Journal of the Marine Biological Association of the United Kingdom

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Original Article

Cite this article: Kondo Y, Suzuki Y, Ohtsuka S, Nagai H, Tanaka H, Srinui K, Miyake H, Nishikawa J (2020). Differences in the cnidomes and toxicities of the oral arms of two commercially harvested rhizostome jellyfish species in Thailand. *Journal of the Marine Biological Association of the United Kingdom* **100**, 701–711. https://doi.org/10.1017/S002531542000065X

Received: 11 March 2020
Revised: 30 June 2020
Accepted: 13 July 2020
First published online: 25 August 2020

Key words:
Cnidome; lethality; nematocyst; rhizostome; tubule

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Differences in the cnidomes and toxicities of the oral arms of two commercially harvested rhizostome jellyfish species in Thailand

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Abstract

In Thailand, two species of rhizostome jellyfish, *Rhopilema hispidum* and *Lobonemoides robustus*, are commercially harvested. The cnidomes, nematocyst size and toxicities were compared between these species. *Rhopilema hispidum* and *L. robustus* each had four types of nematocysts on their oral arms. For *R. hispidum*, these nematocyst types included two types of isorhiza and two types of rhopaloid, while in *L. robustus*, there were three types of isorhiza and one type of rhopaloid. For *R. hispidum*, tubule lengths of the largest nematocyst type (large round isorhiza; mean ± SD = 313.8 ± 62.2 µm) were significantly longer than those of *L. robustus* (large ellipsoid rhopaloid; 162.1 ± 38.5 µm). Using the freshwater shrimp, *Palaemon paucidens*, in a bioassay, we determined that the lethal nematocyst concentrations for *R. hispidum* and *L. robustus* were 5705.3 ± 1118.1 and 3408.3 ± 1032.9 unit g^{-1} wet weight, respectively, and that these concentrations were significantly higher in the former than in the latter.

Introduction

Jellyfish are characterized by their possession of nematocysts (Mariscal, 1974; Hessinger & Lenhoff, 1988; Schuchert, 1993; Kass-Simon & Scappaticci, 2002; Marques & Collins, 2004; Technau *et al*., 2015; Morandini *et al*., 2016). Nematocysts consist of a capsule and an eversible tubule, and are classified into more than 30 morphological types (Östman, 2000). Nematocysts, which contain various proteinaceous toxins, are used to capture prey, and for defence against enemies, such as medusivorous fish (Ates, 1988; Arai, 1997). When the jellyfish's tentacles contact a prey organism, the nematocysts discharge their tubules to sting the prey, thus injecting the toxin into the target's tissues (Burke, 2002). Nematocysts are harmful not only to marine organisms, but also to humans; those of some species are highly dangerous and cause serious health problems to beachgoers and fishers worldwide (Purcell *et al*., 2007). In particular, many fishers suffer stings by jellyfish (Ghosh *et al*., 1990; Al-Rubiay *et al*., 2009; Palmieri *et al*., 2014). They are stung when removing jellyfish from the fishing net during operations (Dong *et al*., 2010; Lucas *et al*., 2014; Palmieri *et al*., 2014). Victims can die in the worst cases (Li *et al*., 2014).

Jellyfish fisheries are intensively exploited in the world's oceans (Kingsford *et al*., 2000; Omori & Nakano, 2001; Omori & Kitamura, 2004; Nishikawa *et al*., 2008, 2015, 2019; Richardson *et al*., 2009; Nishida & Nishikawa, 2011; López-Martínez & Álvarez-Tello, 2013; Fujii *et al*., 2014; Gul *et al*., 2015; Brotz *et al*., 2017; Behera *et al*., 2020). The main target of catch is rhizostome jellyfish, which are used in Chinese cuisine (Kingsford *et al*., 2000; Omori & Nakano, 2001). According to the fisheries statistics of the Food and Agriculture Organization (FAO, 2018), recent annual world jellyfish catches have been more than 500,000 metric tons. China has the highest annual jellyfish catch rate worldwide, followed by the South-east Asian countries, including Thailand, Indonesia, Malaysia and Vietnam (Kingsford *et al*., 2000; Omori & Nakano, 2001; Nishikawa *et al*., 2008, 2015, 2019; Nishida & Nishikawa, 2011; FAO, 2018). Worldwide, at least 17 species of rhizostomes have so far been known as main target species: *Acromitus hardenbergi* Stiasny, 1934; *Cassiopea ndrosia* Agassiz & Mayer, 1899; *Catostylus mosaicus* (Quoy & Gaimard, 1824); *Catostylus perezi* Ranson, 1945; *Cephea cephea* (Forskål, 1775); *Crambione mastigophora* Maas, 1903; *Crambionella annadalei* Rao, 1931; *Crambionella helmbiru* Nishikawa, Mulyadi & Ohtsuka, 2014; *Crambionella orsini* (Vanhöffen, 1888); *Crambionella stuhlmanni* (Chun, 1896); *Lobonema smithi* Mayer, 1910; *Lobonemoides robustus* Stiasny, 1920; *Nemopilema nomurai* Kishinouye, 1922; *Rhizostoma pulmo* (Macri, 1778); *Rhopilema esculentum* Kishinouye, 1891; *Rhopilema hispidum* (Vanhöffen, 1888); *Stomolophus meleagris* Agassiz, 1860 (Brotz, 2016). Of these, *N. nomurai* and *R.*

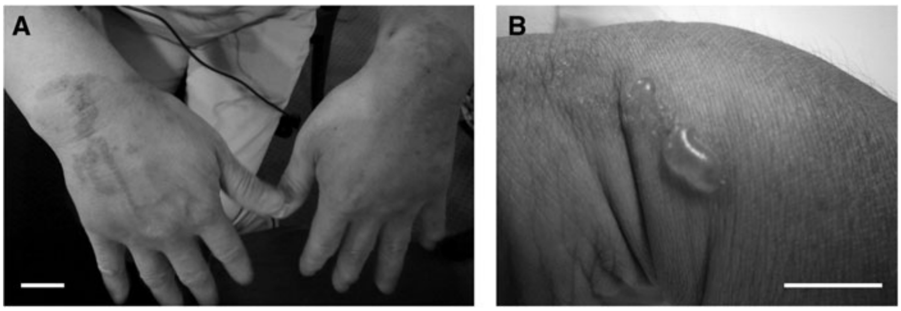

Fig. 1. Dermatitis caused by *Rhopilema hispidum* on 1 July 2013: (A) dermatitis on the backs of a woman's hands; (B) oedema on a man's wrist. Scale bars: A, 3 cm; B, 1 cm.

pulmo have been reported to cause health problems from stings to fishers (Purcell *et al.*, 2007; Mariottini & Pane, 2010). Rhizostome stings are generally reported as mild skin inflammation (Fenner, 1993); however, they can also cause severe health hazards such as erythematous eruption, oedema and burn-like injuries (Figure 1), which have been reported in *Acromitus rabanchatu* Annandale, 1915, *Rhopilema nomadica* Galil, Spanier & Ferguson, 1990, *R. pulmo*, *R. hispidum*, *N. nomurai* and *S. meleagris* (Burnett & Calton, 1985; Galil *et al.*, 1990; Ghosh *et al.*, 1990; Othman *et al.*, 1996; Williamson *et al.*, 1996; Kokelj & Plozzer, 2002; Fenner, 2005; Kawahara *et al.*, 2006; Remigante *et al.*, 2018; present study).

