


Dominance of the coral *Pocillopora acuta* around Phuket Island in the Andaman Sea, Thailand

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Abstract

Pocillopora damicornis (Linnaeus, 1758), a species complex, consists of several genetic lineages, some of which likely represent reproductively isolated species, including the species *Pocillopora acuta* Lamarck, 1816. *Pocillopora acuta* can exhibit similar morphological characteristics as *P. damicornis*, thus making it difficult to identify species-level taxonomic units. To determine whether the *P. damicornis*-like colonies on the reefs in the Andaman Sea (previously often identified as *P. damicornis*) consist of different species, we sampled individual colonies at five sites along a 50 km coastal stretch at Phuket Island and four island sites towards Krabi Province, Thailand. We sequenced 210 coral samples for the mitochondrial open reading frame and identified six distinct haplotypes, all belonging to *P. acuta* according to the literature. Recently, *P. acuta* was observed to efficiently recolonize heat-damaged reefs in Thailand as well as globally, making it a potentially important coral species in future reefs. Specifically in the light of global change, this study underscores the importance of high-resolution molecular species recognition, since taxonomic units are important factors for population genetic studies, and the latter are crucial for management and conservation efforts.

KEYWORDS

biodiversity, haplotypes, Indian Ocean, *Pocillopora*, species delimitation, species diversity

TAXONOMY CLASSIFICATION

Genetics

1 | INTRODUCTION

Pocillopora, a widespread coral genus (Veron, 2000), harbors many fast-growing reef-builders that support a diverse and abundant community of other reef organisms such as echinoderms and crustaceans (Austin et al., 1980; López-Pérez et al., 2017). *Pocillopora damicornis* (Linnaeus, 1758), previously identified solely based on its morphology (D'Croz & Maté, 2004; Mayfield et al., 2013, 2018), is known to be morphologically

highly plastic (Schmidt-Roach et al., 2013; Veron & Pichon, 1976). Phenotypic plasticity allows clonemates of *P. damicornis* genotypes to exhibit different morphologies based on environmental cues (Todd, 2008). This has called into question the ability to accurately identify species based solely on morphology (Flot et al., 2010; Pinzón & Lajeunesse, 2011; Schmidt-Roach et al., 2012; Souter, 2010). Several taxa have been synonymized within *P. damicornis* and subsequently, grouped as *P. damicornis*-like colonies (Pinzón et al., 2013) or the *P. damicornis* species

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complex (Schmidt-Roach et al., 2013). Molecular evidence confirmed the expectations of several taxonomic species within the species complex (Schmidt-Roach et al., 2013) and delineation of species boundaries has been the focus of many publications (e.g., Flot et al., 2010; Forsman et al., 2013; Johnston et al., 2017; Marti-Puig et al., 2014; Oury et al., 2023; Pinzón & Lajeunesse, 2011; Schmidt-Roach et al., 2014). Resolving species taxonomy is crucial, as different species have different functional roles in complex coral reef ecosystems (Boulay et al., 2014) and may respond differently to future changes. To distinguish species, a pocilloporid-specific mitochondrial open reading frame (mtORF), which encodes a transmembrane protein (TMP362; Banguera-Hinestroza et al., 2019), has been shown to be very informative (Flot et al., 2008; Flot & Tillier, 2007; Johnston et al., 2018).

Studies focusing on the Andaman Sea suggested that *P. damicornis*-like corals belong to the *P. damicornis* type β or type γ lineages (Pinzón et al., 2013; Schmidt-Roach et al., 2013) that have now been assigned species status as *P. acuta* Lamarck, 1816 and *P. verrucosa* Ellis & Solander, 1786, respectively (Schmidt-Roach et al., 2014). *Pocillopora damicornis* type β (sensu Schmidt-Roach et al., 2013) corresponds to mtORF Type 5 (sensu Pinzón et al., 2013), Type F (sensu Souter et al., 2009), Type b (sensu Flot et al., 2008) as well as ORF18 and ORF19 found within the Primary Species Hypothesis PSH05 proposed by Gélín, Postaire, et al. (2017). *Pocillopora damicornis* type γ (sensu Schmidt-Roach et al., 2013) corresponds to mtORF Type 3 (sensu Pinzón et al., 2013), Type NF (sensu Souter et al., 2009), as well as ORF 35–48 within the Primary Species Hypothesis PSH13 proposed by Gélín, Postaire, et al. (2017). In the Andaman Sea, several authors refer to the prevalent species as *P. damicornis* (Brown et al., 2019; Kuanui et al., 2008; Phongsuwan & Chansang, 2012; Putchim et al., 2017) whereas others classify it as *P. acuta* (Rinkevich et al., 2016; Ying et al., 2021).

Macromorphological and life-cycle attributes, albeit insufficiently delimiting species within pocilloporids, suggest that *Pocillopora* colonies around Phuket Island are in fact *P. acuta*. These characters include fine and prolonged branches with “acute” branch tips, darker pigmentation surrounding the oral opening of the polyps, a brooding reproductive mode, as well as monthly planulation during or after the new moon (Kuanui et al., 2008; Schmidt-Roach et al., 2012, 2014; Smith et al., 2019; Torres et al., 2020; Figure 1c,f).

Recent studies have highlighted the increasing dominance of pocilloporid corals in coral reef ecosystems (e.g., Poquita-Du et al., 2019), particularly after massive disturbance events like heat waves (Edmunds et al., 2019), making them at least temporary winners of climate change (Laufkötter et al., 2020) and key conservation targets due to their rapid recolonization ability. To confirm, whether *P. acuta* is the dominant pocilloporid around Phuket Island, Thailand, the specific mtORF was amplified for 210 coral samples collected at nine sites. Such taxonomic data is critical for assessing the distribution of this important species and for effective coral reef management and conservation efforts in light of climatic change.

