coral *P. damicornis* at several location in the Gulf of Thailand.

2. Materials and Methods

2.1 Study sites and sample collection

A total of 214 *P. damicornis* samples were collected from five locations throughout the Gulf of Thailand. Three sites within the Mu Ko Sichang, Chonburi Province (Ko Sak, Ko Klung Badan, Ko Khang Khao), one site within the Rayong Province (Hin Phoeng), two sites within the Prachuab Kirikhan Province (Ko Thalu (NW), Ko Thalu (SW)), three sites within the Ko Tao, Chumphon Province (Ao Thein, Ao Hin Wong, Ao Kluatheon) and three sites within the Ko Samui, Surat Thani Province (Ko Taen, Laem Sed, Hin Angwang) (Figure 1). Fragments of *P. damicornis* were collected from 241 colonies; one fragment was taken from each colony. Coral fragments were preserved in 100% ethanol in 1.5 ml eppendorf tubes and then were kept in the laboratory until further processing.

2.2 Genomic DNA Extraction, sequencing and microsatellite genotyping

The coral skeletons from tubes containing coral tissues and were removed, and genomic DNA was extracted from coral tissue samples using DNeasy Blood and Tissue kit as specified by the manufacturer using the instructions for total DNA extraction from animal tissue (Qiagen, Valencia, CA, USA). Samples were genotyped using six microsatellite loci (Table 1) to analyze the genetic structure of *P. damicornis* populations. 10 µL total volumes contained 0.5 µL DNA template. We amplified the extracted DNA by PCR (polymerase chain reaction) method (adding two primer sets to one PCR (Nakajima et al. 2012)) using fluorescently labelled primers (Table 1). The cycling protocol was modified as 94 °C for 5 minutes, followed by 35 cycles at 94 °C for 30 seconds, 54 °C for 30 seconds, 72 °C for 1 minute and a final extension for 30 minutes. Allelic variations were visualized on an ABI 3100 XL sequencer (Applied Biosystems). Genotype calling were analysed using GeneMapper version 4.0 (Applied Biosystems). and each genotype was visually checked.

