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Review of geographical distribution of dinoflagellate cysts in Southeast Asian coasts

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Abstract—Dinoflagellate cysts play an important role in the initiation, recurrence and geographical expansion of harmful algal blooms (HABs). The horizontal distribution and abundance of dinoflagellate cysts in marine sediments provide very essential information in giving early warnings of the presence of toxic species and possible continuing recurrence of HABs in a given area. A review of available bio-geographical information on dinoflagellate cyst assemblages and distributions from the surface sediments of the tropics and Southeast Asian (SEA) waters mainly on the context of HAB dynamics is also provided. Results of review on such studies revealed how cyst mapping activities contributed to understand HAB expansion in SEA region. *Pyrodinium bahamense* var. *compressum* cysts are the most common in the sediments of SEA region, explaining partly the relative wide occurrence of this PSP causative organism in the area. Cysts of *Alexandrium* spp. have also been found in some areas of the region, indicating the risk from the bloom of some toxic species of the genus. The factors and mechanisms of algal bloom expansion in the SEA region, involving the resting stage of causative HAB species, remain to be well understood. High priority should be given to continuing cyst mapping research in the entire SEA region, as the knowledge is so essential in comprehending HABs dispersal and occurrence thereby aiding in HABs management in the area.

Key words: dinoflagellate cyst, cyst mapping, harmful algal bloom, sediment dynamics, Southeast Asia

Introduction

Besides being important primary producers, and therefore an important part of the food chain, some dinoflagellate species are also known for producing lethal toxins and massive blooms, thus causing deleterious effects to human health, economy and a large range of marine life and ecosystem. The life cycle of dinoflagellates includes the dormant resting cyst or hypnozygote formed by sexual reproduction, which serve as protective mechanism against unfavourable conditions, such as nutrient depletion, grazing, competition, and high turbulence (Prakash 1967, Steidinger 1975, Dale 1983, Anderson 1989, Nehring 1993). Many previous experiments have shown that cysts of some species, notably that of *Alexandrium* spp., *Gonyaulax* spp. and *Pyrodinium bahamense* var. *compressum*, can remain vital for several years (Lewis et al. 1979, Dale 2001, Mizushima and Matsuoka 2004).

Of the roughly 2,000 identified motile marine dinoflagellates, there are fewer than 80 species have been known to be toxic (Taylor 1987, Turner and Tester 1989, Turner et al. 1998), while more than 200 species have been known to be cyst-producers (Head 1996, Matsuoka and Fukuyo 2000). These cysts may form a sort of "cyst deposits or seed beds" in sediments of coastal marine waters, which supply the initial inoculums to form plankton blooms once favourable conditions (mainly temperature) are re-established, although endogenous (internal clock, growth factors) and exogenous variables (vitamins, humic acids) could be involved (Pfiester and Anderson 1987). Dinoflagellate cysts are deposited to the sediments of the ocean floor where they undergo a mandatory period of quiescence until conditions are proper for germination to colonize previously unaffected areas (Anderson et al. 1983, 1994, Corrales et al. 1995, Azanza et al. 2004).

Cysts play an important role in the initiation of future plankton bloom and thus provide early warnings of the presence of toxic species in a given area (Anderson et al. 1983, Cembella et al. 1988, Ishikawa and Taniguchi 1996). Together with the wind and natural prevailing physical forces of the water such as tides and currents coupled with sediment transport due to various anthropogenic activities alongside the watersheds, cysts behave as silts and seem to be dispersed and expanded in different areas, which may commonly contaminate the unaffected coastal waters (Anderson et al. 1995). They are remarkably resilient and can survive during transportation in ship's ballast water, in the digestive tracts of spat oysters/mussels shipped from one region to another, and are preserved in sediment for years. Changes in ocean circulation patterns, disturbance of resting cyst populations, and dredging operations can move resting cysts to new regions which may be conducive to growth. Cyst deposits in the sediment also indicate termination of blooms (Steidinger 1975, Wall 1975, Lewis et al. 1979, Yentsch and Mague 1979, Heiskanen 1993). The toxic dinoflagellate cysts can also be a significant source of shellfish intoxication because their toxin content can be higher than the vegetative cells (Dale et al. 1978, Oshima et al. 1982, Schwinghamer et al. 1994). Moreover, variations in the species composition of cyst assemblages are significantly interpreted by palynologists in their studies of dinoflagellate ecology and biogeography for their paleoclimatic change interpretation (Wall et al. 1977, Dale 1983, Ellegaard et al. 1994).