2 | MATERIALS AND METHODS

2.1 | Sampling sites and procedure

Coral samples were taken at nine different sites in the Andaman Sea around Phuket Island, Thailand (Figure 1) located in the Northeastern Indian Ocean, in the Eastern Bay of Bengal. The sampling locations comprise the western edge of Phuket Island (Kamala (KA), Patong North (PN) and Patong South (PS)), four islands towards Krabi Province (Khai Nai (KNA), Khai Nok (KNO), Ko Nung Krabi (KR) and Le Pi (LP)) and two sites around the Panwa peninsula (Panwa (PW) and Tang Khem (TK)). The two sites PW and TK are situated only 0.7 km apart, whereas a larger distance exists between both PW and TK and the sites on the West (18–23 km) as well as the islands towards Krabi Province (15–35 km). For each colony of *P. acuta* sampled, a small branch was clipped and stored in seawater until further processing in the lab at the Phuket Marine Biological Centre (PMBC, Phuket, Thailand). Samples were fixed in a solution of dimethyl sulfoxide, disodium EDTA, and saturated NaCl (DESS buffer; Yoder et al., 2006) and transferred to the lab facilities at GEOMAR Helmholtz Centre for Ocean Research Kiel, for molecular analyses. In total, 210 corals (5–65 per site) were analyzed for a hypervariable mitochondrial open reading frame (mtORF; Flot & Tillier, 2007).

2.2 | Molecular work and data analysis

DNA was extracted from coral tissue samples using an Ethanol precipitation protocol (Baker & Cuning, 2016). DNA quantity and quality from each sample was assessed with a NanoDrop® 2000 spectrophotometer and the quality was further screened from a subsample by gel electrophoresis. An mtORF was amplified using primers developed and described by Flot and Tillier (2007) for corals of the genus *Pocillopora* (FATP6.1 5'-TTTGGGSATTCGTTTAGCAG-3' and RORF 5'-SCCAATAT GTTAAACASCATGTC-3') for determination of mitochondrial haplotype lineages. PCR reactions were conducted as described in Robitzsch et al. (2015): 30 μ L reactions contained 15 μ L Qiagen HotStarTaq Plus Master Mix, 1.88 μ L primers (each primer at 20 μ M, final concentration 1.25 μ M), 8.74 μ L NFW and 2.5 μ L template DNA (10–40 ng/ μ L). Cycle conditions were: 95°C for 5 min + 35 \times [94°C for 30 s, 58°C for 45 s, 72°C for 60 s] + 72°C for 10 min. Gel pictures were taken on 1% agarose gels with 1 kb GeneRuler DNA ladder (Thermo Scientific) as a ladder for all samples. Finally, 25 μ L of each PCR product was sent to the Institute of Clinical Molecular Biology in Kiel (IKMB) for PCR cleanup and bidirectional Sanger sequencing on an ABI 3730xl DNA Analyzer. For the analyses, the respective forward and reverse sequences were assembled, aligned, and trimmed in CodonCode Aligner v9.0.1.3 (CodonCode Corporation). The contigs were checked for gaps and insertion/deletion polymorphisms (indels). Due to low quality, 26 sequences could not be assembled into contigs; therefore, they were excluded from the dataset after comparing readable positions to the unambiguous sequences. Sequences were identified using a