In Thailand, two species are mainly targeted by fisheries: *R. hispidum* and *L. robustus* (Omori & Nakano, 2001; Ohtsuka *et al.*, 2010; Nishida & Nishikawa, 2011; Nishikawa *et al.*, 2019). Both species are distributed in the Gulf of Thailand, while only *L. robustus* appears in the Andaman Sea (Nishikawa *et al.*, 2019). Othman *et al.* (1996) reported that *R. hispidum* nematocysts exhibited toxicity, haemolytic activity and a relaxant effect on phenylephrine-induced smooth muscle contractions in rat aortas. In contrast, *L. robustus* nematocysts have never been analysed toxicologically. This study examined the cnidomes and toxicities

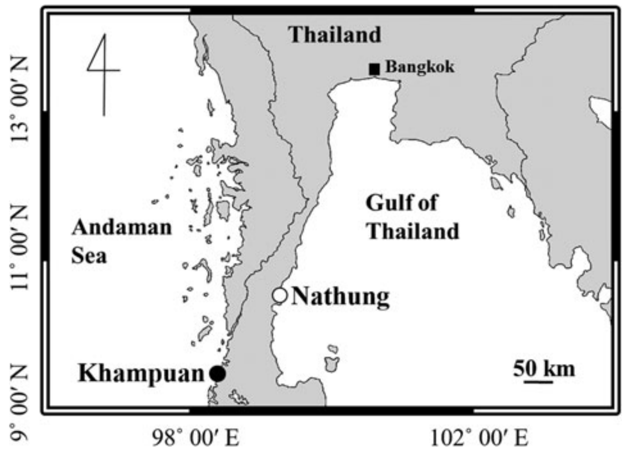

Fig. 2. Sampling sites of jellyfish in Thailand. Open circle and closed circle indicate sampling sites of *Rhopilema hispidum* and *Lobonemoides robustus*, respectively.

of these two species of commercially harvested rhizostome jellyfish in Thailand. The current information on the nematocysts and toxicities of rhizostome jellyfish is insufficient compared with that on other jellyfish (Calder, 1972; Kawahara *et al.*,

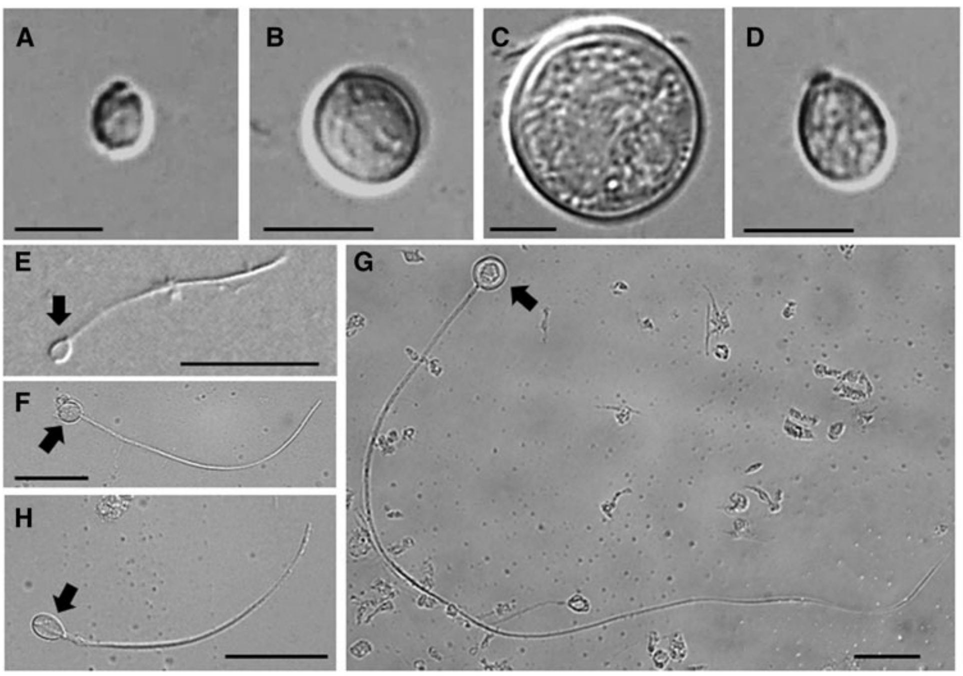

Fig. 3. Nematocysts of the oral arm of *Rhopilema hispidum* collected from the coastal area of Nathung, Thailand on 4 December 2014: (A) undischarged small ellipsoid isorhiza; (B) undischarged medium round isorhiza; (C) undischarged large round isorhiza; (D) undischarged rhopaloid; (E) discharged small ellipsoid isorhiza; (F) discharged medium round isorhiza; (G) discharged large round isorhiza; (H) discharged rhopaloid. Scale bars: A–D, 5 µm; E–H, 20 µm. Capsule indicated by arrow.

https://doi.org/10.1017/S002531542000065X Published online by Cambridge University Press

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Table 1. Size of nematocysts in the oral arms of *Rhopilema hispidum.*