A number of studies on the bio-geographical distribution and changes of dinoflagellate cyst assemblages have been mostly reported from temperate waters (Dale 2001, Head et al. 2001, Matsuoka 1999, Rochon et al. 1999). However, for the past decade, dinoflagellate cysts have been gradually studied in tropical coastal marine waters, mainly in the context of harmful algal bloom dynamics. Through a review of modern dinoflagellate cyst studies mainly carried out in Southeast Asian (SEA) region, we emphasize an importance of "Cyst Mapping" surveys for understanding HAB phenomena in this region.

Geographical distribution and abundance studies of dinoflagellate cysts with special reference to HAB species

The continued threats posed by HABs to wild and farmed fish and shellfish, marine mammals, marine ecosystem and human health cannot be ignored. These HAB phenomena have attracted serious attention from the governments, fisheries and eco-tourism industries, academe, research institutions and the public consumers because of its notorious records in bringing about economic losses in fisheries, human poisoning and even deaths. HAB events have become global and perennial problems as more toxic species, more algal toxins, larger affected areas and higher incidences of affected fisheries and subsequent economic losses are repeatedly reported (Hallegraeff 1993).

Alexandrium cohorticula, A. tamiyavanichii, A. minutum, A. tamarense, *Gymnodinium catenatum* and *Pyrodinium bahamense* var. *compressum* have been identified as causative species of paralytic shellfish poisoning (PSP) and HABs in the SEA region. Most of the above-mentioned dinoflagellate species produce resting cysts triggered by temperature or other environmental changes.

The spatial distributions and relative abundances of dinoflagellate cysts have been investigated in various modern sediments of tropical waters, including few studies conducted in SEA waters. The dinoflagellate cyst assemblages have been described from the Gulf of Thailand and East Coast of Peninsular Malaysia (Lirdwitayaprasit 1997), off Sabah, Sarawak and Brunei Darussalam waters (Lirdwitayaprasit 1998), Jakarta Bay, off Flores Island, Larantuka and off Udjung, Pandang, Indonesia (Matsuoka et al. 1999), off Mangalore, SW India (Godhe et al. 2000), Manila Bay (Furio 1995, Azanza et al. 2004), Sunda Shelf, South China Sea (Kawamura 2004), coastal waters of Sabah, Malaysia (Furio et al. 2006), Hurun and Kao Bays, Indonesia; estuary of Mekong River and off Nha Trang, Vietnam (Mizushima 2007), the mariculture areas in Pangasinan, NW Philippines (Baula et al. 2008); several basins and estuaries (Bolinao Bay, Malampaya Sound, Sorsogon Bay and Juag Lagoon) in the Philippines (Reotita et al. 2008). The available studies in the tropics of the SEA region as described above are summarized in Table 1 and Fig. 1.

Cyst diversity in Southeast Asia

The cyst assemblages present an overall relatively high diversity which vary from 13 to approximately 50 cyst-type taxa (Fig. 2) in the SEA sediments, where they are mostly dominated with undifferentiated morphotype 'round brown' cysts without processes *Protoperidinium* spp. (*Brigantedinium** spp.). (Species names marked with asterisk and enclosed in parentheses are in paleontological systematics.) These are accompanied mainly by the cysts of *Gonyaulax spinifera* complex (*Spiniferites** spp.), *Lingulodinium polyedrum* (*Lingulodinium machaerophorum**), *P. bahamense* var. *compressum* (*Polysphaeridium zoharyii**), *Protoceratium reticulatum* (*Operculodinium centrocarpum**), *Protoperidinium denticulatum* (*Brigantedinium irregulare**), *P. leonis* (*Quenquecuspis concreta**), *P. claudicans* (*Votadinium spinosum**), *P. oblongum* (*V. calvum*) with *A.* cf. *minutum*, *A.* cf. *tamiyavanichii*, *A.* cf. *tamarense*, *A.* cf. *pseudogonyaulax*, and *A.* cf. *affine*, being present in few counts. Variations in species richness among the dinoflagellate cyst assemblages obtained in the region are shown in Fig. 3. In general, the species diversity in coastal areas is higher than in off-shore areas. The species of dinoflagellate cysts which are commonly found from the modern surface sediments in the region are shown in Fig. 2 and listed in Table 2.

Cyst density

In terms of total cysts abundances, modern sediments from Indonesian waters contained relatively high total cyst abundances varying from 87 to 2,668 cysts g^{-1} in Hurun Bay and from 5 to 3,691 cysts g^{-1} in Kao Bay (Mizushima 2007); and those cyst abundances described by Baula et al. (2008) in the mariculture areas of Pangasinan, NW Philippines with total cyst abundances ranging from 43 to 1,940 cysts g^{-1} (Fig. 4). The other areas show generally lower cyst densities such

Table 1. A summary of available data on dinoflagellate cyst assemblages in surface modern sediments of tropics and/or Southeast Asian region.