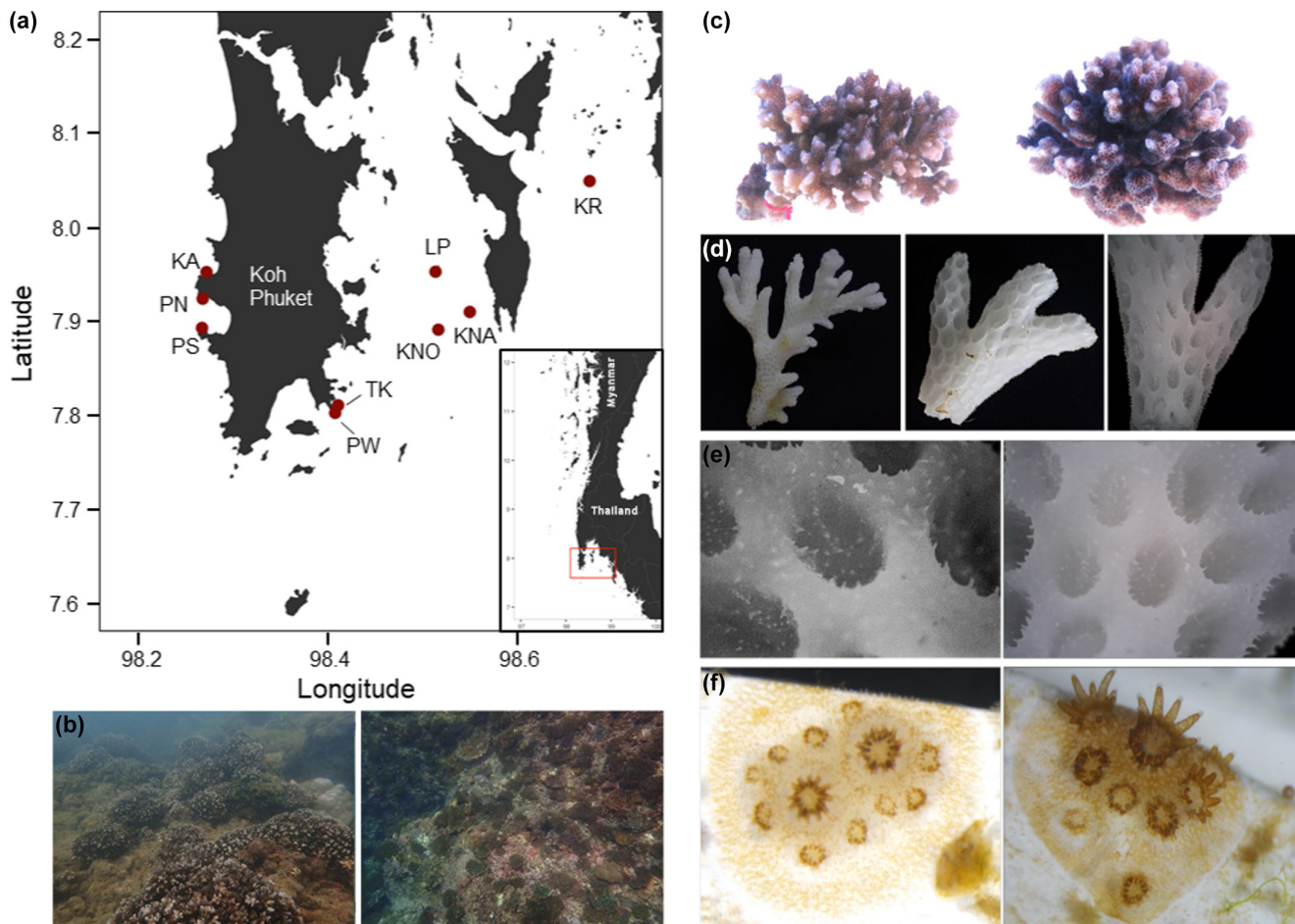


FIGURE 1 Map of the sampling sites of *Pocillopora acuta* around Phuket Island, Thailand. Site codes are: KA Kamala, KNA Khai Nai, KNO Khai Nok, KR Koh Nung Krabi, LP Le Pi, PN Patong North, PS Patong South, PW Panwa and TK Tang Khem. *Pocillopora* species were collected for this study from different reefs in the Thai Andaman Sea (a), where in-situ *Pocillopora* can be quite dominant (b). Their branches are elongated with “acute” tips (c–d) and their skeletal calyx is oval as observed for both *P. damicornis* and *P. acuta* (e; Schmidt-Roach et al., 2014). Coral recruits are formed from brooded larvae (collected from TK, PW) and colonies can fuse at early stage forming (f). Maps (a) were created with publicly available data from GADM.org.

BLAST search against the blastn database using the NCBI website (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>). The resulting alignment of unambiguous, high-quality reads was converted in MEGA X (Stecher et al., 2020) for further analysis of distinct haplotypes in DNAsp v6 (Rozas et al., 2017). Thereafter, the resulting NEXUS file was exported into Network 10.2.0.0 (<https://fluxus-engineering.com>) to build a median-joining network (Bandelt et al., 1999). Therefore, sequences of the sister species *P. verrucosa* from the Indo-Pacific (GenBank accession number: KP238128) and *P. damicornis* from the Great Barrier Reef (GenBank accession number: JX625077) were obtained from GenBank (Figure 2; Pinzón et al., 2013; Schmidt-Roach et al., 2013).

3 | RESULTS AND DISCUSSION

Corals of the genus *Pocillopora* exhibit a high phenotypic plasticity, fostering the application of molecular techniques such as markers targeting mtORF or internal transcribed spacer (ITS) regions (Flot et al., 2008; Flot & Tillier, 2007; Marti-Puig et al., 2014) for species

identification. Furthermore, concepts like the Primary Species Hypothesis (PSH), which relies on morphological discriminations and/or molecular markers coupled with criteria such as biological or ecological considerations (Pante et al., 2015), can lead to the possible delineation of new species. In this study, 210 *P. acuta* colonies were sampled and a fragment of the mtORF (828 bp; GenBank accession numbers: MZ465117–MZ465326) was sequenced to identify the dominant species within the *P. damicornis* species complex around Phuket Island, Thailand. Unambiguous, high-quality alignments were identified as *P. acuta* and compared to GenBank sequences of *P. damicornis* type β , now *P. acuta*, from La Réunion (accession numbers: KT879932–KT880039) and *P. acuta* from the Philippines (accession numbers: MH064356–MH064390). This dataset provided six distinct haplotypes (Figure 2). A total of 210 colonies yielded 204 samples corresponding to haplotype 1, which corresponds to one of four *P. acuta* haplotypes that were described in the Philippine archipelago by Torres and Ravago-Gotanco (2018; GenBank accession number: MH064356) and ORF18 found in La Réunion (sensu Gélín, Fauvelot, et al., 2017;

