Genetic diversities of commercially harvested jellyfish, *Rhopilema hispidum* and *Lobonemoides robustus* in Southeast Asia

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**Abstract:** The rhizostome jellyfishes, *Rhopilema hispidum* and *Lobonemoides robustus*, are two of the most abundant and commercially important species in Southeast Asia. However, information on genetic diversity and continuities among local populations remains totally unknown. We explored the genetic structure and population continuities of *R. hispidum* and *L. robustus* using genetic markers (COI & ITS1 regions) at 11 locations in four countries in Southeast Asia where fisheries were conducted. *Rhopilema* populations showed genetic distances ($\Phi_{ST}$) among locations correlated positively with geographic distances, suggesting that they are in the isolation-by-distance (IBD). In *Lobonemoides*, molecular analysis revealed three distinct clades corresponding to sampling locations. Genetic distances among locations in *L. robustus* suggested that all populations maintain significant isolation. Our study reveals that these two blooming species have different phylogeographic patterns and differ in genetic diversity and continuities. Eustatic sea level changes during the Pleistocene and present ocean current systems, as well as differences in biological characteristics of these two species may explain these phylogeographic differences. Our results also suggest that jellyfish fisheries need to be carefully managed to avoid extinction of local populations and maintain the genetic diversity of these species, especially for *L. robustus*, which exhibits considerable genetic diversity in each location.

**Key words:** Jellyfish bloom, Jellyfish fisheries, Phylogeography, Sundaland, Southeast Asia

**Introduction**

Mass occurrences of jellyfish have been reported in various regions of the world (Brotz et al. 2012), although glob-
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2000, Omori & Nakano 2001, Omori & Kitamura 2004, Nishikawa et al. 2008, Nishikawa et al. 2009, Richardson et al. 2009, Nishida & Nishikawa 2011, López-Martínez & Álvarez-Tello 2013, Fujii et al. 2014, Gul et al. 2015, Nishikawa et al. 2015, Brotz & Pauly 2017, Nishikawa et al. 2019, Behera et al. 2020).

*Rhopilema hispidum* (Vanhöffen, 1888) and *Lobonemoides robustus* Stiasny, 1920 are two of the most commercially important jellyfish species in Southeast Asia (Nishikawa et al. 2008, Kitamura & Omori 2010, Nishikawa et al. 2019). *Rhopilema hispidum* is distributed from temperate to tropical zones in the Indo-West Pacific from Japan, China, and Southeast Asia to Pakistan and the Red Sea. It is harvested in Vietnam, Thailand, Malaysia, and Pakistan (Omori & Nakano 2001, Nishikawa et al. 2008, Kitamura & Omori 2010, Gul & Morandini 2015, Nishikawa et al. 2019). On the other hand, *L. robustus* occurs mainly in the tropical zone from the Bay of Bengal to Southeast Asia, and is harvested in Malaysia, Thailand, Myanmar, and the Philippines (Kramp 1961, Kitamura & Omori 2010, Nishida & Nishikawa 2011, Kondo et al. 2014, Nishikawa et al. 2019). Both species bloom in various parts of Southeast Asia, contributing significantly to local and regional economies (Nishikawa et al. 2008, 2019). However, genetic diversity of local populations and geographic continuity of these species have not been well examined. Nonetheless, such information is needed not only to better understand mechanisms of bloom formation, but also to guide conservation of these commercially harvested species.

Southeast Asia has some of the highest biological diversity in the world (Hoeksema 2007, Bellwood et al. 2012), and it has been suggested that this reflects complex geological history (Hall 2002). In particular, the glacial cycle during the Pleistocene caused significant sea-level changes, resulting in the appearance of land-bridges, i.e., Sundaland (Voris 2000), which limited dispersion of marine organisms between the Indian and Pacific Oceans, promoting not only speciation, but also differentiation at the cryptic species level. After the glacial period, population dispersion resulted in overlapping populations and high diversity in the two regions (Hoeksema 2007, Gaither & Rocha 2013).

The aim of this study was to clarify genetic structures of local populations of these two blooming jellyfish species and to quantify genetic continuity among populations in Southeast Asia. Biological and physical processes that may have shaped spatial patterns of genetic diversity are also discussed.