LOCATION	SPECIES RICHNESS/DIVERSITY	CYST ABUNDANCE	AUTOTROPHIC & HETEROTROPHIC RATIO	DOMINANT SPECIES
Gulf of Thailand and East Coast of Peninsular Malaysia (Lirdwitayaprasit, 1997)	20 cyst-types	6 to 278 cysts cm^{-3}		Toxic: not so clear but morphotype *Alexandrium* spp. are present Common: *Scrippsiella* spp.
off Sabah, Sarawak and Brunei Darussalam waters (Lirdwitayaprasit, 1998)	18 cyst-types	6 to 278 cysts cm^{-3}		Toxic: not so clear but morphotype *Alexandrium* spp. are present Common: *Spiniferites bulloideus*
Coastal waters of Indonesia (Matsuoka, et al., 1999)	Jakarta Bay: 22 cyst-types	Jakarta Bay: 30 to 580 cysts ml^{-1} wet sediment		Toxic: *Pyrodinium bahamense* var. *compressum* Common: *Protoperidinium* spp., *Brigantedinium* cf. *cariocoense*, *Gonyaulax scrippsae*, *Scrippsiella* spp.
	Off Flores Island: 5 cyst-types	off Flores Island: 270 cysts per 1 ml wet sediment		Toxic: *Protoceratium reticulatum* Common: *Protoperidinium* spp., *Gonyaulax scrippsae*, *Protoperdinium oblongum*
	Udjung, Pandang, Larantuka: 11 cyst-types	Ujung Pandang: 210 to 410 cysts per 1 ml wet sediment		Toxic: *Pyrodinium bahamense* var. *compressum* Common: *Protoperidinium* spp., *Scrippsiella* spp.
off Mangalore, SW India (Godhe, et al., 2000) (outside SE Asia)	43 cysts taxa	122 cysts g^{-1} (quantified only in one station and the remaining stations are qualified)		Toxic: *Alexandrium minutum*, *A. tamarense* and *A.* cf. *tamiyavanichii*, *Gymnodinium catenatum* Common: *A. minutum*, *A. tamarense*, *A.* cf. *tamiyavanichii*, *Gymnodinium catenatum*, *Protoperidinium avellana*, cf. *Pentapharsodinium dalei*, *Protoceratium reticulatum*, *Lingulodinium polyedrum*, *Scrippsiella trochoidea* and/or *Protoperidinium* cf. *minutum*
Manila Bay, Philippines (Azanza, et al., 2004)	23 cysts taxa	30 to 793 cells cm^{-3}	A*=5 cyst taxa H*=70%	Toxic: *Pyrodinium bahamense* var. *compressum* Common: *Protoperidinium* spp. *Pyrodinium bahamense* var. *compressum*, *Diplopsalis* spp., *L. polyedrum*, *Gonyaulax* spp., *Pyrophacus steinii*, and *P. reticulatum*
Sunda Shelf, South China Sea (Kawamura, 2004)	35 cysts taxa	86 to 817 cysts ml^{-1}		Toxic: *Alexandrium* spp. *Oligotrophic tropical Sunda* Shelf: Common: *Spiniferites* spp. (*Gonyaulax scrippsae*, *G. spinifera*, *S. ramosus*, *S. hyperacanthus*, *S. membtanaceus*), *P. reticulatum*, *O. Israelianum*, *Protoperidinium* spp.

Table 1. (Continued).