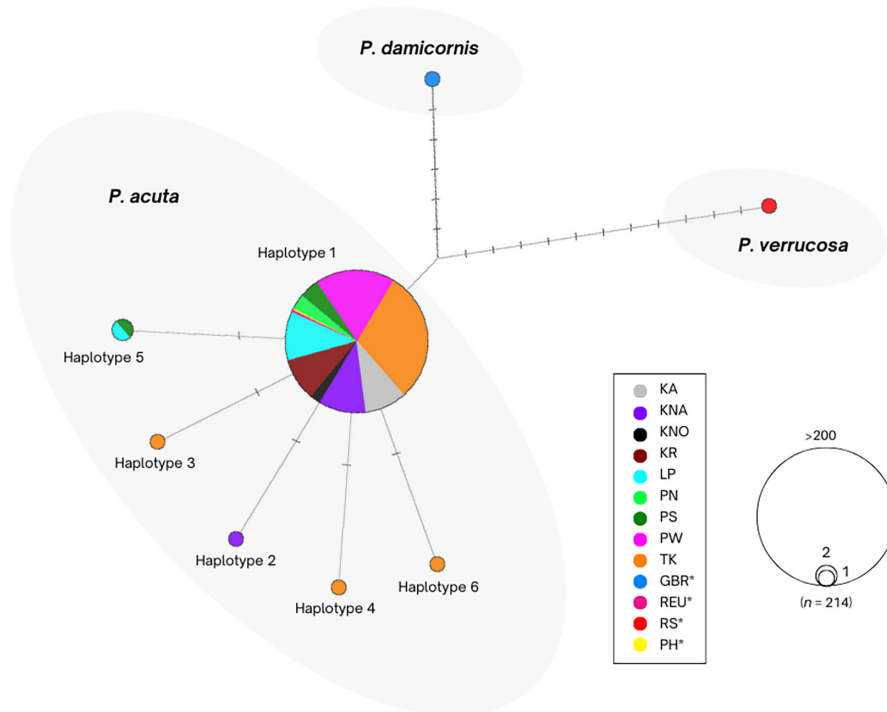


FIGURE 2 Minimum-spanning haplotype network of mtORF DNA sequences from nine sampling sites around Phuket Island, Thailand. The alignment consisted of 210 sequences, 828 bp length, from several distinct reefs (KA Kamala, KNA Khai Nai, KNO Khai Nok, KR Koh Nung Krabi, LP Le Pi, PN Patong North, PS Patong South, PW Panwa and TK Tang Khem; see Figure 1). Sequences were referenced against two distinct *P. acuta* haplotypes found in the Philippine archipelago (PH) by Torres and Ravago-Gotanco (2018) and on La Réunion (REU) by Gélín, Fauvelot, et al. (2017). *P. verrucosa* and *P. damicornis* references are from the Red Sea (RS) identified by Robitzsch et al. (2015) and from the Great Barrier Reef (GBR) identified by Schmidt-Roach et al. (2013), respectively. *Sequences obtained from GenBank.

GenBank accession number: [KT879932](https://www.ncbi.nlm.nih.gov/nuccore/KT879932)). Two of 210 samples corresponded to haplotype 5 and one sample each coincided with haplotypes 2, 3, 4, and 6. Interestingly, haplotypes 2–6 are novel haplotypes not yet found on other Andaman Sea reefs. However, this may be due to the lack of molecular data for *Pocillopora* corals in the region rather than the absence of corresponding haplotypes. For instance, the same haplotypes of *P. damicornis* type α and β could be found on either side of the Australian continent at Ningaloo Reef sites (Western Australia) and on the Great Barrier Reef (Eastern Australia; Thomas et al., 2014). On the contrary, Noreen et al. (2015) found distinct *Pocillopora* haplotypes at higher latitude subtropical and lower latitude tropical reefs on the Great Barrier Reef, despite prevalent oceanographic exchange via the Eastern Australian Current towards the subtropics. Only within a transition zone, both tropical and subtropical haplotypes coexisted.

Accurate species identification is critical for the widely distributed and researched genus *Pocillopora* to identify cryptic species and endemism since these have direct implications for conservation policies. Furthermore, the delimitation of taxonomic units for population genetic studies is crucial to avoid inaccurate estimations of genetic divergence and connectivity (Pante et al., 2015), which are the foundation of management and conservation programs. Here, of particular importance is the effect of reproduction on clonal structure, on larval dispersal potential and, therefore, on population connectivity. Ecological studies benefit from the ability to identify species, which allows for the characterization of significant differences and temporal variability in molecular physiological profiles between species (e.g., *P. damicornis* and *P. acuta*), with implications for resilience under long-term stress (Mayfield et al., 2018). Furthermore, the inability to accurately characterize species as well as genetic clusters within

species greatly reduces the ability to detect a response of the biota at various levels of hierarchy to ongoing climate change and undermines efforts guiding conservation efforts.

The findings within this study demonstrated the widespread occurrence of *Pocillopora acuta* around the island of Phuket, Thailand. Previous studies documented the existence of *P. acuta* in the Gulf of Thailand (Pinzón et al., 2013), the Indian Ocean (Gélín et al., 2018; Gélín, Fauvelot, et al., 2017) as well as the South China Sea (Poquita-Du et al., 2017). Other studies have recently documented the dominance of this species on many coral reefs globally: A study conducted in Singapore evidenced that out of five pocilloporid species recorded since 1838, only colonies of *P. acuta* are remaining to date (Poquita-Du et al., 2019). Since at least the 1970s, Mo'orea has experienced substantial reduction in coral cover, resulting in a predominant recovery of corals of the genus *Pocillopora* following each disturbance (Adjeroud et al., 2018; Berumen & Pratchett, 2006; Holbrook et al., 2018; McWilliam et al., 2020). A mass bleaching event in 2010 resulted in 100% reduction of coral cover (Edmunds et al., 2019); however, a high density of sexually reproduced offspring of *Pocillopora* colonies accelerated coral community recovery, followed by the recovery of other coral taxa. The impact of the 2010 mass bleaching event was heterogeneous across ocean basins with the Indian Ocean and Australasia more severely affected than the Pacific Ocean (Alemu & Clement, 2014; Guest et al., 2012; Hoeksema et al., 2012; Sutthacheep et al., 2013). Overall coral cover decline of up to 90% occurred in Southeast Asia, specifically in reefs around Indonesia, Malaysia, and Thailand (Tun et al., 2010). Around Phuket Island, specifically at the site TK, coral species diversity was high until 2007 and the genus *Pocillopora* comprised only a minor fraction (5% of total coral cover; Brown et al., 2019). A follow-up survey in

2016 found a major shift in species composition, with *Pocillopora* colonies dominating (55% of total coral cover; Brown et al., 2019). Furthermore, fast-growing corals like *Acropora* and *Pocillopora* were severely harmed in the bleaching event in 2010 but coped well with thermal stress during the subsequent bleaching episode in 2016 (Putchim et al., 2017). As a result of the 2010 bleaching event, adapted genotypes might have recolonized reefs around Phuket Island, therefore establishing the dominance of *Pocillopora acuta* colonies in the area (Fiesinger et al., 2023).