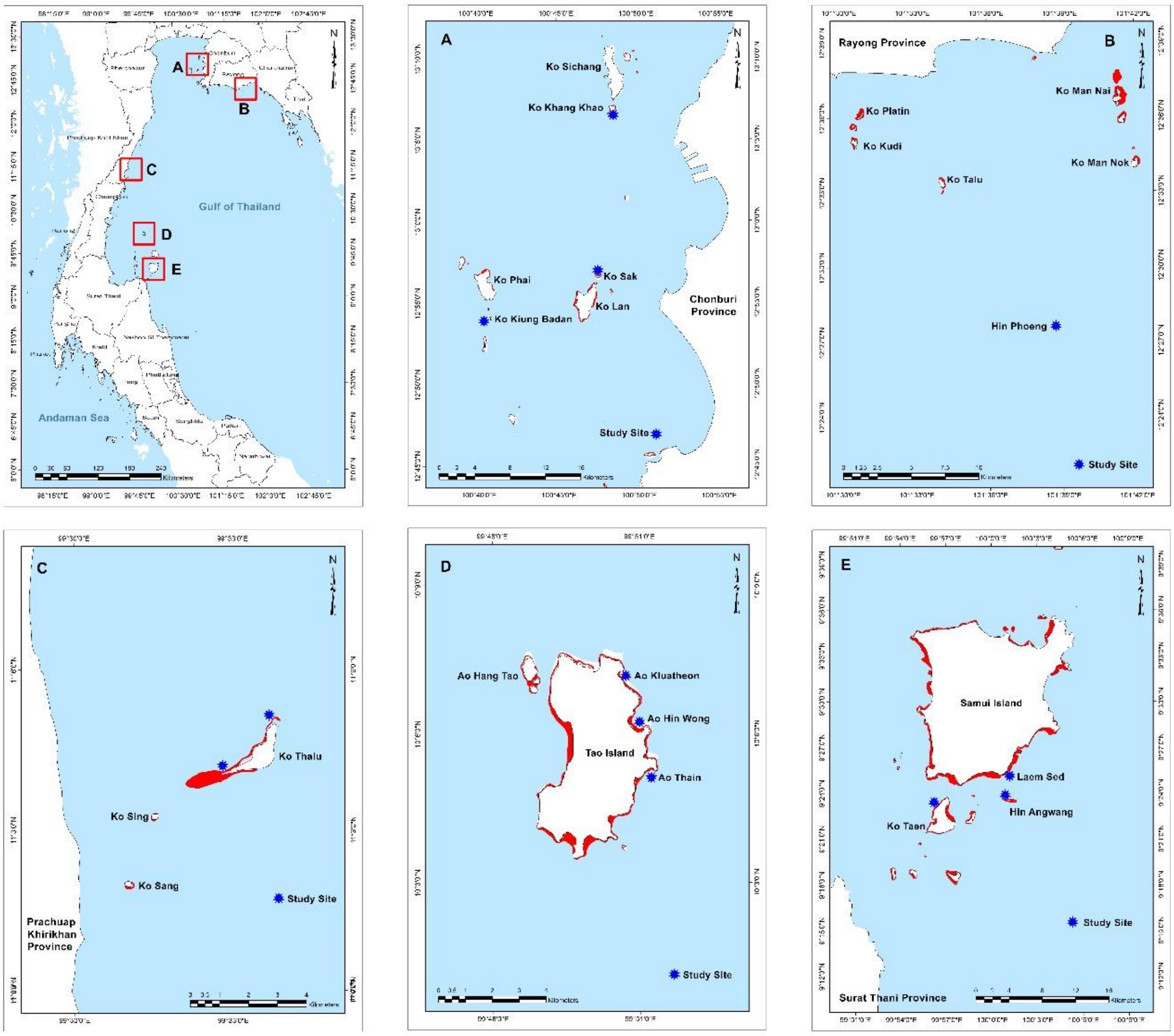

Figure 1. Map of the Gulf of Thailand showing twelve study sites: (A) Ko Sak (KS), Ko Klung Badan (KB), Ko Khang Khao (KK), the Inner Gulf of Thailand, (B) Hin Phoeng (HP), the Eastern Gulf of Thailand, (C) Ko Thalu (northwest, TNW) and Ko Thalu (southwest, TSW), the Western Gulf of Thailand, (D) Ao Thein, (AT) , Ko Tao, Ao Hin Wong, (HWO) , Ko Tao, Ao Kluatheon (AKT), Ko Tao, the Western Gulf of Thailand, (E) Ko Taen (Kta), Ko Samui, Laem Sed (LS), Ko Samui, Hin Angwang (HWA), Ko Samui, the Western Gulf of Thailand.

2.3 Statistical analyses

The numbers of alleles, allele frequencies, observed heterozygosity (H_o) and expected heterozygosity (H_e), number of private alleles, and inbreeding coefficient (F_{IS}) values (Peakall and Smouse 2012) were calculated using the GenAlEx software (version 6.5). F_{IS} values were applied to examine the deviation from Hardy-Weinberg equilibrium (HWE) because gaps between H_o and H_e under HWE are in proportion to the value of F_{IS}. F-statistics via analysis of molecular variance (AMOVA) was used to test the significance of all estimates based on 999 random permutations in order to measure the proportion of genetic variation between sites. A low pairwise F_{ST} indicates a high extent of gene flow and vice versa. Statistical significance levels for all pairwise tests were $P<0.05$. Pairwise geographic distances between sites were also calculated by GenAlEx software to estimate the scale of populations analyzed (Nakajima et al. 2009)

3. Results

A total of 214 complete multilocus genotypes from 241 coral fragments of *P. damicornis* were gathered. Mean H_o and H_e values for all loci across sites ranged from 0.125 to 1.000

Table 1. Details for six polymorphic microsatellite loci developed for Pocillopora damicornis as calculated from genotypes of 38 individuals