LOCATION	SPECIES RICHNESS/DIVERSITY	CYST ABUNDANCE	AUTOTROPHIC & HETEROTROPHIC RATIO	DOMINANT SPECIES
Coastal Waters of Sabah, Malaysia (Furio, et al., 2006)	Kota Kinabalu Bay: 25 cyst-types	Kota Kinabalu Bay: 103 to 451 cysts g^{-1}	A* = 378 cysts g^{-1} (35.44%) H* = 690 cysts g^{-1} (64.56%)	Toxic: *Pyrodinium bahamense* var. *compressum* Common: *Protoperdinium* spp., *Alexandrium affine*-type, *Protoperidinium leonis*, Pbc, *Gonyaulax* spp., *L. polydrum*, *Protoperidinium conicum*, *P. oblongum*
	Tuaran Estuary: 11 cyst-types	Tuaran Estuary: 8 to 184 cysts g^{-1}	A* = 54 cysts g^{-1} (18.98%) H* = 230 cysts g^{-1} (81.02%)	Toxic: *Pyrodinium bahamense* var. *compressum* Common: *Protoperidinium* spp., *Protoperidinium claudicans*, *Gonyaulax* spp., *P. subinerme*, Pbc
	Sipitang Bay: 24 cyst-types	Sipitang Bay: 35 to 411 cysts g^{-1}	A* = 717 cysts g^{-1} (68.38%) H* = 338 cysts g^{-1} (32.25%)	*Toxic: Pyrodinium bahamense* var. *compressum* Common: *Alexandrium affine*-type, *Protoperidinium* spp., Pbc, *Alexandrium pseudogonyaulax*, *L. polyedrum*
	Kuala Penyu Lagoon: 22 cyst-types	Kuala Penyu Lagoon: 2 to 62 cysts g^{-1}	A* = 74 cysts g^{-1} (45.75%) H* = 87 cysts g^{-1} (54.25%)	Toxic: *Pyrodinium bahamense* var. *compressum* Common: *P. reticulatum*, *Protoperidinium* spp., *Protoperidinium conicoides*, *Deplopelta parva*, *P. denticulatum*, *Alexandrium* spp., Pbc
Coastal waters in Indonesia and few estuaries in Vietnam (Mizushima, 2007)	Hurun Bay: 33 cyst-types	Hurun: 87 to 2,668 cysts g^{-1} Bay	A* = 5831 cysts g^{-1} H* = 7306 cysts g^{-1}	Toxic: *Pyrodinium bahamense* var. *Compressum* Common: Pbc, *Protoperidinium* spp., *P. reticulatum*, *Alexandrium affine*-type, *Protoperidinium conicum*, *P. denticulatum*, *P. subinerme*, *Scrippsiella* spp.
	Kao Bay: 35 cyst-types	Kao Bay: 5 to 3,691 cysts g^{-1}	A* = 15,111 cysts g^{-1} H* = 7,521 cysts g^{-1}	Toxic: *Pyrodinium bahamense* var. *compressum* Common: Pbc, *Brigantedinium assymetricum*, *Protoperidinium leonis*, *P. subinerme*, *Spiniferites* spp., *P. steinnii*
	Mekong River and off Nha Trang: 29 cyst-types	Mekong River and off Nha Trang: 70 to 206 cysts g^{-1}	A* = 717 cysts g^{-1} H* = 793 cysts g^{-1}	
the mariculture area in Pangasinan, NW Philippines (Abstract, Baula, et al., 2008)	50 cyst-types (Bolinao, Anda, Bani and Alaminos)	43 to 1,940 cysts g^{-1}		Toxic: *Alexandrium minutum* Common: *Spiniferites bulloideus*, *Algidasphaeridium minutum* var. *minutum* and *Brigantedinium majusculum*.

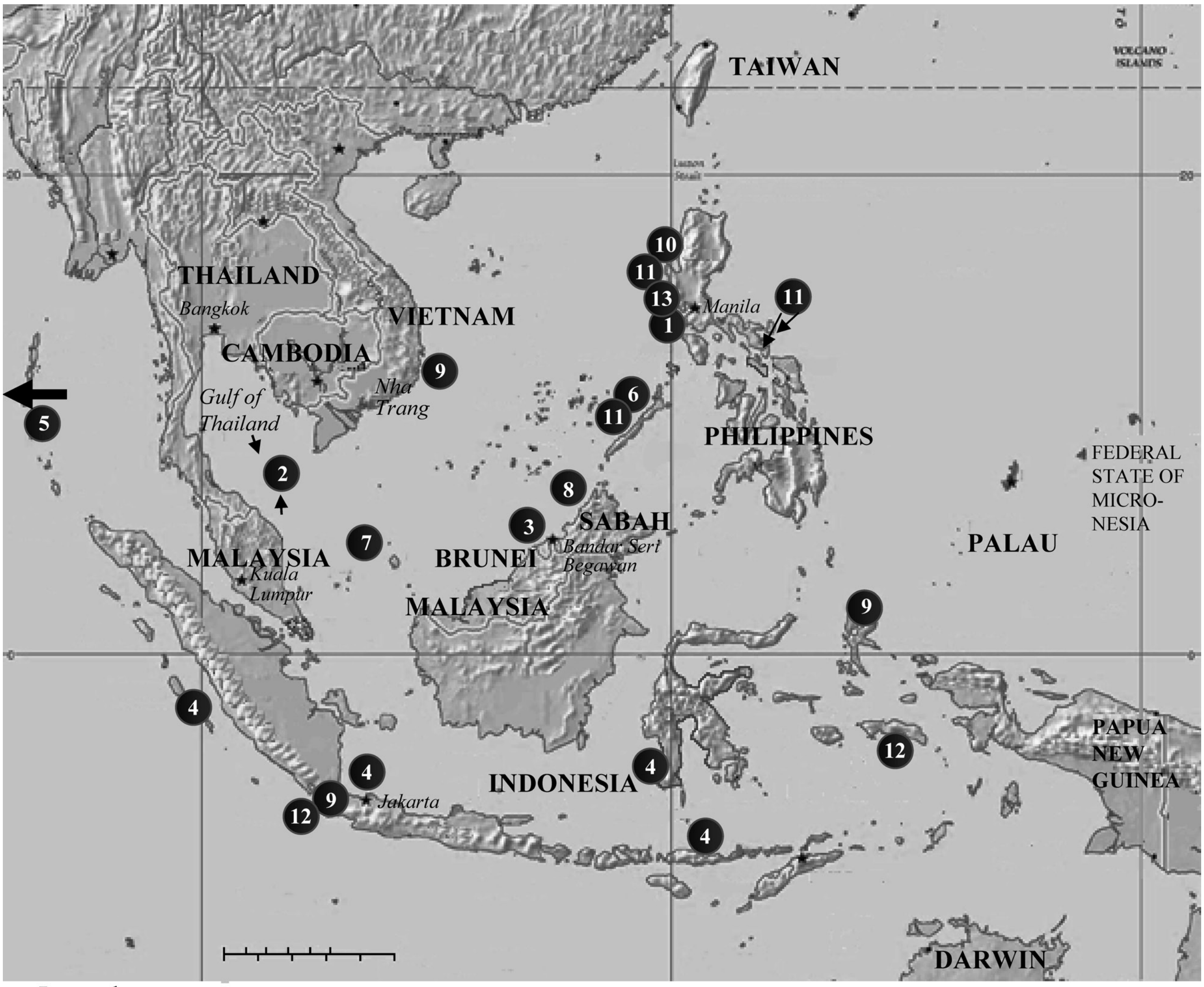
Table 1. (Continued).