Since the genus *Pocillopora* comprises many species (Pinzón et al., 2013), it is likely that not all are able to withstand the ongoing and escalating climatic perturbations predicted for the upcoming decades. However, the species and more specifically the genotypes that do survive might be more suitable and thus, selected for future warming conditions (Hume et al., 2022). By identifying the highly connected and more stress-tolerant species and genotypes within the genus, such as *P. acuta*, targeted management efforts may facilitate rapid recolonization of future reefs thereby catalyzing their recovery (Hume et al., 2022). Because many ecosystems are naturally prone to pulse disturbances, “regeneration taxa,” which are able to rapidly recolonize an area after severe disturbance events, are critical (McWilliam et al., 2020). However, a shift away from long-lived taxa to rapid recolonizers alters the functional trait assemblage of coral reef ecosystems (Lavorel et al., 1997; McWilliam et al., 2020). In this context, it is necessary to point out that *P. acuta* has been shown to express special properties: intracolony genetic variability such as mosaicism and chimerism (Oury et al., 2020; Rinkevich et al., 2016) as well as polyploidy (Stephens et al., 2023). While coral chimerism may enhance within-colony biodiversity that may counter the detrimental effects of changing ecosystems on genetic and phenotypic diversity (Rinkevich, 2019), triploidy may under certain circumstances outcompete diploid genotypes (Stephens et al., 2023) through beneficial traits as observed in aquaculture (e.g., increased growth, pathogen resistance; Guo & Allen, 1994; Zhou & Gui, 2017) but may come at the cost of infertility (as observed in other invertebrates; Kang et al., 2013). Therefore, the dominance of a single coral species together with its peculiar characteristics may have implications for the functioning of Andaman Sea reefs that need to be the focus of future studies.

In conclusion, the coral reefs around Phuket Island are dominated by *P. acuta* colonies and it is likely that recent monitoring efforts have identified these as *P. damicornis*. However, it cannot be discounted that in the past, different species within the *P. damicornis* species complex possibly coexisted that have since been outcompeted by fast-growing *P. acuta* colonies after massive bleaching events. It would be desirable to expand the sampling area and include more offshore sites that potentially comprise a higher pocilloporid diversity. Ancient DNA from museum samples or coral skeletons could provide an overview of which *Pocillopora* species were present in the area in the past. We should treat species delimitation carefully as it can be challenging and shift in a changing ocean. A more integrative

approach should be followed in the future by combining molecular markers with additional physiological and biological criteria assessments to build up evolutionary species units. Such identifications are key for coral reef management and local as well as regional restoration efforts and can facilitate the identification of those genotypes that are most likely to withstand future climate conditions.

AUTHOR CONTRIBUTIONS

Anna Fiesinger: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (equal); methodology (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Christoph Held:** Formal analysis (equal); investigation (equal); methodology (equal); software (equal); supervision (equal); validation (equal); writing – original draft (supporting); writing – review and editing (supporting). **Andrea L. Schmidt:** Data curation (supporting); resources (supporting); writing – review and editing (supporting). **Lalita Putchim:** Data curation (equal); funding acquisition (supporting); project administration (supporting); resources (equal); writing – review and editing (equal). **Frank Melzner:** Funding acquisition (lead); investigation (equal); project administration (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal). **Marlene Wall:** Conceptualization (lead); data curation (supporting); funding acquisition (lead); investigation (lead); methodology (supporting); project administration (lead); supervision (lead); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The sequences obtained for the coral colonies analyzed in this study can be obtained from GenBank with the accession numbers [MZ465117–MZ465326](#).