Individual number		No. 1			No. 2			No. 3			
		BD (cm)	WW (kg)	Sex	BD (cm)	WW (kg)	Sex	BD (cm)	WW (kg)	Sex	
		38.5	4.56	♀	39.0	6.01	♀	57.9	12.64	♀	
Nematocyst type (Number of nematocysts examined)		Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Average
Small ellipsoid isorhiza (N = 10)	Capsule length (μm)	3.5	5.0	4.1 ± 0.4	3.5	6.1	4.5 ± 0.8	3.7	5.3	4.4 ± 0.6	4.3 ± 0.6
	Capsule width (μm)	2.6	3.4	2.9 ± 0.2	2.5	3.5	2.8 ± 0.4	2.1	3.5	2.9 ± 0.4	2.9 ± 0.4
	Tubule length (μm)	26.4	54.8	44.5 ± 8.5	30.1	54.5	45.7 ± 7.7	20.5	77.2	38.1 ± 15.7	42.8 ± 11.3
Medium round isorhiza (N = 10)	Capsule length (μm)	5.4	7.2	6.3 ± 0.5	5.6	6.7	6.2 ± 0.3	5.0	7.6	6.3 ± 0.7	6.3 ± 0.5
	Capsule width (μm)	4.7	6.4	5.8 ± 0.5	5.3	6.3	5.8 ± 0.3	5.0	7.1	5.8 ± 0.7	5.8 ± 0.5
	Tubule length (μm)	50.3	94.4	70.2 ± 12.6	61.5	90.7	74.6 ± 9.1	64.5	95.5	77.5 ± 9.3	74.1 ± 10.5
Large round isorhiza (N = 10)	Capsule length (μm)	12.6	15.1	13.8 ± 0.8	13.3	15.6	14.8 ± 0.8	12.2	15.0	13.9 ± 1.0	14.1 ± 1.0
	Capsule width (μm)	10.4	13.3	12.3 ± 0.8	11.6	15.0	13.2 ± 0.9	11.0	14.9	13.0 ± 1.2	12.8 ± 1.0
	Tubule length (μm)	233.7	329.5	295.7 ± 29.1	249.2	416.9	353.2 ± 60.0	209.8	414.0	292.6 ± 73.7	313.8 ± 62.2
Rhopaloid (N = 10)	Capsule length (μm)	6.0	7.5	6.9 ± 0.5	5.3	6.9	6.3 ± 0.5	6.0	7.1	6.6 ± 0.4	6.6 ± 0.5
	Capsule width (μm)	3.8	4.8	4.5 ± 0.4	4.0	4.8	4.4 ± 0.3	4.3	5.0	4.6 ± 0.2	4.5 ± 0.3
	Tubule length (μm)	55.7	94.7	72.7 ± 13.1	40.7	100.0	67.0 ± 19.1	58.7	96.7	73.1 ± 11.7	70.9 ± 14.7

BD, bell diameter; WW, wet weight.

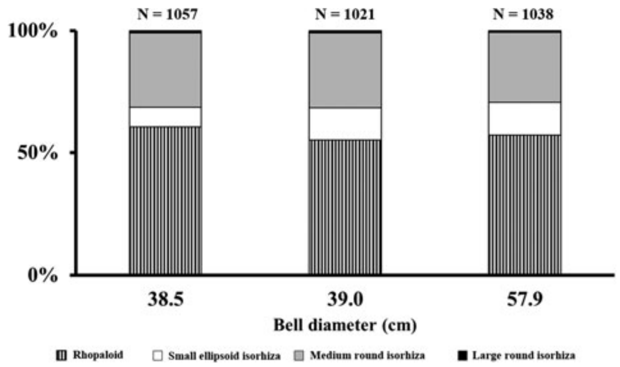

Fig. 4. Nematocyst compositions and proportions from *Rhopilema hispidum* collected from the coastal area of Nathung, Thailand on 4 December 2014.

2006). The purpose of this study is to accumulate basic data to prevent sting injuries caused by jellyfish.

Materials and methods

Cnidomes

Rhopilema hispidum and *L. robustus* were collected from the coastal areas of Khampuan, Suksamran District, Ranong Province (9°21′43″–9°23′27″N 98°22′49″–98°23′33″E) and Nathung, Muang District, Chumphon Province (10°29′30″–10°29′52″N 99° 14′42″–99°15′32″E), Thailand, on 3 and 4 December 2014, respectively (Figure 2). Each jellyfish was scooped with a 2-mm mesh scoop net with a long handle of ~1.5 m. The bell diameters and wet weights of the captured jellyfish were measured *in situ* immediately after collection. The marginal parts of the oral arms from each jellyfish were excised from fresh individuals, using clean scissors for cnidome analysis and toxicity bioassays.

To examine the cnidomes from each jellyfish species, a small piece of the oral arm was cut off with scissors and immersed in vinegar to discharge the nematocysts (Birsa *et al.*, 2010), then subsequently fixed in 5% neutralized formalin/seawater. Approximately 1000 nematocysts per individual were counted and classified by type, capsule size and shape following Östman (2000) under an optical microscope BX53 (Olympus Corporation, Hachioji, Tokyo, Japan). The sizes and tubule lengths of the discharged nematocysts were measured using a microscope digital camera DP21 (Olympus Corporation, Hachioji, Tokyo, Japan) and image-processing software ImageJ, version 1.48 (Wayne Rasband National Institutes of Health, USA). In two species, 10 nematocysts of each type per individual were examined to measure the capsule lengths, widths and tubule lengths. The capsule size of each nematocyst type was compared using a Tukey test and Welch's *t*-test in R, version 3.0.1 (R Core Team, 2016). The differences in tubule lengths between *R. hispidum* and *L. robustus* were also analysed via Welch's *t*-test in R, version 3.0.1. Capsule volumes were estimated following Purcell (1984) based on capsule length and width from previous and present studies. The correlation between capsule volume and tubule length was determined using Spearman's rank correlation coefficient test in R, version 3.0.1.

Toxicity

Marginal parts from the oral arms of the two jellyfish species were used in the toxicity bioassays. Oral arm parts were frozen on dry