LOCATION	SPECIES RICHNESS/DIVERSITY	CYST ABUNDANCE	AUTOTROPHIC & HETEROTROPHIC RATIO	DOMINANT SPECIES
Northwestern and Central Philippines (Furio, et al., undated, in press)	Masinloc Bay: 30 cyst-types	Masinloc Bay: 148 to 866 cysts g^{-1}	A*=1847 cysts g^{-1} H*=2024 cysts g^{-1}	Toxic: *Pyrodinium bahamense* var. *compressum* Common: Pbc, *Brigantedinium* spp., *Protoperidinium conicum*, *P. denticulatum*, *Spiniferites* spp., *Diplopelta parva*, *Protoperidinium conicum*, *Alexandrium affine*-type, *Protoperdinium oblongum*
	Subic Bay: 29 cyst-types	Subic Bay: 53 to138 cysts g^{-1}	A*=156 cysts g^{-1} H*=382 cysts g^{-1}	Toxic: *Pyrodinium bahamense* var. *compressum* Common: *Brigantedinium* spp., Pbc, *Diplopelta parva*, *L. polyedrum*, *Protoperdinium denticulatum*, *Alexandrium affine*-type, *Spiniferites* spp.
	Maqueda & Villareal Bays: 33 cyst-types	Maqueda & Villareal Bays: 155 to 684 cysts g^{-1}	A*=1620 cysts g^{-1} H*=1676 cysts g^{-1}	Toxic: *Pyrodinium bahamense* var. *compressum* Common: Pbc, *Brigantedinium* spp., *Protoperidinium leonis*, *P. denticulatum*, *P. subinerme*, *Spiniferites* spp.
Several basins in the Philippines (Reotita, et al. 2008)	All studied basins: 35 cyst-types	Bolinao waters: 8 to 82 cysts ml^{-1}		Toxic: *Alexandrium*-type spp. Common: *Brigantedinium* spp., *L. polyedrum*, *P. reticulatum*
		Malampaya Sound: 37 to 396 cysts ml^{-1}		Toxic: *Pyrodinium bahamense* var. *Compressum*, *Gymnodinium catenatum*, Common: Pbc, *Brigantedinium* spp., *L. polyedrum*, *Pyrophacus steinnii*, *P. reticulatum*, *Cochlodinium* spp.
		Sorsogon Bay: 22 to 116 cysts ml^{-1}		Toxic: *Pyrodinium bahamense* var. compressum Common: Pbc, *Brigantedinium* spp., *L. polyedrum*, *Pyrophacus steinnii*, *P. reticulatum*, *Cochlodinium* spp.
		Juag Lagoon: 44 to 137 cysts ml^{-1}		Toxic: *Pyrodinium bahamense* var. *compressum*, *G. catenatum* Common: Pbc, *Brigantedinium* spp., *L. polyedrum*, *P. steinnii*,

as those described by Furio et al. (2006) in surface sediments of Sabah coastal waters, particularly off Kota Kinabalu (103–451 cysts g^{-1}), Sipitang Bay (35–411 cysts g^{-1}), Tuaran Bay (8–184 cysts g^{-1}).