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REFERENCES

- Adjeroud, M., Kayal, M., Iborra-Cantonnet, C., Vercelloni, J., Bosserelle, P., Liao, V., Chancerelle, Y., Claudet, J., & Penin, L. (2018). Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. *Scientific Reports*, *8*, 9680.
- Alemu, J. B., & Clement, Y. (2014). Mass coral bleaching in 2010 in the Southern Caribbean. *PLoS One*, *9*, e83829.
- Austin, A., Austin, S., & Sale, P. (1980). Community structure of the fauna associated with the coral *Pocillopora damicornis* (L.) on the great barrier reef. *Marine and Freshwater Research*, *31*, 163.
- Baker, A., & Cuning, R. (2016). Bulk gDNA extraction from coral samples. *Protocols.io*, 1–6. <https://dx.doi.org/10.17504/protocols.io.dyq7vv>
- Bandelt, H. J., Forster, P., & Röhl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, *16*, 37–48.
- Banguera-Hinestroza, E., Ferrada, E., Sawall, Y., & Flot, J.-F. (2019). Computational characterization of the mtORF of pocilloporid corals: Insights into protein structure and function in *Stylophora* lineages from contrasting environments. *Genes*, *10*, 324. <https://doi.org/10.3390/genes10050324>
- Berumen, M. L., & Pratchett, M. S. (2006). Recovery without resilience: Persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs*, *25*, 647–653.
- Boulay, J. N., Hellberg, M. E., Cortés, J., & Baums, I. B. (2014). Unrecognized coral species diversity masks differences in functional ecology. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20131580.
- Brown, B. E., Dunne, R. P., Somerfield, P. J., Edwards, A. J., Simons, W. J. F., Phongsuwan, N., Putschim, L., Anderson, L., & Naeije, M. C. (2019). Long-term impacts of rising sea temperature and sea level on shallow water coral communities over a ~40 year period. *Scientific Reports*, *9*, 8826.
- D'Croz, L., & Maté, J. L. (2004). Experimental responses to elevated water temperature in genotypes of the reef coral *Pocillopora damicornis* from upwelling and non-upwelling environments in Panama. *Coral Reefs*, *23*, 473–483. <https://doi.org/10.1007/s00338-004-0397-7>
- Edmunds, P., Adam, T., Baker, A., Doo, S., Glynn, P., Manzello, D., Silbiger, N., Smith, T., & Fong, P. (2019). Why more comparative approaches are required in time-series analyses of coral reef ecosystems. *Marine Ecology Progress Series*, *608*, 297–306.
- Fiesinger, A., Held, C., Melzner, F., Putschim, L., Reusch, T. B. H., & Wall, M. (2023). Population genetic differentiation of the ubiquitous brooding coral *Pocillopora acuta* along Phuket Island reefs in the Andaman Sea, Thailand. *BMC Ecology and Evolution*, *23*(1), 42. <https://doi.org/10.1186/s12862-023-02153-7>
- Flot, J.-F., Couloux, A., & Tillier, S. (2010). Haplowebs as a graphical tool for delimiting species: A revival of Doyle's "field for recombination" approach and its application to the coral genus *Pocillopora* in Clipperton. *BMC Evolutionary Biology*, *10*, 372.
- Flot, J. F., Magalon, H., Cruaud, C., Couloux, A., & Tillier, S. (2008). Patterns of genetic structure among Hawaiian corals of the genus *Pocillopora* yield clusters of individuals that are compatible with morphology. *Comptes Rendus Biologies*, *331*, 239–247.
- Flot, J.-F., & Tillier, S. (2007). The mitochondrial genome of *Pocillopora* (Cnidaria: Scleractinia) contains two variable regions: The putative D-loop and a novel ORF of unknown function. *Gene*, *401*, 80–87.
- Forsman, Z. H., Johnston, E. C., Brooks, A. J., Adam, T. C., & Toonen, R. J. (2013). Genetic evidence for regional isolation of *Pocillopora* corals from Moorea. *Oceanography*, *26*, 153–155.
- Gélin, P., Fauvelot, C., Mehn, V., Bureau, S., Rouzé, H., & Magalon, H. (2017). Superclone expansion, long-distance clonal dispersal and local genetic structuring in the coral *Pocillopora damicornis* type β in Reunion Island, South Western Indian Ocean. *PLoS One*, *12*, e0169692.
- Gélin, P., Pirog, A., Fauvelot, C., & Magalon, H. (2018). High genetic differentiation and low connectivity in the coral *Pocillopora damicornis* type β at different spatial scales in the Southwestern Indian Ocean and the Tropical Southwestern Pacific. *Marine Biology*, *165*, 167.
- Gélin, P., Postaire, B., Fauvelot, C., & Magalon, H. (2017). Reevaluating species number, distribution and endemism of the coral genus *Pocillopora* Lamarck, 1816 using species delimitation methods and microsatellites. *Molecular Phylogenetics and Evolution*, *109*, 430–446.
- Guest, J. R., Baird, A. H., Maynard, J. A., Muttaqin, E., Edwards, A. J., Campbell, S. J., Yewdall, K., Affendi, Y. A., & Chou, L. M. (2012). Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS One*, *7*, e33353.
- Guo, X., & Allen, S. K. (1994). Sex determination and polyploid gigantism in the dwarf surfclam (*Mulinia lateralis* Say). *Genetics*, *138*, 1199–1206.
- Hoeksema, B. W., Matthews, J. L., & Yeemin, T. (2012). The 2010 coral bleaching event and its impact on the mushroom coral fauna of Koh Tao, Western Gulf of Thailand. *Phuket Marine Biological Centre Research Bulletin*, *71*, 71–81.
- Holbrook, S. J., Adam, T. C., Edmunds, P. J., Schmitt, R. J., Carpenter, R. C., Brooks, A. J., Lenihan, H. S., & Briggs, C. J. (2018). Recruitment drives spatial variation in recovery rates of resilient coral reefs. *Scientific Reports*, *8*, 7338.
- Hume, B. C. C., Voolstra, C. R., Armstrong, E., Mitushasi, G., Porro, B., Oury, N., Agostini, S., Boissin, E., Poulain, J., Carradec, Q., Paz-García, D. A., Zoccola, D., Magalon, H., Moulin, C., Bourdin, G., Iwankow, G., Romac, S., Banaigs, B., Boss, E., ... Forcioli, D. (2022). Disparate patterns of genetic divergence in three widespread corals across a pan-Pacific environmental gradient highlights species-specific adaptation trajectories. *npj Biodiversity*, *2*, 15.
- Johnston, E. C., Forsman, Z. H., Flot, J.-F., Schmidt-Roach, S., Pinzón, J. H., Knapp, I. S. S., & Toonen, R. J. (2017). A genomic glance through the fog of plasticity and diversification in *Pocillopora*. *Scientific Reports*, *7*, 5991. <https://doi.org/10.1038/s41598-017-06085-3>
- Johnston, E. C., Forsman, Z. H., & Toonen, R. J. (2018). A simple molecular technique for distinguishing species reveals frequent misidentification of Hawaiian corals in the genus *Pocillopora*. *PeerJ*, *6*, e4355.
- Kang, J.-H., Lim, H. J., Kang, H.-S., Lee, J.-M., Baby, S., & Kim, J.-J. (2013). Development of genetic markers for triploid verification of the Pacific oyster, *Crassostrea gigas*. *Asian-Australasian Journal of Animal Sciences*, *26*, 916–920.
- Kuanui, P., Chavanich, S., Raksasab, C., & Viyakarn, V. (2008). Lunar periodicity of larval release and larval development of *Pocillopora damicornis* in Thailand: 11.
- Lauffkötter, C., Zscheischler, J., & Fröhlicher, T. L. (2020). High-impact marine heatwaves attributable to human-induced global