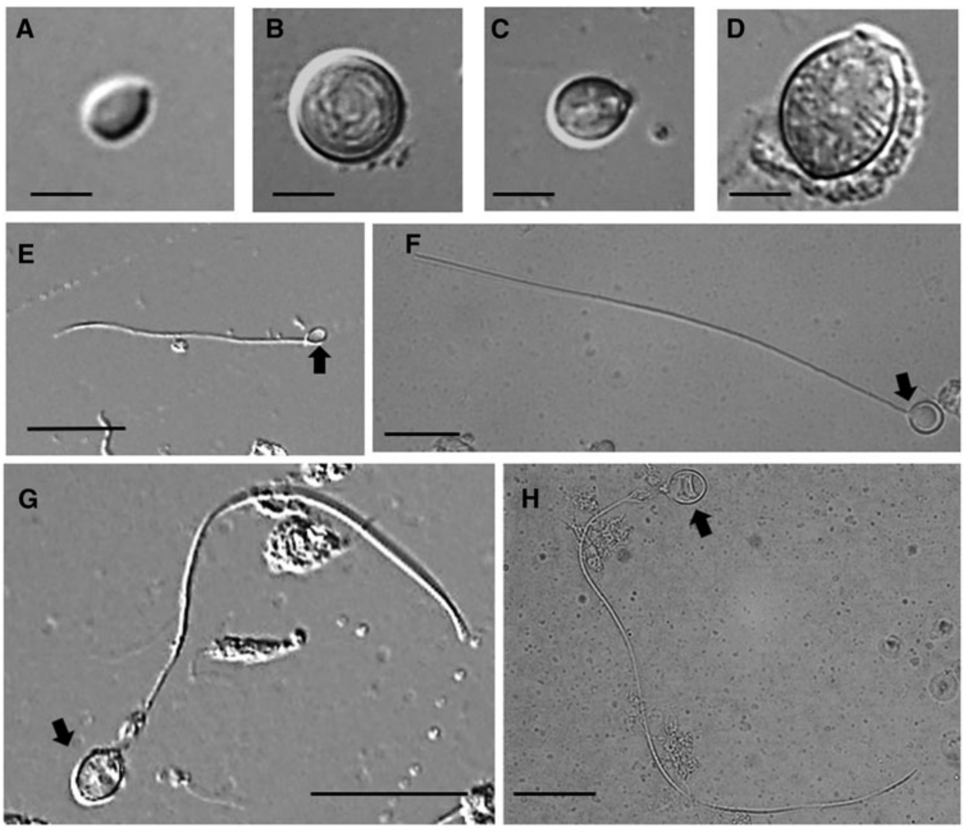

Fig. 5. Nematocysts from the oral arms of *Lobonemoides robustus* collected from the coastal area of Khampuan, Thailand on 3 December 2014: (A) undischarged small ellipsoid isorhiza; (B) undischarged large round isorhiza; (C) undischarged small ellipsoid rhopaloid; (D) undischarged large ellipsoid rhopaloid; (E) discharged small ellipsoid isorhiza; (F) discharged large round isorhiza; (G) discharged small ellipsoid rhopaloid; (H) discharged large ellipsoid rhopaloid. Scale bars: A–D, 5 µm; E–H, 20 µm. Capsule indicated by arrow.

Table 2. Size of nematocysts in the oral arm of *Lobonemoides robustus*.

Individual number		No. 1			No. 2			No. 3			No. 4			
		BD (cm)	WW (kg)	Sex	BD (cm)	WW (kg)	Sex	BD (cm)	WW (kg)	Sex	BD (cm)	WW (kg)	Sex	
		40.2	7.76	♀	42.5	7.64	♂	45.8	10.56	♂	47.9	7.23	♀	
Nematocyst type (Number of nematocysts examined)		Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Average
Small ellipsoid isorhiza	Capsule length (μm)	3.1	4.7	4.0 ± 0.5	3.1	5.1	4.1 ± 0.7	3.6	5.2	4.4 ± 0.5	4.7	6.9	5.5 ± 0.8	4.5 ± 0.8
(N = 10)	Capsule width (μm)	2.5	3.9	2.9 ± 0.5	2.3	3.6	2.8 ± 0.4	2.6	4.0	3.1 ± 0.4	3.0	4.2	3.7 ± 0.4	3.1 ± 0.5
	Tubule length (μm)	28.7	72.1	47.5 ± 5.1	28.0	69.6	45.7 ± 14.2	28.4	90.4	49.8 ± 21.4	24.4	96.2	64.3 ± 25.8	51.8 ± 20.3
Large round isorhiza	Capsule length (μm)	7.9	9.2	8.6 ± 0.4	8.4	9.4	8.9 ± 0.5	8.0	10.2	9.1 ± 0.6	8.6	9.8	9.3 ± 0.4	9.0 ± 0.5
(N = 10)	Capsule width (μm)	6.7	8.9	7.8 ± 0.7	7.3	8.8	8.0 ± 0.5	6.7	9.0	7.9 ± 0.8	7.5	9.1	8.1 ± 0.5	8.0 ± 0.6
	Tubule length (μm)	80.7	205.2	111.7 ± 40.8	111.5	210.2	157.6 ± 33.3	98.8	160.4	116.5 ± 18.9	100.4	172.6	133.7 ± 24.7	129.9 ± 34.6
Small ellipsoid rhopaloid	Capsule length (μm)	6.2	8.1	7.3 ± 0.5	5.3	7.4	6.5 ± 0.7	6.3	7.1	6.7 ± 0.3	6.6	7.4	7.1 ± 0.3	6.9 ± 0.6
(N = 10)	Capsule width (μm)	4.6	6.3	5.2 ± 0.5	4.4	6.2	4.9 ± 0.5	4.4	6.0	5.1 ± 0.6	4.4	5.5	5.1 ± 0.5	5.1 ± 0.5
	Tubule length (μm)	53.5	116.1	70.8 ± 17.2	59.7	107.7	77.3 ± 18.8	49.7	98.1	76.2 ± 13.3	52.7	98.3	76.5 ± 11.9	75.2 ± 15.2
Large ellipsoid rhopaloid	Capsule length (μm)	9.0	15.0	11.1 ± 1.8	11.3	15.5	13.0 ± 1.5	9.2	15.1	11.9 ± 1.7	9.7	13.5	11.9 ± 1.1	12.0 ± 1.8
(N = 10)	Capsule width (μm)	7.2	9.5	8.1 ± 0.8	7.7	11.6	9.5 ± 1.3	7.4	11.9	9.3 ± 1.2	7.0	9.6	8.3 ± 1.0	8.8 ± 1.2
	Tubule length (μm)	104.2	175.4	149.5 ± 23.1	134.6	248.7	173.8 ± 34.4	114.0	275.0	164.5 ± 53.2	108.1	198.7	160.6 ± 39.1	162.1 ± 38.5

BD, bell diameter; WW, wet weight.

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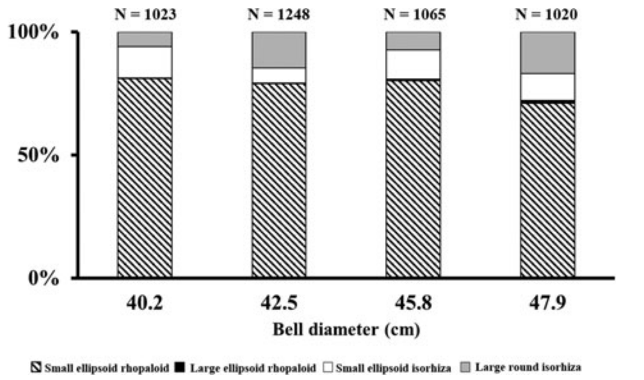

Fig. 6. Nematocyst compositions and proportions of *Lobonemoides robustus* collected from the coastal area of Khampuan, Thailand on 3 December 2014.