Other cyst mapping studies in the sediments of Gulf of Thailand and East Coast of Peninsular Malaysia (Lirdwitayaprasit 1997); off Sabah, Sarawak and Brunei Darussalam waters (Lirdwitayaprasit 1998); off Jakarta Bay; off Flores Is., Larantuka; and off Udjung, Pandang, Indonesia (Matsuoka et al. 1999); off Mangalore, SW India (Godhe et al. 2000), Manila Bay (Azanza et al. 2004), Sunda Shelf, South China Sea (Kawamura 2004) and in several basins (Bolinao Bay, Malampaya Sound, Sorsogon Bay and Juag Lagoon) in the Philippines (Reotita, et al. 2008) are not comparable with the above-mentioned studies as the units used for cyst densities are different. However, in off-shore areas of the above-mentioned localities, such as the Gulf of Thailand, off Sabah, Sarawak and others, cyst densities are generally lower than those in coastal areas.

Likewise, such findings are comparable to other modern dinoflagellate cyst assemblages in the sediments of tropical Atlantic and adjacent seas, which also contained lower cyst density (Wall et al. 1977). It is generally inferred that the surface sediments contained lower density in the tropics than in



Legend

1. Manila Bay, Philippines (Furio 1995; Corrales and Crisostomo 1996; Azanza et al. 2004)
2. Gulf of Thailand and east coast of Peninsular Malaysia (Lirdwitayaprasit 1997)
3. Off Sabah, Sarawak, Malaysia and Brunnei Darussalam (Lirdwitayaprasit 1998)
4. Jakarta Bay, off Flores Island, Larantuka; and Udjung Padang, Indonesia; (Matsuoka et al. 1999)
5. Off Mangalore, Southwest India (Godhe et al. 2000); the location is outside the map.
6. Malampaya Sound, Palawan, Philippines (Borja et al. 2000; Sombrito et al. 2004; Reotita et al., 2008)
7. Sunda Shelf, South China Sea (Kawamura, 2004)
8. Coastal waters of Sabah (Kota Kinabalu Bay, Tuaran Estuary, Sipitang Bay and Kuala Penyu Lagoon) (Furio et al. 2006)
9. Hurun Bay and Kao Bay, Halmahera, Indonesia; and off Nha Trang and estuary off Mekong River, Vietnam (Mizushima et al. 2007)
10. Mariculture areas NW Philippines (Bolinao, Anda and Alaminos Bay) (Baula et al. 2008)
11. Bolinao Bay, Malampaya Sound, Sorsogon Bay and Juag Lagoon, Philippines (Reotita et al. 2008)
12. Ambon and Hurun Bays, Indonesia (Mizushima et al. 2007)
13. Masinloc and Subic Bays, NW and Western Samar Bays, Central Philippines (Furio et al. in press)

Fig. 1. Dinoflagellate cyst mapping study sites in Southeast Asian region.

Table 2. List of dinoflagellate cyst assemblages from the modern surface sediments in Southeast Asian waters.