**Materials and Methods**

**Sample collection and DNA extraction**

Jellyfish tissues were sampled at 11 locations in four countries in Southeast Asia from 2010 to 2018 (Fig. 1, Table 1). At each location/time, adult jellyfish were collected with a scoop net from a fisherman’s boat or a chartered boat at blooming locations. In addition to sampling at sea, jellyfish tissues were also sampled at ports where fishing boats return. Tissue samples of exumbrellas or oral-arms were taken and preserved in 99% ethanol and frozen at −30°C until DNA extraction. Due to the high water-content in jellyfish, ethanol used for tissue preservation...
### Table 1

List of sample information and mitochondrial molecular indices for two species: locations, site abbreviation, year, map coordinates, sample size of mitochondrial DNA (mtDNA) and nuclear DNA (nDNA), and indices diversity. Site abbreviation is corresponding to Fig. 1.

| Location                  | Site abbreviation | Year | Latitude (N) | Longitude (E) | Sample size | mtDNA          | nDNA          | Indices diversity of mitochondrial DNA |
|---------------------------|-------------------|------|--------------|---------------|-------------|----------------|---------------|----------------------------------------|
| **Rhopilema hispidum**    |                   |      |              |               |             |                |               |                                        |
| Malaysia                  | Kukup             | MK   | 2011         | 1°19'32.94"   | 103°26'36.42" | 36            | 13            | 0.794 $\pm$ 0.066 0.506 $\pm$ 0.309 |
| Thailand                  | Songkhla          | TS   | 2013         | 7°13'17.97"   | 100°37'19.22" | 32            | 5             | 0.750 $\pm$ 0.068 0.359 $\pm$ 0.236 |
| Phetchaburi              |                   | TP   | 2010, 2016   | 13°1'23.35"   | 100°5'5.17"   | 28            | 15            | 0.783 $\pm$ 0.079 0.351 $\pm$ 0.233 |
| Si Racha & Ang Sila      |                   | TSA  | 2010, 2016   | 13°9'28.92"   | 100°54'13.14" | 30            | 12            | 0.749 $\pm$ 0.084 0.341 $\pm$ 0.227 |
| Vietnam                  | Do Son            | VD   | 2011         | 20°43'14.04"  | 106°47'35.58" | 29            | 7             | 0.879 $\pm$ 0.040 0.351 $\pm$ 0.233 |
| Do Son                   |                   | VD2  | 2016         | 13°1'21.7"    | 100°44'44.1"  | 32            | 8             | 0.829 $\pm$ 0.052 0.259 $\pm$ 0.183 |
| Vietnam                  | Thanh Hoa         | VT   | 2011         | 19°43'14.82"  | 105°53'18.18" | 2             | 1             | 1.000 $\pm$ 0.500 0.197 $\pm$ 0.278 |
| **Lobonemoides robustus**|                   |      |              |               |             |                |               |                                        |
| Malaysia                  | Bako              | MB   | 2015         | 1°39'52.91"   | 110°25'51.97" | 37            | 27            | 0.647 $\pm$ 0.090 0.196 $\pm$ 0.146 |
| Thailand                  | Phetchaburi       | TP   | 2016         | 13°1'21.7"    | 100°04'44.1"  | 8             |               | 0.786 $\pm$ 0.151 1.063 $\pm$ 0.645 |
| Phetchaburi              |                   | TP2  | 2018         | 13°1'21.7"    | 100°04'44.1"  | 20            |               | 0.926 $\pm$ 0.041 1.174 $\pm$ 0.646 |
| Suk Samran               |                   | TA   | 2011         | 9°22'56.47"   | 98°23'29.17"  | 31            | 27            | 0.630 $\pm$ 0.102 0.147 $\pm$ 0.120 |
| Philippines              | Lagen Island      | PL   | 2015, 2017   | 11°4'33.54"   | 119°24'34.72" | 42            | 25            | 0.824 $\pm$ 0.055 0.566 $\pm$ 0.331 |
| Carigara Bay             |                   | PC   | 2013         | 11°22'53.06"  | 124°39'48.71" | 6             |               | 0.600 $\pm$ 0.215 0.880 $\pm$ 0.575 |

$h =$ Haplotype diversity  
$\pi% =$ Nucleotide diversity
was replaced with new 99% ethanol several times. DNA was extracted using the protocol described in Iida et al. (2021).