Locus	Primer sequence (5′-3′)	Repeat motif	Size (bp)	Fluorescence tag
PV2	F: GCCAGGACCCATTTATACTCC R: TGCAGTGTTCTACTTGTCAGTGC	$(GA)_{20}$	130-196	FAM
Pd3-002	F: ATCCGAATACAAGCGAAACG R: CAAAGCTTCTATCAGAAAATGCAA	(AAC)10	195–243	NED
Pd3-004	F: ACCAGACAGAAACACGCACA R: GCAATGTGTAACAGAGGTGGAA	$(ATG)_8$	160-180	VIC
Pd3-005	F: AGAGTGTGGACAGCGAGGAT R: GTTCCTTCGCCTTCGATTTT	$(TGA)_9$	200-230	VIC
Pd3-EF65	F: TGTGCAGGTGTTGTGACTGA R: TGTCTTTTTCACTTTTGCTTCAA	(GTT)5, (TGC)11	259–281	FAM
Pd2-AB79	F: GGAGATGGATGGAGACTGCT R: U19-AGTGCACGCACTAGATAGA	$(GT)_5(CT)_2$ $GT(CT)_3$	140-170	VIC

Table 2. Population statistic (± sd); N = total number of sample colonies, H_o = observed heterozygosity (Mean ±SD), H_e = expected heterozygosity (Mean ±SD); departures from Hardy–Weinberg equilibrium are expressed as F_{IS} (Mean ±SD)

Study site	N	Mean H_o	Mean H_e	Mean F_{IS}
Inner Gulf of Thailand (IG)				
Ko Sak (KS)	16	1.000	0.654	-0.531
Ko Klung Badan (KB)	15	0.967	0.572	-0.689
Ko Khang Khao (KK)	17	0.941	0.621	-0.533
Eastern Gulf of Thailand (EG)				
Hin Phoeng (HP)	30	0.900	0.761	-0.186
Western Gulf of Thailand (WG)				
Ko Thalu (northwest, TNW)	23	0.935	0.619	-0.533
Ko Thalu (southwest, TSW)	18	0.361	0.759	0.522
Ao Thein, Ko Tao (AT)	16	0.125	0.117	-0.067
Ao Hin Wong, Ko Tao (HWO)	16	0.750	0.803	0.061
Ao Kluatheon, Ko Tao (AKT)	21	0.952	0.769	-0.238
Ko Taen, Ko Samui (Kta)	20	0.975	0.671	-0.458
Laem Sed, Ko Samui (LS)	14	1.000	0.561	-0.803
Hin Angwang, Ko Samui (HWA)	8	0.813	0.648	-0.256
Total or mean (±SD)	**214**	**0.810±0.060**	**0.630±0.038**	**-0.309±0.080**

and 0.117 to 0.561, respectively, and the total mean values were 0.810±0.060 (±SD) and 0.630±0.038 (±SD), respectively (Table 2). Departures in population heterozygosity from HWE were indicated by mean F_{IS} values, which ranged from -0.067 to -0.803 at all sites (Table 2).

The variance calculated by AMOVA was 0.149 (15 %) for among regions and 0.820 (85 %) within populations (total value: 0.969). A significant difference was detected among populations (P < 0.001) (Table 3).

Population differentiation among sampling sites was examined using pairwise F_{ST} comparison (Table 4). Pairwise F_{ST} values across study sites ranged from 0.004 to 0.425. The highest F_{ST} values were found between Ko Khang Khao samples (the Inner Gulf of Thailand) and Ao Thien, Ko Tao samples (the Western Gulf of Thailand),

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

Source	df	Sum of squares	Est. Var.	% of the total variances	*P*
Among populations	11	63.4	0.149	15%	<0.001
Among individuals within populations	214	175.5	0.820	85%	<0.001
Total	225	238.9	0.969		

Table 4. Pairwise F_{ST} values for all 12 populations as indices of genetic differentiation (below diagonal) and pairwise geographic distance (km) based on geographic coordinates of sampling sites (above diagonal)