Biological Names	Paleontological Names
GONYAULACALES	GONYAULACALES
Alexandrium affine-type (Inoue et Fukuyo) Balech	
Alexandrium minutum Halim	
Alexandrium pseudogonyaulax (Biecheler) Horiguchi ex Kita & Fukuyo	*Impagidinium* spp.
Gonyaulax digitalis (Poichet) Kofoid	*Spiniferites* sp.
Gonyaulax sp.	*Spiniferites hyperacanthus* (Deflandre & Cookson) Cookson & Eisenack
Gonyaulax spinifera complex (Claparède et Lachmann) Diesing	*Spiniferites* cf. *delicates*
Gonyaulax scrippsae Kofoid	*Spiniferites bulloideus* (Deflandre & Cookson) Sarjeant
Lingulodinium polyedrum (Stein) Dodge	*Lingulodinium machaerophorum* (Deflandre and Cookson) Wall
Protoceratium reticulatum (Claparède et Lachmann) Bütschli	*Operculodinium centrocarpum* (Deflandre and Cookson) Wall sensu Wall and Dale
Pyrodinium bahamense var. *compressum* (Böhm) Steidinger, Tester and Taylor	*Polysphaeridium zoharyi* (Wall)
Pyrophacus steinii (Stein) Wall and Dale	*Tuberculodinium vancampoae* (Rossignol) Wall
GYMNODINIALES	GYMNODINIALES
Pheopolykrikos hartmannii (Zimmerman) Matsuoka & Fukuyo	
Polykrikoides kofoidii	
PERIDINIALES	PERIDINIALES
Calciodinellid group	Calciodinellid group
Scrippsiella spp.	
Protoperidinioid group	Protoperidinioid group
Protoperidinium denticulatum (Gran et Braarud) Balech	*Brigantedinium irregulare* Matsuoka
Protoperidinium spp.	*Brigantedinium* spp.
Protoperidinium claudicans Paulsen	*Votadinium spinosum* (Wall) Reid
Protoperidinium compressum (Abé) Balech	*Steladinium reidii* (Wall & Dale) Reid
Protoperidinium conicum (Gran) Balech	*Selenopemphix quanta* (Bradford) Matsuoka
Protoperidinium leonis (Pavillard) Balech	*Quinquecuspis concretum* (Reid) Harland
Protoperidinium pentagonum (Gran) Balech	*Trinovantedinium capitatum* Reid
Protoperidinium sp.	*Steladinium abei* Matsuoka
Protoperidinium subinerme (Paulsen) Loeblich III	*Selenopemphix nephroides* Benedek
Protoperidinium oblongum (Aurivillus) Park et Dodge	*Votadinium calvum* Reid
Protoperidinium spp. (round-brown cyst)	*Brigantedinium* spp.
Diplopsalid group	Diplopsalid group
Oblea acanthocysta Kawami, Iwataki et Matsuoka	
Preperidnium spp.	*Dubridinium* spp.

the temperate zone (Wall et al. 1977, Orlova et al. 2004). The results indicated above are distinctly lower than the cyst abundance in the sub-tropical estuarine system, such as those in Rookey Bay, west coast of Florida, USA, ranging from 1,300 to 8,500 cysts g^{-1} (Cremer et al. 2007). These variations in cyst abundance, assemblage, composition and geographical distribution in different areas were attributed to the following factors: (1) differences in abundance of vegetative cells in the water column and in their cyst production efficiencies, (2) differences in the sedimentary regime; and/or (3) depositional process affected by water currents.

A database on phytoplankton composition of Masinloc and Subic Bays from the Fisheries Resources and Ecological Assessment Project (NFRDI Accomplishment Report CY 2006–2008 funded-project) showed that diatoms were most dominant than dinoflagellates. It had been well documented that many previous red tide events in the area since 1987 was due to high biomass of toxic dinoflagellates *P. bahamense* var. *compressum* (Gonzales 1989, Gonzales, et al. 1989, Corrales and Gomez 1990, Bajarias 1995). Other dinoflagellate species that formed blooms in these areas were non-cyst forming genera, e.g. *Noctiluca, Ceratium* and *Prorocentrum*. It was reflected in the cyst records of these areas by relatively low cyst abundance and by fewer cyst species in the assemblages that were moderately dominated by heterotrophic species. Thus, the low dinoflagellate cyst production could have been attributed to the dominance of diatoms and other phytoplankton groups rather than dinoflagellates.