**Mitochondrial DNA (mtDNA) analysis**

MitDNA cytochrome oxidase c subunit I (COI) fragments from *Rhoplema h isp idum* were amplified using LCO1490 and HCO2198 (Folmer et al. 1994). *Lobonemoides robustus* COI genes were amplified using newly-designed primers (LorCOL: 5′-TTT GGC GCC TCC TCG GCC ATG-3′, LorCOH: 5′-TCC TGC AGG GTC AAA GAA AG-3′). Polymerase chain reactions (PCR) of *R. hispidum* and *L. robustus* were carried out using a T100 Thermal Cycler (BioRad) under the following conditions: initial denaturation at 95°C for 2 min, followed by 30–35 cycles of 95°C for 30 s, 50–55°C for 30 s, 72°C for 1.5 min, and a final extension at 72°C for 5 min. The PCR reaction mixture was composed of 1.5 µL forward and reverse primers (10 µM), 1.5 µL 10× EX buffer, 1.5 µL dNTP, 0.075 µL Ex Taq HS, 7.425 µL PCR grade water, and 1.5 µL template DNA. PCR products were visualized on 2% agarose gels stained with MIDORI Green Direct (Nippon Genetics Co., Ltd.).

PCR products were purified using Exo-Sap IT (Affymetrix) and directly sequenced using BigDye terminator kit because of unclear sequences obtained. ITS1 fragments had insertions/deletions at two positions (Fig. S1). Thus, newly-designed primers LorITS1F1 (5′-CGG AAG GAT CAT TAC CGA AC-3′) and LorITS1R1 (5′-CAG TCC TCG GTC AGT AAG TCA G-3′), and LorITS1F2 (5′-GCC ACT GTG AAC TTG TAC CC-3′) and LorITS1R2 (5′-CGG AGA GCC GAG AGG TG-3′, Blacket et al. 2012) tails, and reverse primers included a pig-tail (5′-GTT TCT T-3′, Brownstein et al. 1996) to obtain the sharp fragment peaks. PCR for fragment analysis was carried out in a total volume of 10 µL containing 5.35 µL DW, 1 µL 10× EX buffer, 1 µL dNTP, 0.2 µL two forward primers (5 µM), 0.4 µL two reverse primers (5 µM), 0.2 µL FAM and PET primer, 0.05 µL Ex Taq HS and 1 µL template DNA. PCR was carried out at 95°C for 3 min followed by 45 cycles of 95°C for 30 s, 59°C for 30 s, 72°C for 30 s, and final extension at 72°C for 5 min. Fragment size was scored using 500 LIZ size standards and checked with Peak Scanner ver. 3.0.2.

**Data analysis**

Nucleotide sequences were checked by eye and edited using MEGA ver. 6 (Tamura et al. 2013). The number of haplotypes was checked with FaBox (Villesen 2007), and haplotype networks were constructed using statistical parsimony in TCS ver. 1.21 (Clement et al. 2000). Haplotype (h) and nucleotide (π%) diversities were calculated in Arlequin ver. 3.5 (Excoffier & Lischer 2010). Genetic differentiation between locations was examined with pairwise ΦST values using 1,000 permutations in Arlequin, and significance levels for multiple comparisons were adjusted using the Bonferroni correction. In addition, tests for population expansion based on Tajima’s D and a mismatch distribution analysis, which identifies characteristic ‘waves’ in the shape of the distribution resulting from population expansion (Rogers & Harpending 1992) were carried out in Arlequin. For the COI of *R. hispidum*, the relationship between geographic distance (coastline) and genetic distance (ΦST) was examined with a Mantel test. In *L. robustus*, the genetic distances among MB, TA, and PL with more than 30 samples were calculated with the Kimura 2-Parameter model (K2P, Kimura 1980) using MEGA ver. 6. These analyses excluded VT because the sample size at VT was too small.