- warming. *Science*, 369, 1621–1625. <https://doi.org/10.1126/science.aba0690>
- Lavorel, S., McIntyre, S., Landsberg, J., & Forbes, T. D. A. (1997). Plant functional classifications: From general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution*, 12, 474–478.
- López-Pérez, A., Granja-Fernández, R., Benítez-Villalobos, F., & Jiménez-Antonio, O. (2017). Pocillopora damicornis-associated echinoderm fauna: Richness and community structure across the southern Mexican Pacific. *Marine Biodiversity*, 47, 481–490.
- Marti-Puig, P., Forsman, Z. H., Haverkort-Yeh, R. D., Knapp, I. S. S., Maragos, J. E., & Toonen, R. J. (2014). Extreme phenotypic polymorphism in the coral genus *Pocillopora*; micro-morphology corresponds to mitochondrial groups, while colony morphology does not. *Bulletin of Marine Science*, 90, 211–231.
- Mayfield, A. B., Chen, Y.-J., Lu, C.-Y., & Chen, C.-S. (2018). The proteomic response of the reef coral *Pocillopora acuta* to experimentally elevated temperatures. *PLoS One*, 13, e0192001.
- Mayfield, A. B., Fan, T. Y., & Chen, C. S. (2013). Physiological acclimation to elevated temperature in a reef-building coral from an upwelling environment. *Coral Reefs*, 32, 909–921. <https://doi.org/10.1007/s00338-013-1067-4>
- McWilliam, M., Pratchett, M. S., Hoogenboom, M. O., & Hughes, T. P. (2020). Deficits in functional trait diversity following recovery on coral reefs. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20192628.
- Noreen, A. M. E., Schmidt-Roach, S., Harrison, P. L., & van Oppen, M. J. H. (2015). Diverse associations among coral host haplotypes and algal endosymbionts may drive adaptation at geographically peripheral and ecologically marginal locations. *Journal of Biogeography*, 40, 1639–1650.
- Oury, N., Gélín, P., & Magalon, H. (2020). Together stronger: Intracolony genetic variability occurrence in *Pocillopora* corals suggests potential benefits. *Ecology and Evolution*, 10, 5208–5218. <https://doi.org/10.1002/ece3.5807>
- Oury, N., Noël, C., Mona, S., Aurelle, D., & Magalon, H. (2023). From genomics to integrative species delimitation? The case study of the Indo-Pacific *Pocillopora* corals. *Molecular Phylogenetics and Evolution*, 184, 107803. <https://doi.org/10.1016/j.ympev.2023.107803>
- Pante, E., Puillandre, N., Viricel, A., Arnaud-Haond, S., Aurelle, D., Castelin, M., Chenuil, A., Destombe, C., Forcioli, D., Valero, M., Viard, F., & Samadi, S. (2015). Species are hypotheses: Avoid connectivity assessments based on pillars of sand. *Molecular Ecology*, 24, 525–544.
- Phongsuwan, N., & Chansang, H. (2012). Repeated coral bleaching in the Andaman Sea, Thailand, during the last two decades. *Phuket Marine Biological Center Research Bulletin*, 71, 19–41.
- Pinzón, J. H., & Lajeunesse, T. C. (2011). Species delimitation of common reef corals in the genus *Pocillopora* using nucleotide sequence phylogenies, population genetics and symbiosis ecology. *Molecular Ecology*, 20, 311–325.
- Pinzón, J. H., Sampayo, E., Cox, E., Chauka, L. J., Chen, C. A., Voolstra, C. R., & Lajeunesse, T. C. (2013). Blind to morphology: Genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *Journal of Biogeography*, 40, 1595–1608.
- Poquita-Du, R., Ng, C. S. L., Loo, J. B., Afiq-Rosli, L., Tay, Y. C., Todd, P., Chou, L. M., & Huang, D. (2017). New evidence shows that *Pocillopora* 'damicornis-like' corals in Singapore are actually *Pocillopora acuta* (Scleractinia: Pocilloporidae). *Biodiversity Data Journal*, 5, e11407.
- Poquita-Du, R. C., Quek, Z. B. R., Jain, S. S., Schmidt-Roach, S., Tun, K., Heery, E. C., Chou, L. M., Todd, P. A., & Huang, D. (2019). Last species standing: Loss of Pocilloporidae corals associated with coastal urbanization in a tropical city state. *Marine Biodiversity*, 49, 1727–1741.
- Putchim, L., Phongsuwan, N., Yaemarnpattana, C., Thongtham, N., & Richter, C. (2017). Long-term changes in the susceptibility of corals to thermal stress around Phuket, Thailand. *PeerJ Preprints*. <https://doi.org/10.7287/peerj.preprints.2979v1>
- Rinkevich, B. (2019). Coral chimerism as an evolutionary rescue mechanism to mitigate global climate change impacts. *Global Change Biology*, 25, 1198–1206.
- Rinkevich, B., Shaish, L., Douek, J., & Ben-Shlomo, R. (2016). Venturing in coral larval chimerism: A compact functional domain with fostered genotypic diversity. *Scientific Reports*, 6, 19493.
- Robitzsch, V., Banguera-Hinestroza, E., Sawall, Y., Al-Sofyani, A., & Voolstra, C. R. (2015). Absence of genetic differentiation in the coral *Pocillopora verrucosa* along environmental gradients of the Saudi Arabian Red Sea. *Frontiers in Marine Science*, 2, 1–10.
- Rozas, J., Ferrer-Mata, A., Sanchez-DelBarrio, J. C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S. E., & Sanchez-Gracia, A. (2017). DnaSP 6: DNA sequence polymorphism analysis of large data sets. *Molecular Biology and Evolution*, 34, 3299–3302.
- Schmidt-Roach, S., Lundgren, P., Miller, K. J., Gerlach, G., Noreen, A. M. E., & Andreakis, N. (2013). Assessing hidden species diversity in the coral *Pocillopora damicornis* from Eastern Australia. *Coral Reefs*, 32, 161–172.
- Schmidt-Roach, S., Miller, K. J., Lundgren, P., & Andreakis, N. (2014). With eyes wide open: A revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia: Pocilloporidae) using morphology and genetics. *Zoological Journal of the Linnean Society*, 170, 1–33.
- Schmidt-Roach, S., Miller, K. J., Woolsey, E., Gerlach, G., & Baird, A. H. (2012). Broadcast spawning by *Pocillopora* species on the great barrier reef. *PLoS One*, 7, e50847.
- Smith, H. A., Moya, A., Cantin, N. E., van Oppen, M. J. H., & Torda, G. (2019). Observations of simultaneous sperm release and larval planulation suggest reproductive assurance in the coral *Pocillopora acuta*. *Frontiers in Marine Science*, 6, 362.
- Souter, P. (2010). Hidden genetic diversity in a key model species of coral. *Marine Biology*, 157, 875–885. <https://doi.org/10.1007/s00227-009-1370-3>
- Souter, P., Henriksson, O., Olsson, N., & Grahn, M. (2009). Patterns of genetic structuring in the coral *Pocillopora damicornis* on reefs in East Africa. *BMC Ecology*, 9, 1–13.
- Stecher, G., Tamura, K., & Kumar, S. (2020). Molecular evolutionary genetics analysis (MEGA) for macOS. *Molecular Biology and Evolution*, 37, 1237–1239.
- Stephens, T. G., Strand, E. L., Putnam, H. M., & Bhattacharya, D. (2023). Ploidy Variation and Its Implications for Reproduction and Population Dynamics in Two Sympatric Hawaiian Coral Species. *Genome Biology and Evolution*, 15(8). <https://doi.org/10.1093/gbe/evad149>
- Sutthacheep, M., Yucharoen, M., Klinthong, W., Pengsakun, S., Sangmanee, K., & Yeemin, T. (2013). Impacts of the 1998 and 2010 mass coral bleaching events on the Western Gulf of Thailand. *Deep Sea Research Part II: Topical Studies in Oceanography*, 96, 25–31.
- Thomas, L., Kendrick, G., Stat, M., Travaille, K., Shedrawi, G., & Kennington, W. (2014). Population genetic structure of the *Pocillopora damicornis* morphospecies along Ningaloo Reef, Western Australia. *Marine Ecology Progress Series*, 513, 111–119.
- Todd, P. A. (2008). Morphological plasticity in scleractinian corals. *Biological Reviews*, 83, 315–337.
- Torres, A. F., Forsman, Z. H., & Ravago-Gotanco, R. (2020). Shifts in coral clonality along a gradient of disturbance: Insights on reproduction and dispersal of *Pocillopora acuta*. *Marine Biology*, 167, 161.