ice in the field, the wet weights were measured, and the arm parts were then lyophilized using a freeze-dryer FreeZone 6 (Labconco Corporation, Kansas City, USA) in the laboratory. The dry weights of the freeze-dried oral arms were recorded using an electronic scale PB602-S (Mettler Toledo International, Inc., Taito City, Tokyo, Japan), then homogenized with a spatula. The oral arm homogenate (mass ~0.10–0.25 g) was then placed in a 2-ml vial together with 1 ml of glass beads (diameter: 0.5 mm). The bottle was then filled with a 0.15 M NaCl 0.01 M phosphate buffer solution at pH 7.0. The bottle was placed in a homogenizer Mini-Beadbeater-1 (Bio Spec Products, Inc., Bartesville, USA) and run through 20 vibration cycles at 4800 rpm for 30 s, then cooled on crushed ice for 60 s. The samples were then moved to microtubes and run through two centrifugation cycles at 62,000 rpm for 30 s, then cooled for 30 s. The supernatant was recovered and diluted 1, 5, 10 and 15 times for *R. hispidum* and 1, 3, 5 and 7

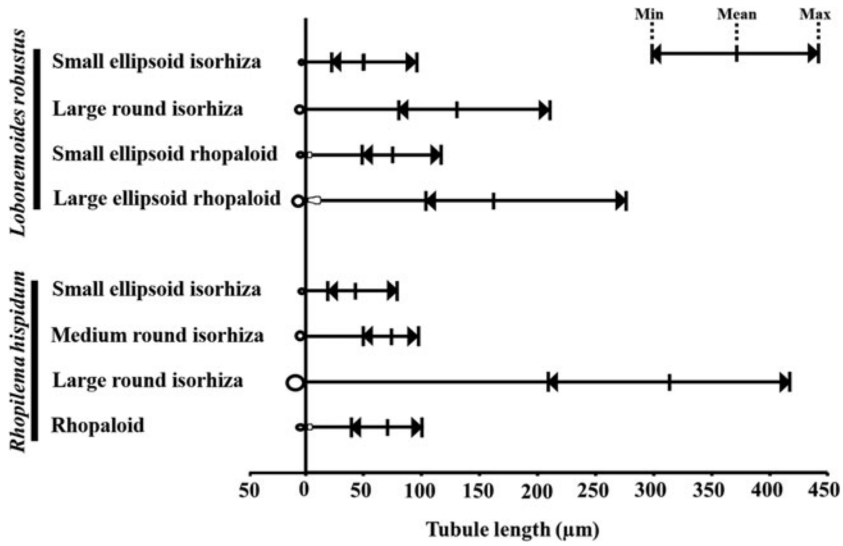

Fig. 7. Comparison of mean tubule length between *Rhopilema hispidum* and *Lobonemoides robustus*.

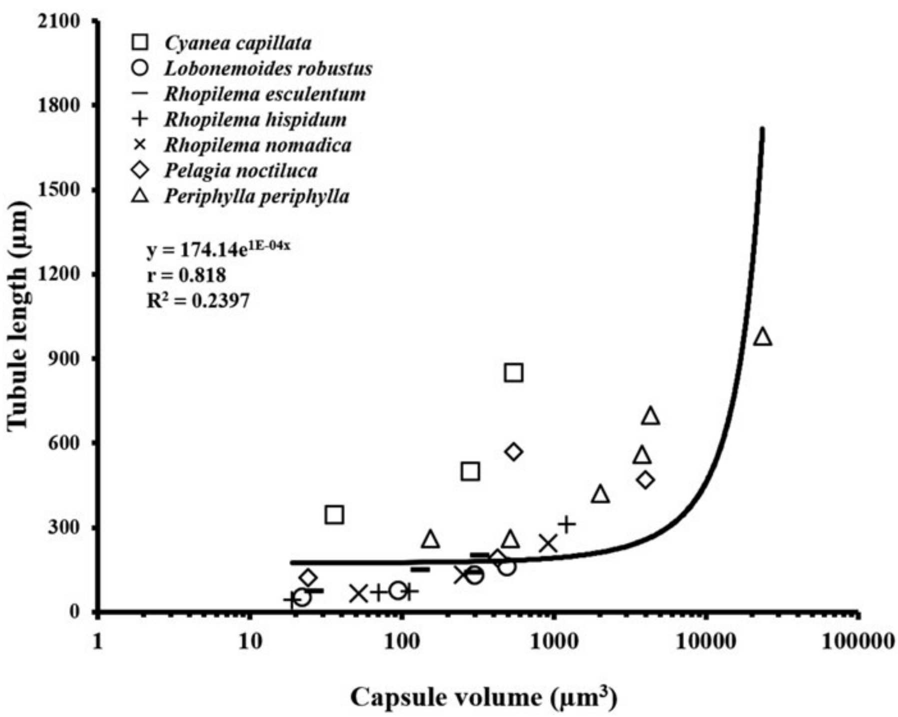

Fig. 8. Correlation between capsule volume and tubule length of nematocysts.

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Table 3. Types, capsule sizes, volumes and tubule lengths of scyphomedusae nematocysts.