The allele network of the ITS1 gene region for *R. hispidum* was constructed with TCS. On the other hand, ITS1 fragments for *L. robustus* were genotyped with a Peak Scanner ver. 3.0.2 (ABI). Hierarchical Bayesian clustering analysis with STRUCTURE ver. 2.3.4 (Pritchard et al. 2000) was performed using the admixture model with uncorrelated allele frequencies. The most likely number of clusters was tested based on probabilities of K=1 to 11. Each replicate run consisted of 10,000 Markov chain
Monte Carlo (MCMC) samples and a burn-in of 10,000 iterations. Structure Harvester ver. 0.6.93 (Earl & von Holdt 2012) was used to determine the most likely value of K, based on the largest LnP (D).

**Results**

**Rhopilema hispidum**

In *R. hispidum*, mitochondrial COI sequences (509 bp) obtained from 189 individuals revealed 48 haplotypes from six locations in Southeast Asia (Fig. 2A). Network analysis of COI haplotypes showed two distinct clades. The main clade (Clade Ra) showed a star-shaped network composed of an ancestral haplotype separated by one-mutation haplotypes. The smaller clade (Clade Rb) was composed mostly of individuals in Malaysia (MK). Individuals collected from two locations in Vietnam (VD, VD2, VT) were not included. Haplotype (h) and nucleotide (π%) diversity ranged from 0.749 (TSA) to 0.879 (VD), and from 0.259 (VD2) to 0.506 (MK), respectively (Table 1).

Population-pairwise $\Phi_{ST}$ values in *R. hispidum* ranged from $-0.005$ (VD vs. VD2) to $0.145$ (MK vs. VD2, Table 2A). Populations in Vietnam (VD and VD2) showed significant differences from those in MK and TS (Bonferroni corrections, $p < 0.05$). Genetic distances among locations were significantly correlated with geographic distances (Spearman’s rank coefficient test, $\rho = 0.718$, $p < 0.01$. Fig. 3). Tajima’s $D$ was significantly negative ($D = -2.291$, $p < 0.001$). The observed mismatch distribution analysis of all samples did not differ significantly from the distribution expected for a recent population expansion model (Sum of Squared deviation $S = 0.005$, $p = 0.051$, Harpending’s Raggedness index $hr = 0.039$, $p = 0.404$). However, the mismatch distribution analysis of each population, VD and VD2 differed significantly (VD: $S = 0.016$, $p = 0.010$, $hr = 0.115$, $p = 0.010$. VD2: $S = 0.012$, $p = 0.006$, $hr = 0.116$).

**Table 2.** Population-pairwise $\Phi_{ST}$ values of COI from *Rhopilema hispidum* (A) and *Lobonemoides robustus* (B).

|       | MK  | TS  | TP  | TSA | VD  |
|-------|-----|-----|-----|-----|-----|
| MK    | 0.067|     |     |     |     |
| TS    | 0.063| 0.007|     |     |     |
| TP    | 0.073| 0.012| -0.01|     |     |
| VD    | 0.135*| 0.053*| 0.035| 0.036|     |
| VD2   | 0.145*| 0.060*| 0.038| 0.038| -0.005|

|       | MB  | TP  | TP2 | TA  | PL  |
|-------|-----|-----|-----|-----|-----|
| MB    |     |     |     |     |     |
| TP    | 0.302**|   |     |     |     |
| TP2   | 0.329**| -0.036|     |     |     |
| TA    | 0.753**| 0.467**| 0.377**|     |     |
| PL    | 0.876**| 0.794**| 0.767**| 0.869**|     |
| PC    | 0.879**| 0.633**| 0.609**| 0.882**| 0.717**|

* $p < 0.05$, ** $p < 0.001$

Following Bonferroni corrections for Type I errors.