Region	**IG**	**IG**	**WG**	**IG**	**EG**	**WG**	**WG**	**WG**	**WG**	**WG**	**WG**	**WG**
Study site	KS	KB	AT	KK	HP	TSW	HWO	AKT	TNW	Kta	LS	HWA
KS		16.1	362.6	25.3	51.5	241.5	324.4	323.2	240.4	401.2	395.6	396.5
KB	0.105		319.8	11.2	54. 5	234.10	318.1	316.1	232.3	398.4	390.9	396.0
AT	0.310	0.215		349.9	284.5	116.5	2.3	2.83	114.3	81.70	78.1	80.8
KK	0.074	0.157	0.425		83.6	263.9	347.9	347.7	262.9	426.06	419.8	420.8
HP	0.045	0.053	0.236	0.051		203.4	302.3	256.9	211.5	370.14	347.6	358.3
TSW	0.110	0.118	0.260	0.147	0.078		113.9	110.4	1.41	192.5	188.9	191.7
HWO	0.092	0.073	0.245	0.104	0.042	0.036		2.2	113.5	81.2	75.9	78.4
AKT	0.057	0.071	0.257	0.100	0.036	0.074	0.043		110.8	83.34	81.3	82.1
TNW	0.109	0.004	0.237	0.144	0.047	0.113	0.060	0.062		192.81	189.7	192.5
Kta	0.136	0.154	0.413	0.089	0.090	0.082	0.073	0.087	0.138		6.59	3.51
LS	0.102	0.018	0.273	0.169	0.070	0.131	0.086	0.074	0.023	0.152		3.67
HWA	0.172	0.100	0.416	0.155	0.103	0.133	0.094	0.122	0.080	0.155	0.103	

whereas the lowest value was found between Ko Thalu (northwest, the Western Gulf of Thailand) samples and Ko Klung Badan (the Inner Gulf of Thailand) samples.

Principle coordinate analysis (PCA) based on F_{ST} values revealed that genetic connectivity was not associated with the geographic location and distance between sites (Figure 2). For example, Ao Thian site was located far from Ao Hin Wong and Ao Klua Theon, although these three sites are located on the eastern side of Ko Tao.

4. Discussion

Based on our findings, ten of the twelve populations of *P. damicornis*, collected from the Gulf of Thailand, showed the negative F_{IS} values at each locus, showing that there was heterozygosity excess compared to the HWE expectation. According to the study of the genetic population in French Polynesia, the heterozygote excess may be due to the effect of clonality in *P. damicornis* (Adjeroud et al. 2014). Hence, heterozygotes with better characteristics such as proper size, high clonal growth rate, high survival rate, etc., can enhance the success of their clonal propagation, leading to natural