Jellyfish	Nematocsyt type	Length (μm)	Width (μm)	Volume (μm³)	Tubule length (μm)	Reference
Aurelia aurita	Atrichous isorhiza	-	-	-	44.7 ± 30.2	Kitatani *et al.* (2015)
	Heterotrichous microbasic eurytele	-	-	-	51.2 ± 32.0	
	Unidentified nematocyst	-	-	-	34.1 ± 6.97	
Crysaora pacifica	Atrichous isorhiza	-	-	-	92.0 ± 42.5	Kitatani *et al.* (2015)
	Heterotrichous microbasic eurytele	-	-	-	133.3 ± 71.1	
	Unidentified nematocyst	-	-	-	87.9 ± 41.4	
Cyanea capillata	Basitrichous isorhiza	5.4 ± 0.84	3.55 ± 0.2	35.8*	220–470	Heeger *et al.* (1992)
	Holotrichous isorhiza	11.62 ± 1.21	9.41 ± 0.72	539.9*	< 850	
	Heterotrichous microbasic eurytele	10.35 ± 0.96	7.21 ± 0.53	282.7*	< 500	
Lobonemoides robustus	Small ellipsoid isorhiza	4.5 ± 0.8	3.1 ± 0.5	21.9*	51.8 ± 20.3	Present study
	Large round isorhiza	9.0 ± 0.5	8.0 ± 0.6	301.6*	129.9 ± 34.6	
	Small ellipsoid rhopaloid	6.9 ± 0.6	5.1 ± 0.5	94.0*	75.2 ± 15.2	
	Large ellipsoid rhopaloid	12.0 ± 1.8	8.8 ± 1.2	486.6*	162.1 ± 38.5	
Rhopilema esculentum	a-isorhiza	4.9	3.2	26.3*	75	Chen & Ding (1981)
	o-isorhiza	9.9	7.9	323.5*	200	
	e-isorhiza	10.5	4.9	132.0*	150	
	Eurytele	10.1	7.5	297.5*	140	
Rhopilema hispidum	Small ellipsoid isorhiza	4.3 ± 0.6	2.9 ± 0.4	18.9*	42.8 ± 11.3	Present study
	Medium round isorhiza	6.3 ± 0.5	5.8 ± 0.5	111.0*	74.1 ± 10.5	
	Large round isorhiza	14.1 ± 1.0	12.8 ± 1.0	1209.6*	313.8 ± 62.2	
	Rhopaloid	6.6 ± 0.5	4.5 ± 0.3	70.0*	70.9 ± 14.7	
Rhopilema nomadica	Small holotrichous isorhiza	5.57 ± 0.56	5.11 ± 0.38	51.34 ± 14.95	68.86 ± 16.31	Avian *et al.* (1995)
	Large holotrichous isorhiza	12.55 ± 0.97	10.82 ± 0.95	906.09 ± 207.63	247.25 ± 50.31	
	Heterotrichous microbasic eurytele	8.46 ± 1.20	6.26 ± 1.16	248.99 ± 97.00	134.28 ± 37.34	
Pelagia noctiluca	Heterotrichous microbasic eurytele	12.88 ± 0.9	8.90 ± 0.77	541.28 ± 110.97	570.05	Avian *et al.* (1991)
	Heterotrichous isorhiza	14.32 ± 1.40	7.48 ± 0.67	423.84 ± 89.26	190.02	
	Holotrichous O-isorhiza	20.82 ± 1.94	18.87 ± 1.91	3987.25 ± 1110.81	470.51	
	Atrichous a-isorhiza	5.03 ± 0.39	3.00 ± 0.27	23.93 ± 5.23	123.38	
Periphylla periphylla	Holotrichous isorhiza	11.3–15.6	7.3–9.8	516.4*	> 260	Jarms *et al.* (2002)
	Small holotrichous isorhiza	7.9	6.1	153.9*	> 260	
	Round heterotrichous microbasic eurytele	17.6–21.8	13–15	2021.7*	> 420	
	Long ellipsoid heterotrichous microbasic eurytele	16–62	13–16	4293.4*	> 700	
	Giant ellipsoid heterotrichous microbasic eurytele	38–100	24–27	23492.4*	800–1160	
	Short ellipsoid heterotrichous microbasic eurytele	21.8–25.8	16.3–18.5	3772.9*	> 560	

*, Volumes estimated following Purcell (1984) based on capsule length and width.

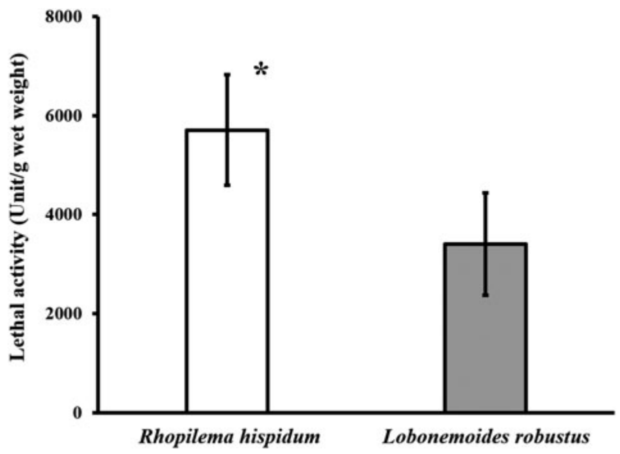

Fig. 9. Comparison of lethal activity between *Rhopilema hispidum* and *Lobonemoides robustus*. Asterisk indicates significant difference (Welch's *t*-test, $P < 0.05$).

times for *L. robustus* with a 0.15 M NaCl 0.01 M phosphate buffer solution at pH 7.0. For the lethality assay, the diluted solution was injected into the abdomens of three individual freshwater shrimp *Palaemon paucidens* De Haan, 1844 per each diluted concentration extracted from one individual jellyfish. The injection volume was calculated as 0.2 µl per 0.5 g of shrimp wet weight. Lethality (one unit) was defined as the minimum amount of venom that killed the tested shrimp within 4 h. The dilution ratio at which the shrimp died within 4 h was 5, 5, 10 times for *R. hispidum* and 3, 3, 3, 5 times for *L. robustus*, respectively. The shrimps injected with saline were used as a negative control to confirm that the shrimp did not die within 4 h. The lethality per gram of wet weight of the oral arm was formulated as follows:

Lethality per oral arm wet weight (unit g^{-1} wet weight) = lethality (unit)/homogenized oral arm (g) × [wet weight of fresh oral arm (g)/dry weight of freeze-dried oral arm (g)].

Differences in the toxicities between *R. hispidum* and *L. robustus* were tested via Welch's *t*-test in R, version 3.0.1.

Result

Cnidomes

Rhopilema hispidum cnidomes were composed of four nematocyst types: small ellipsoid isorhizas (Figure 3A, E), medium round isorhizas (Figure 3B, F), large round isorhizas (Figure 3C, G) and rhopaloids (Figure 3D, H) (Table 1). The average capsule dimensions were 4.3 ± 0.6 (length) × 2.9 ± 0.4 (width) µm (N = 30) for small ellipsoid isorhizas, 6.3 ± 0.5 × 5.8 ± 0.5 µm (N = 30) for medium round isorhizas, 14.1 ± 1.0 × 12.8 ± 1.0 µm (N = 30) for large round isorhizas, and 6.6 ± 0.5 × 4.5 ± 0.3 µm (N = 30) for rhopaloids (Figure 3A–H, Table 1). All three isorhiza capsule dimensions are significantly different (Tukey's test, $P < 0.05$). Tubule lengths were 42.8 ± 11.3 µm (N = 30) for small ellipsoid isorhizas, 74.1 ± 10.5 µm (N = 30) for medium round isorhizas, 313.8 ± 62.2 µm (N = 30) for large round isorhizas, and 70.9 ± 14.7 µm (N = 30) for rhopaloids (Table 1). The rhopaloids and medium round isorhizas were the major components of *R. hispidum* nematocysts, constituting 55.2–60.5% and 28.6–30.9%, respectively, irrespective of bell diameter (Figure 4). The small ellipsoid and large round isorhizas were less prevalent and comprised only 8.0–13.4% and 0.8–0.9% of the cnidomes, respectively (Figure 4).