![Fig. 2. Parsimony COI haplotype networks of (A) *Rhopilema hispidum* and (B) *Lobonemoides robustus*. Sizes of circles are proportional to haplotype frequencies and circle colors indicate their geographic origins (Fig. 1). Each branch represents a one-nucleotide mutation. Small, empty circles symbolize hypothetical haplotypes. Site abbreviations correspond to Fig. 1 and Table 1.](image)

![Fig. 3. Mantel test of relationships between pairwise $\Phi_{ST}$ values and geographic distances (coastal line) for *Rhopilema hispidum* COI. Significant correlation was shown (Spearman’s rank coefficient test, $\rho = 0.718$, $p < 0.01$).](image)
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$p = 0.006$. Fig. S2A). MK did not differ significantly ($S = 0.034$, $p = 0.274$, $hr = 0.066$, $p = 0.634$), but it showed a bimodal distribution (Fig. S2A). On the other hand, the mismatch distribution analysis for Thailand showed no significant difference ($S > 0.002$, $p > 0.570$, $hr > 0.021$, $p > 0.928$; Fig. S2A).

In the ITS1 region of R. hispidum, five alleles based on the 349-bp nucleotide sequence were detected from 59 individuals (Fig. 4). ITS1 haplotypes showed no differences between locations or clades.

**Lobonemoides robustus**

*Lobonemoides robustus* specimens were collected at Bako, Malaysia (MB), Phetchaburi (TP, TP2) and Suk Samran (TA) in Thailand, Lagen Island (PL) and Carigara Bay (PC) in the Philippines (Fig. 1, Table 1). Most fishing grounds of this species were different from those of *R. hispidum*, except for Phetchaburi, Thailand where both species are harvested and processed. Mitochondrial COI sequences (568 bp) of *L. robustus* obtained from 144 individuals revealed 57 haplotypes from five locations (Fig. 2B). Network analysis of COI haplotypes showed three major, distinct clades. Clade La included mainly Bako, Malaysia (MB). Clade Lb consisted of Suk Samran, Thailand (TA), and Clade Lc consisted mainly of Legan Island, Philippines (PL). Clade La and -b exhibited star-shaped networks. Haplotype ($h$) and nucleotide ($\pi$ %) diversities ranged from 0.600 (PC) to 0.824 (PL), and from 0.147 (TA) to 1.174 (TP2), respectively (Table 1). In *L. robustus*, population-pairwise $\Phi_{ST}$ calculated for all pairs of samples ranged from $-0.036$ (TP vs. TP2) to $0.882$ (TA vs. PC, Table 2B). All locations paired except for TP and TP2, which were significantly different (Bonferroni corrections, $p < 0.001$). Tajima’s $D$ showed that MB and TA were significantly negative ($p < 0.05$). Mismatch distribution analysis was carried out for MB, TA, TP2, and PL. Although there was no significant difference between observed and expected distributions ($p > 0.16$), PL showed a bimodal distribution (Fig. S2B). Genetic distances (K2P) based on COI sequences between locations were as follows: 3.26±0.69% between MB and PL, 3.09±0.65% between TA and PL, and 0.828±0.30% between MB and TA.

**Discussion**

Two sets of genetic markers, mtDNA COI and nDNA ITS1, were used in this study. While these markers are often used in studies of population genetics targeting rhizostome jellyfish, lower genetic mutation rates in ITS1 than those in COI have been reported (Stopar et al. 2010, Ramšak et al. 2012, Dong et al. 2016). In *L. robustus*, our newly-designed primer sets enabled PCR to obtain sequences for COI and ITS1, and both genetic markers...
showed similar patterns with regard to genetic isolation.

Ranges of haplotype diversity in *R. hispidum* and *L. robustus* were similar to those reported in other rhizostome species (see Table S1, Dawson & Hamner 2005, Ramšak et al. 2012, Lee et al. 2013, Glynn et al. 2015, Dong et al. 2016, Gotoh et al. 2017). On the other hand, nucleotide diversity in *L. robustus* was higher than in other species (Table S1), which probably reflects the divergent clades in this species (Fig. 2B).