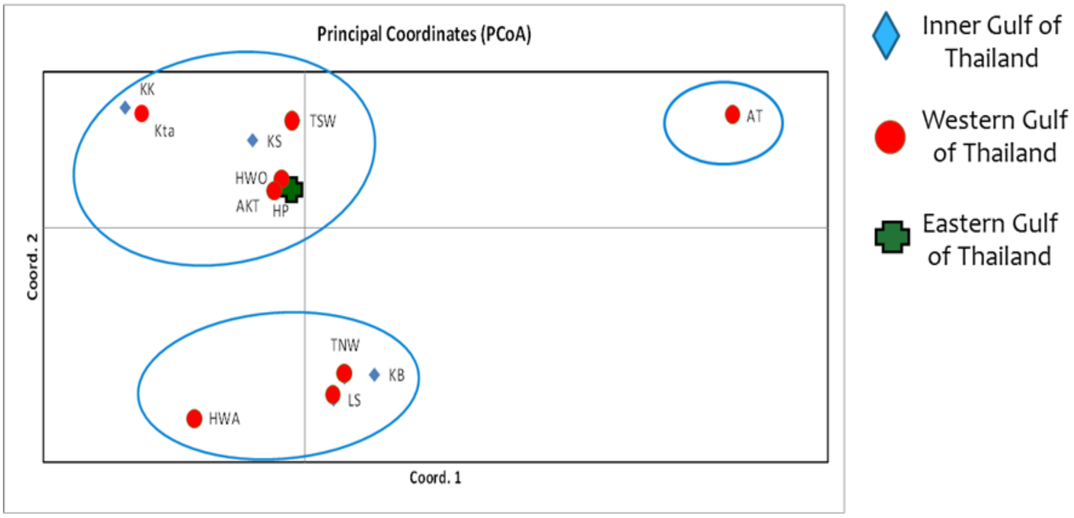

Fig. 2. Plot of the principal coordinate analysis based on a co-variance with standardized data; Ko Sak (KS), Ko Klung Badan (KB), Ko Khang Khao (KK), the inner Gulf of Thailand, Hin Phoeng (HP), the eastern Gulf of Thailand, Ko Thalu (northwest, TNW), Ko Thalu (southwest, TSW), Ao Thein, (AT), Ao Hin Wong, (HWO), Ao Kluatheon (AKT), Ko Taen (Kta), Laem Sed (LS), Hin Angwang (HWA), the western Gulf of Thailand.

coral populations. On the other hand, some coral populations and loci exhibited a significantly positive F_{IS} value, illustrating the occurrence of heterozygote deficiency. This may be influenced by several factors, e. g. null alleles and inbreeding as it was found in *P. damicornis* along the Great Barrier Reef, Australia (Ayre et al. 1997). Furthermore, the occurrence of micro-scale Wahlund effects can also induce the heterozygote deficiency because of genetic patchiness, i.e., the admixture of several differentiated cohorts, as observed in some reef organisms (Selkoe et al. 2010).

In this study, the observed coral populations had a low level of genotypic diversity, indicating that this may result from asexual reproduction in coral recruitment and population maintenance of *P. damicornis* in the Gulf of Thailand. These findings are in accordance with the results of some previous publications that observed *P. damicornis* in several geographical regions, for example, Australia, East Africa, Hawaii and Okinawa (Stoddart 1984; Adjeroud and Tsuchiya 1999; Souter et al. 2009; Gorospe and Karl 2013). Conversely, several works conducted in the Great Barrier Reef, West Papua New-Guinea, Indonesia and the tropical Eastern Pacific reported that the high levels of genotypic richness in the population of *P. damicornis* are derived from its predominance of sexual reproduction (Ayre et al. 1997; Starger et al. 2008). Our findings also reveal that the degrees of asexual reproduction and clonality in *P. damicornis* varied geographically.

In the Gulf of Thailand, the colonies of *P. damicornis* are generally distributed in the form of abundant patchy populations in shallow fringing reefs. Because the skeleton of *P. damicornis* is fragile, some human activities such as trampling, gleaning, fishing and anchoring, can generate negative impacts on leading to the high fragmentation rates and the survival rates of coral fragments. This might promote the high levels of clonality within local populations (Pinzón et al. 2012; Adjeroud et al. 2014). The observed study sites in the Gulf of Thailand, however, had a low level of fragmentation of *P. damicornis*, implying that the fragmentation of *P. damicornis* colonies is probably less common the Gulf of Thailand. It is possible that a high level of clonality could result from the production of asexual (pathenogenetic) larvae of *P. damicornis*.

Twelve coral populations in the Gulf of Thailand observed in this study had a significant genetic differentiation, which can be linked to the marked variability in the reproductive strategies and genetic structure of *P. damicornis* across the geographic range in the Gulf of Thailand. The maintenance of local populations of *P. damicornis* in the Gulf of Thailand may be mainly enhanced by its asexual reproduction, contributing to the elevation of clonality within populations and significant genetic differentiation among populations. However, gene flow among some populations in the Gulf of Thailand can also be observed, based on our analysis. Our findings agree with what Bell (1982) found on modelling the dispersal and population maintenance in a species with mixed modes of reproduction and mentioned that larvae generated from sexual reproduction tended to provide long-distance colonists and gene flow between distant populations. In contrast, asexual reproduction serves as a vital contributor for maintaining local populations (Adjeroud and Tsuchiya 1999; Adjeroud et al. 2014). Understanding of population genetic studies on scleractinian corals in the Gulf of Thailand is still limited and most researches were implemented as in an initial phase. Detailed studies are highly required and further findings should provide a clear explanation in various aspects, for example, genetic diversity, clonality and connectivity of other coral species in a marine ecosystem.

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