Lobonemoides robustus cnidomes were also composed of four nematocyst types, but their compositions differed from those of *R. hispidum*: small ellipsoid isorhizas (Figure 5A, E), large round isorhizas (Figure 5B, F), small ellipsoid rhopaloids (Figure 5C, G) and large ellipsoid rhopaloids (Figure 5D, H) (Table 2). The average capsule dimensions were 4.5 ± 0.8 (length) × 3.1 ± 0.5 (width) µm (N = 40) for small ellipsoid isorhizas, 9.0 ± 0.5 × 8.0 ± 0.6 µm (N = 40) for large round isorhizas, 6.9 ± 0.6 × 5.1 ± 0.5 µm (N = 40) for small ellipsoid rhopaloids and 12.0 ± 1.8 × 8.8 ± 1.2 µm (N = 40) for large ellipsoid rhopaloids (Figure 5A–H, Table 2). There was a significant difference between the capsule dimensions of the two isorhizas (Welch's *t*-test, $P > 0.05$). The two rhopaloids are also significantly different (Welch's *t*-test, $P > 0.05$). The tubule lengths were 51.8 ± 20.3 µm (N = 40) for small ellipsoid isorhizas, 129.9 ± 34.6 µm (N = 40) for large round isorhizas, 75.2 ± 15.2 µm (N = 40) for small ellipsoid rhopaloids and 162.1 ± 38.5 µm (N = 40) for large ellipsoid rhopaloids (Table 2). The small ellipsoid rhopaloids were the most dominant nematocysts in *L. robustus*, constituting over 70% of the cnidome, irrespective of bell diameter (Figure 6). The small ellipsoid isorhizas and large round isorhizas comprised 6.3–12.8% and 5.9–17.0% of the total cnidome, respectively (Figure 6). The large ellipsoid rhopaloids comprised <1% of the nematocysts in the cnidome (Figure 6).

The tubule lengths of the most dominant nematocyst types did not differ significantly between *R. hispidum* (rhopaloids) and *L. robustus* (small ellipsoid rhopaloids) (Welch's *t*-test, $P > 0.05$) (Figure 7, Tables 1 and 2). However, tubule lengths of the large round isorhizas in *R. hispidum* were significantly longer than those of the large ellipsoid rhopaloids in *L. robustus* (Welch's *t*-test, $P < 0.05$) (Figure 7, Tables 1 and 2).

The capsule volume and tubule length of several scyphozoans were significantly positively correlated (Spearman's rank correlation coefficient test, $P < 0.05$, $r = 0.82$) (Figure 8, Table 3). The following equation was obtained from the relationship between capsule volume (x) and tubule length (y): $y = 174.14{\times}10^{-1E-04x}$.

Toxicity

In *R. hispidum*, the lethality per wet weight (g) of the oral arms ranged from 5020.0–6995.6 unit g^{-1} wet weight (mean ± SD = 5705.3 ± 1118.1 unit g^{-1} wet weight, N = 3). In *L. robustus*, the lethal activity ranged from 2871.5–4956.6 unit g^{-1} wet weight (3408.3 ± 1032.9 unit g^{-1} wet weight, N = 4) (Figure 9). The lethal activity of *R. hispidum* was significantly greater than that of *L. robustus* (Welch's *t*-test, $P < 0.05$).

Discussion

Scyphozoans, including rhizostomes, have fewer nematocyst types than do anthozoans and hydrozoans (Kubota, 1985; Purcell & Mills, 1988). In many scyphozoans, isorhizas and rhopaloids are the main components (Arai, 1997). *Rhopilema hispidum* and *L. robustus* cnidomes were also composed of isorhizas and rhopaloids. *Rhopilema hispidum* had three isorhiza types and one rhopaloid type, while *L. robustus* had two of each type. Othman *et al.* (1996) observed three nematocyst types (atrichous isorhizas, holotrichous isorhizas and heterotrichous microbasic euryteles) in *R. hispidum* tentacles. This differed from the nematocyst composition of the oral arm, suggesting that *R. hispidum* cnidomes vary among body parts. Previous studies have reported that rhizostome jellyfish have between two and five nematocyst types (Table 4). Mastigophores are rare (Table 4). Cnidomes from five species of the genus *Rhopilema* have been reported: *Rhopilema verrilli* (Fewkes, 1887) (Calder, 1972); *R. esculentum* (Chen & Ding, 1981); *R. hispidum* (Othman *et al.*, 1996; present study); *R. nomadica* (Avian *et al.*, 1995). Previous and present studies have revealed that cnidomes of the genus *Rhopilema*

https://doi.org/10.1017/S002531542000065X Published online by Cambridge University Press

Table 4. Capsule size of Rhizostomeae species nematocysts.