In *R. hispidum*, genetic distances (ΦST) among locations correlated positively with geographic distances, suggesting that this species may be in the state of isolation-by-distance (IBD, Wright 1943, Slatkin 1993) in Southeast Asia. On the other hand, Clade Rb, which differs by two mutations from Clade Ra, is composed of haplotypes from a part of Malaysia (MK) and Thailand (TS, TP, and TAS). Mismatch-distribution analysis showed a bimodal shape in MK, which implies that secondary contact has occurred between differentiated clades (Fig. S2A). Although the origin of Clade Rb is unknown, due to the limited geographic coverage of our study, it may have been introduced from another region, such as the Indian Ocean, where this species occurs (Omori & Nakano 2001, Omori & Kitamura 2004, Nishikawa et al. 2008, Gulp & Morandini 2015). Mismatch-distribution analysis for Thailand showed no significant differences, suggesting that those populations have experienced rapid population growth in the past. This result may reflect bottlenecks due to environmental changes (discussed below) and subsequent population growth and dispersal. In the ITS1 region, differences in genetic structure between locations or clades were less obvious because of the low mutation rate.

In contrast to the results for *R. hispidum*, genetic distance (ΦST) values in *L. robustus* exhibited significant differentiation among all locations studied. This local independence in genetic structure was also supported by nDNA results. In COI, mutations between Clade La, composed mainly of the Malaysian population (MB), and Clade Lb, composed of the Andaman Sea population (TA), were low, and the K2P genetic distance between MB and TA was approximately 1%. On the other hand, Clade Lc, composed of PL, contained relatively many mutations, and K2Ps between PL and other locations (MB and TA) were ~3%. In previous studies, K2P genetic distances within species in the Medusozoa are <5.7% (Ortman et al. 2010). Also, detailed morphological comparisons of individuals between TP and PL showed no clear differences in several characters examined (Iida et al. unpalish). These results suggest that local genetic differences observed in this species are intra-specific variation rather than inter-specific, although further detailed morphological examination, including from other sampling locations, is needed.

In this study, *R. hispidum* and *L. robustus* showed different phylogeographic patterns. While *R. hispidum* exhibited a population in equilibrium (i.e., IBD state) throughout the sampling locations, *L. robustus* appears genetically isolated in each location. The oceans, including the coastal environment of Southeast Asia, have been affected by repeated changes in the marine environment during glacial and interglacial cycles of the Pleistocene (ca. 2.5 Ma–10 Ka) (Jankov et al. 2007, Bowen et al. 2016, Choo et al. 2021). In the Southeast Asian region, during glacial periods, the shallow continental shelf was exposed, accompanied by low sea-levels, forming land bridges through the Indonesian Archipelago, known as Sundaland (Fig. 1B, Voris 2000). During the appearance of Sundaland, seawater exchange between the Indian and Pacific Oceans was limited, and the South China Sea was more influenced by freshwater from large rivers and lakes (Voris 2000, Sathi-amurthy & Voris 2006). These environmental changes may have affected the distribution not only of medusae, but also of polyps, which lived by attaching themselves to substrates such as sea floors and acted as a population bottleneck. During the low sea-level period, *R. hispidum* populations in various locations rapidly colonized the South China Sea (Fig. 1B). On the other hand, the appearance of Sundaland seems to have split local populations of *L. robustus* into three regions. Although the number of sampling locations in this study was relatively limited, differences in blooming locations and migration patterns between two species with eustatic changes during the Pleistocene may be one cause for their different genetic structures.

Sundaland may have facilitated allopatric divergence in both species from the Indian and Pacific Oceans, and this may have affected the *R. hispidum* and *L. robustus* populations in the Andaman Sea, which formed Clades Rb and Lb. After the low sea-level period, both species may have dispersed to their present ranges, and populations of both species in the Andaman Sea and the South China Sea mixed in the area around the Malay Peninsula. Genetic differentiation and sister species have been reported in several other marine organisms due to separation of the Indian and Pacific Ocean by Sundaland (Fleminger 1986, Benzie 1998, Gaither & Rocha 2013).