- Torres, A. F., & Ravago-Gotanco, R. (2018). Rarity of the “common” coral *Pocillopora damicornis* in the western Philippine archipelago. *Coral Reefs*, 37, 1209–1216.
- Tun, K., Chou, L. M., Low, J., Yeemin, T., Phongsuwan, N., Setiasih, N., Wilson, J., Amri, A. Y., Abdul Adzis, K. A., Lane, D., van Bochove, J.-W., Kluskens, B., Long, N. V., Tuan, V. S., & Gomez, E. (2010). A regional overview on the 2010 CORAL bleaching event in Southeast Asia. In *Page status of coral reefs in east Asian seas region: 2010*. Global Coral Reef Monitoring Network.
- Veron, J. E. N. (2000). *Coral reefs of the world*. Page Australian Institute of Marine Science (AIMS).
- Veron, J. E. N., & Pichon, M. (1976). *Scleractinia of Eastern Australia, part 1*. Australian Institute of Marine Science (AIMS), Australian Government Publishing Service.
- Ying, L., Sinutok, S., Pramneechote, P., Aiyarak, P., Ralph, P. J., & Chotikarn, P. (2021). Physiological responses of *Pocillopora acuta* and *Porites lutea* under plastic and fishing net stress. *Frontiers in Marine Science*, 8, 712214.
- Yoder, M., Tandingan De Ley, I., King, I. W., Mundo-Ocampo, M., Mann, J., Blaxter, M., Poiras, L., & De Ley, P. (2006). DESS: A versatile solution for preserving morphology and extractable DNA of nematodes. *Nematology*, 8, 367–376.
- Zhou, L., & Gui, J. (2017). Natural and artificial polyploids in aquaculture. *Aquaculture and Fisheries*, 2, 103–111.

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