Jellyfish	Nematocyst type	Capsule length (μm)	Capsule width (μm)	Reference
Cassiopea andromeda	a-isorhiza	4.15–8.29	2.68–4.88	Heins *et al.* (2015)
	O-isorhiza	5.37–9.02	4.88–8.54	
	Rhopaloid	5.97–17.80	4.52–15.85	
	Lemon-shaped microbasic birhopaloid	4.63–9.27	2.93–5.85	
Catostylus mosaicus	Oval-shaped holotrichous isorhiza	3.9–4.8	2.9–3.4	Peach & Pitt (2005)
	Pear-shaped holotrichous isorhiza	5.8–8.7	2.4–3.0	
	Rhopaloid	7.1–9.3	4.9–6.6	
	Birhopaloid	14.0–15.9	9.5–10.2	
Lobonemoides robstus	Small ellipsoid isorhiza	3.1–6.9	2.3–4.2	Present study
	Large round isorhiza	7.9–10.2	6.7–9.1	
	Small ellipsoid rhopaloid	5.3–8.1	4.4–6.3	
	Large ellipsoid rhopaloid	9.0–15.5	7.0–11.9	
Nemopilema nomurai	Holotrichous anisorhiza	25.0–30.0	24.0–26.0	Kubota *et al.* (2006)
	Microbasic mastigophore	17.0–22.0	11.0–14.0	
	Large atrichous isorhiza	13.7–15.8	3.74–4.15	
	Small atrichous isorhiza	8.47–10.8	5.40–7.06	
Phyllorhiza punctata	Round holotrichous isorhiza	5.6–5.8	4.9	Peach & Pitt (2005)
	Oval holotrichous isorhiza	5.1–5.7	3.4–3.8	
	Medium rhopaloid	7.2–7.7	4.7–5.5	
	Large rhopaloid	12.5–14.7	8.4–10.9	
	Birhopaloid	13.5–14.6	10.0–10.5	
Rhizostoma octopus	Atrichous haploneme	3.5–6.5	2.3–5.3	Holst *et al.* (2007)
	Heterotrichous microbasic eurytele	5.8–10.2	4.1–7.8	
Rhizostoma plumo	Heterotrichous microbasic eurytele	5.9–8.0	3.5–6.0	Avian *et al.* (1991)
	Holotrichous isorhiza	3.0–4.0	2.0–2.5	
	Atrichous a-isorhiza	3.0–3.5	2.0–3.0	
	Atrichous α-isorhiza	3.3–4.0	1.1–1.4	
Rhopilema esculentum	a-isorhiza	2.9–7.5	2.0–5.0	Chen & Ding (1981)
	o-anisorhiza	5.9–15.0	3.9–12.5	
	e-anisorhiza	4.5–12.8	2.5–6.7	
	Eurytele	4.4–16.0	2.9–11.5	
Rhopilema hispidum	Small ellipsoid isorhiza	3.5–6.1	2.1–3.5	Present study
	Medium round isorhiza	5.0–7.6	4.7–5.0	
	Large round isorhiza	12.2–13.3	10.4–15.0	
	Rhopaloid	5.3–7.5	3.8–5.0	
Rhopilema nomadica	Small holotrichous isorhiza	4.20–8.50	2.90–5.56	Avian *et al.* (1995)
	Large holotrichous isorhiza	10.50–18.30	10.10–16.80	
	Heterotrichous microbasic eurytele	6.10–12.70	4.10–10.50	
Rhopilema verrilli	a-atrichous isorhiza	5.3–6.9	3.3–4.5	Calder (1972)
	Holotrichous haploneme (isorhiza or anisorhiza)	6.9–8.9	5.4–7.4	
	Microbasic heterotrichous eurytele	7.6–10.1	5.0–7.1	
Stomolophus meleagris	a-isorhiza	3.8–4.8	2.4–31.	Calder (1983)
	Small eurytele	6.4–10.1	4.5–6.5	
	Medium-large eurytele	10.5–12.6	7.3–9.0	
	Large eurytele	13.2–17.8	8.0–10.3	

https://doi.org/10.1017/S002531542000065X Published online by Cambridge University Press

mainly consist of isorhizas and rhopaloids (Table 4). The cnidome of *L. robustus* was first recorded in the rhizostome family, Lobonemidae. They have two nematocyst types, isorhizas and rhopaloids (present study). In both jellyfish species examined in this study, small nematocysts of >10 µm in capsule length dominated the oral arms cnidome, while relatively large nematocysts were rare. Similar cnidomes were found in other rhizostomes, such as *S. meleagris* (Calder, 1983), *R. nomadica* (Avian *et al.*, 1995), *C. mosaicus* and *Phyllorhiza punctata* von Lendenfeld, 1884 (Peach & Pitt, 2005).

The types and tubule lengths of scyphozoan nematocysts were compiled from previous studies (Table 3). The purple jellyfish, *Pelagia noctiluca* (Forsskål, 1775), is a highly venomous species, with nematocysts containing tubules longer than 400 µm (Avian *et al.*, 1991; Mariottini *et al.*, 2008). The lion's mane jellyfish, *Cyanea capillata* (Linnaeus, 1758), which occasionally causes serious damage to humans, has nematocysts with tubule lengths that reach ~850 µm (Heeger *et al.*, 1992). Kitatani *et al.* (2015) clarified that nematocyst tubule length is directly correlated with pain in humans; stings from longer tubules exert more severe pain. The average longest tubules in *R. hispidum* (313.8 µm) and *L. robustus* (162.1 µm) were longer than those in the harmful Japanese sea nettle, *Chrysaora pacifica* (Goette, 1886) (133.3 µm) (Yasuda *et al.*, 2003; Kitatani *et al.*, 2015; present study). Therefore, these two species of edible jellyfish can potentially cause damage in humans. Our results showed that the tubule lengths of the large round isorhizas in *R. hispidum* were significantly longer than those of the large ellipsoid rhopaloids of *L. robustus*, suggesting that *R. hispidum* is more harmful than *L. robustus*. Our lethality bioassay also showed that the toxicity of the former was approximately twice that of the latter. *Rhopilema hispidum* has longer tubules than do other *Rhopilema* species (Chen & Ding, 1981; Avian *et al.*, 1995; present study) (see Table 3). Othman *et al.* (1996), Williamson *et al.* (1996) and Kawahara *et al.* (2006) reported that *R. hispidum* caused considerable damage to human skin. In fact, when one of the authors and one of the aquarium staff were stung by *R. hispidum* in Thailand on 1 July 2013, dermatitis and oedema occurred on their hands (Figure 1). In contrast, *L. robustus* has not been observed to cause such severe damage since we first studied it in 2009. The nematocyst volume and tubule length were significantly positively correlated (Figure 8, Table 3). The tubule is helically coiled in the capsule before discharge (Avian *et al.*, 1991, 1995; Östman, 2000). Purcell (1984) suggested that large-volume capsules could accommodate longer tubules and could more effectively penetrate and capture prey animals. Jellyfish with large capsules and long tubules are highly likely to be dangerous species.

This study revealed the cnidomes and toxicities of two commercially harvested rhizostome jellyfish in Thailand. *Rhopilema hispidum* causes more severe symptoms because its toxicity is stronger than that of *L. robustus*. Fortunately, no fatal stings by rhizostomes have been reported in Thai waters (Fenner *et al.*, 2010). Stings from rhizostomes such as *Catostylus*, *Lobonema* and *Phyllorhiza* are usually relatively mild (Halstead, 1965; Williamson *et al.*, 1996; Marsh & Slack-Smith, 2010); however, the sting of *N. nomurai* has been reported to be fatal in the worst cases (Williamson *et al.*, 1996; Dong *et al.*, 2010; Kim *et al.*, 2018). Further research is needed, as toxicity varies by jellyfish species. This study is the first report to investigate the toxicity and cnidome of *L. robustus,* but the rhizostome toxicity information is insufficient. Understanding cnidome biology, toxins and jellyfish behaviour is important in preventing stings to fishers and beachgoers.

Acknowledgements. We thank the members of Enoshima Aquarium for providing us with the pictures. We would like to express our sincere thanks to Prof. Shuhei Nishida for encouragement throughout this study.

Financial support. This study was partially supported by grants from the Japan Society of Promotion of Science (JSPS), KAKEN (grant numbers 20380110, 25304031, 26304030 and 18K05688), and the Core to Core Program (B. Asia-Africa Science Platforms).

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