Clade Lc in *L. robustus*, composed mainly by the individuals from the Philippines, showed a distant and complex haplotype network, suggesting populations with a long evolutionary history (Fig. 2B). In the mismatch distribution analysis, PL did not show any significant difference between the measured and the estimated values of population expansion. Therefore, PL may have experienced secondary contacts with different populations (Fig. S2B). A biogeographical barrier called Huxley’s line has been reported in the east part of Palawan Island, Philippines (Fig. 1B, Huxley 1868). There were no extensive continental shelves, and there were large rivers in the eastern part of Huxley’s line; thus, environmental changes east of Huxley’s line may have been more limited than those along the Sunda Shelf (Kakioka et al. 2018). Clade Lc of *L. robustus*, composed of populations near Huxley’s line, may also have expanded from refugia near the Philippines. In
addition, a longnose seahorse, *Hippocampus trimaculatus* Leach, 1814, showed higher genetic diversity in the Philippine-Australia lineage, suggesting that it was divided into smaller, isolated populations and subject to drift (Lourie & Vincent 2004).

The contrasting genetic structures of the two blooming jellyfish species, revealed in this study, may also have been caused by oceanographic conditions during the Holocene and by their dispersal abilities. Strong and seasonally reversed current systems driven by the monsoon occur in Southeast Asia (Fig. 1A, Wyrki 1961). Most blooming locations, i.e., fishery grounds of *R. hispidum*, are located in an area where strong seasonal currents occur. *Rhopilema* populations in the upper Gulf of Thailand (TSA, TP) and southwest part of the Gulf (TS) share similar genetic compositions (Table 2A), suggesting that reversed currents driven by monsoon winds transported and mixed populations on both sides of the Gulf. According to local fishermen, the appearance of jellyfish in the Gulf of Thailand is associated with monsoon winds, and empirically, jellyfish are caught in large numbers on the west coast during the northeast monsoon and in the east or deepest part of the Gulf during the southwest monsoon (Nishikawa et al. 2019). In contrast, at locations where *L. robustus* is collected, currents are not as strong as those in the range of *R. hispidum* (Fig. 1A), which may weaken dispersal of the species. In situ measurements of swimming speeds of *R. hispidum* and *L. robustus* showed differences in their swimming abilities (*R. hispidum*: 4.05 ± 2.13 m min⁻¹, *L. robustus*: 2.45 ± 2.00 m min⁻¹. Kondo et al. unpublished). This could also affect dispersal ability, and thus genetic structure. On the other hand, there seem to be some differences in the environmental preferences for the somatic growth of polyps between *R. hispidum* and *L. robustus*. Our preliminary laboratory experiments indicate that *R. hispidum* polyps show higher growth at lower temperatures and higher salinities than *L. robustus* (Iida et al. in preparation). These differences in biological characteristics may be associated with the genetic patterns of the two jellyfish species. However, biological/ecological information on these species is very limited.

Mechanisms of bloom formation may be inferred from the present genetic results for the two fishery species. In previous studies, two main mechanisms of bloom formation were suggested: (1) life cycle and suitable environmental conditions (true bloom) or (2) temporary or transient chemical or physical phenomena (apparent bloom, Graham et al. 2001, Hamner & Dawson 2009). In this study, *L. robustus* showed low gene flow, with independent genetic structures maintained within each location. This suggests that blooms are formed by each local population, not elsewhere; thus, these are “true blooms.” In contrast, *R. hispidum* exhibits relatively high genetic continuity between locations. It is difficult to conclude that blooms in this species are formed by local populations. These jellyfish must be transported from other locations in “apparent blooms”. Different fishing seasons corresponding to different geographic areas may be attributed to transportation of jellyfish by currents (Table S2, Omori & Kitamura 2004, Nishikawa et al. 2008, Nishida & Nishikawa 2011, Nishikawa et al. 2019).

*Rhopilema hispidum* and *Lobonemoides robustus* are both commercially harvested in various locations in Southeast Asia. In northern Vietnam, 0.8–1.2 million *R. hispidum* were caught during a single fishing season (Nishikawa et al. 2008). Since 1997, the global catch of this jellyfish exceeds 500,000 tons annually (Brotz et al. 2017). In spite of this high fishing pressure based on increasing demands for edible jellyfish, no resource management of these two jellyfish is currently being attempted in Southeast Asia. Our results suggest that jellyfish fisheries, especially for *L. robustus*, which exhibits considerable location-based genetic diversity, need to be carefully managed to avoid extinction of local populations and to maintain genetic diversity of this species, as well as to achieve sustainable fisheries.

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