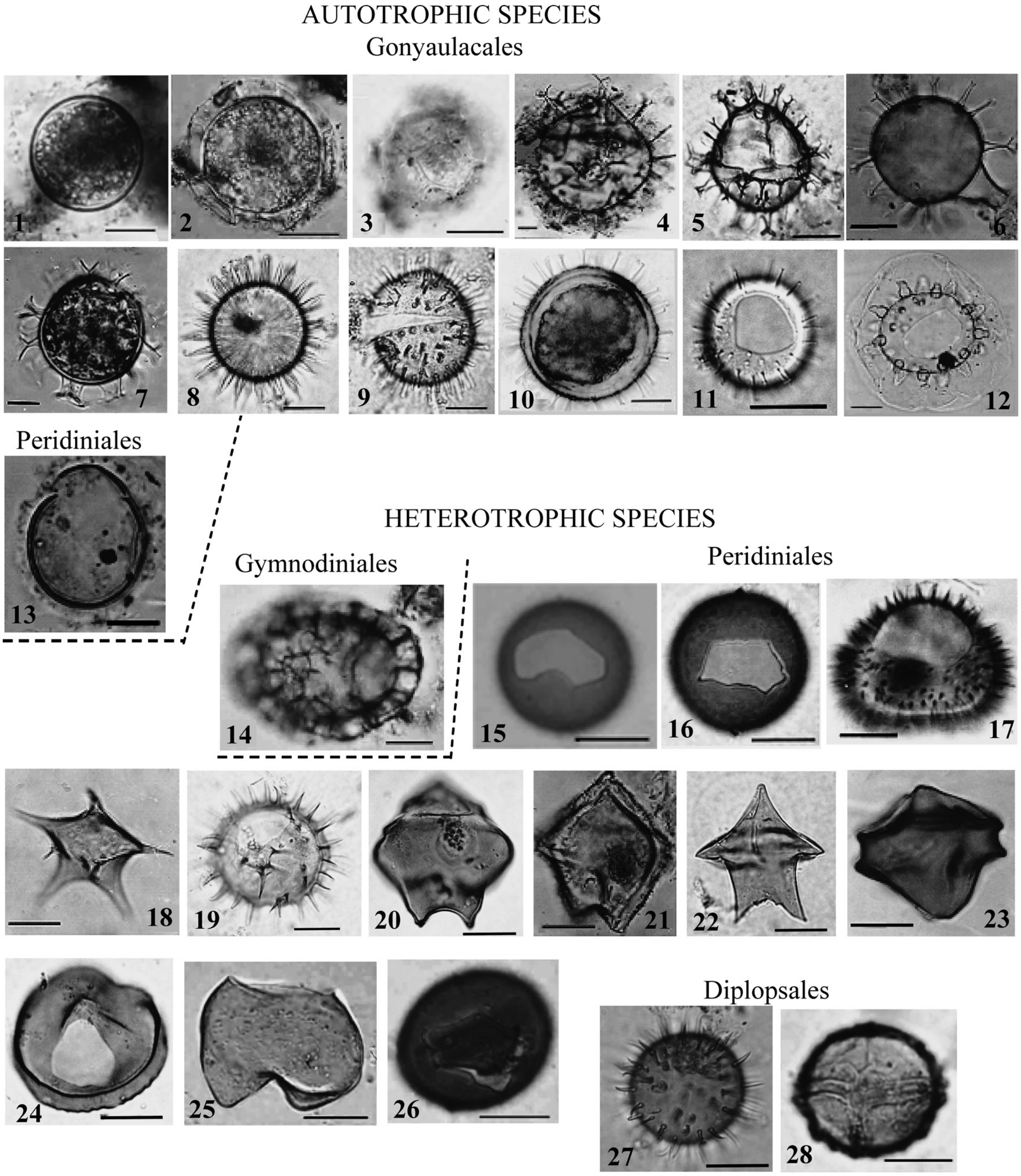


Fig. 2. Dominant cysts identified in Southeast Asia surface sediment: 1. *Alexandrium affine*-type; 2–3. *Alexandrium pseudogonyaulax*; 4. *Gonyaulax digitalis* (*Spiniferites* sp.*); 5. *Gonyaulax* sp.; 6. *Gonyaulax spinifera* (*Spiniferites* cf. *delicates**); 7. *Gonyaulax scrippsae* (*Spiniferites bulloides**); 8. *Lingulodinium polyedrum*; 9-10. *Pyrodinium bahamense* var. *compressum*; 11. *Protoceratium reticulatum*; 12. *Pyrophacus steinee*; 13. *Scrippsiella* sp.; 14. *Polykrikos kofoidii*; 15. *Protoperidinium denticulatum*; 16. *Protoperidinium* sp.; 17. *Protoperidinium claudicans*; 18. *Protoperidinium compressum*; 19. *Protoperidinium conicum*; 20. *Protoperidinium leonis*; 21. *Protoperidinium pentagonum*; 22. *Protoperidinium* sp. (*Stelladinium abei**); 23-24. *Protoperidinium subinerme*; 25. *Protoperidinium oblongum*; 26. *Protoperidinium* sp.; 27. *Oblea acanthocysta*; 28. *Dubridinium caperatum**. Asterisk mark (*) indicates a scientific name under system for micropaleontology. Scale bar shows 20 mm.

Abundance and distribution of the cysts of toxic species

Blooms of *P. bahamense* var. *compressum* (Pbc) had been well documented and described in SEA region. Pbc cysts were widespread in relatively high concentrations in the sediments of most coastal waters in the region (Fig. 5) but had not been recorded from the estuary of Mekong River and off Nha Trang, Vietnam (Mizushima 2007); off Mangalore, SW India (Godhe et al. 2000); Sunda Shelf, South China Sea (Kawamura 2004); and the mariculture areas in Pangasinan, NW Philippines (Baula et al. 2008).

Cysts of other toxic dinoflagellates are present at significantly low counts as follows: *A.* cf. *minutum, A.* cf. *tamarense, A.* cf. *tamiyavanichii* and *P. reticulatum* in the

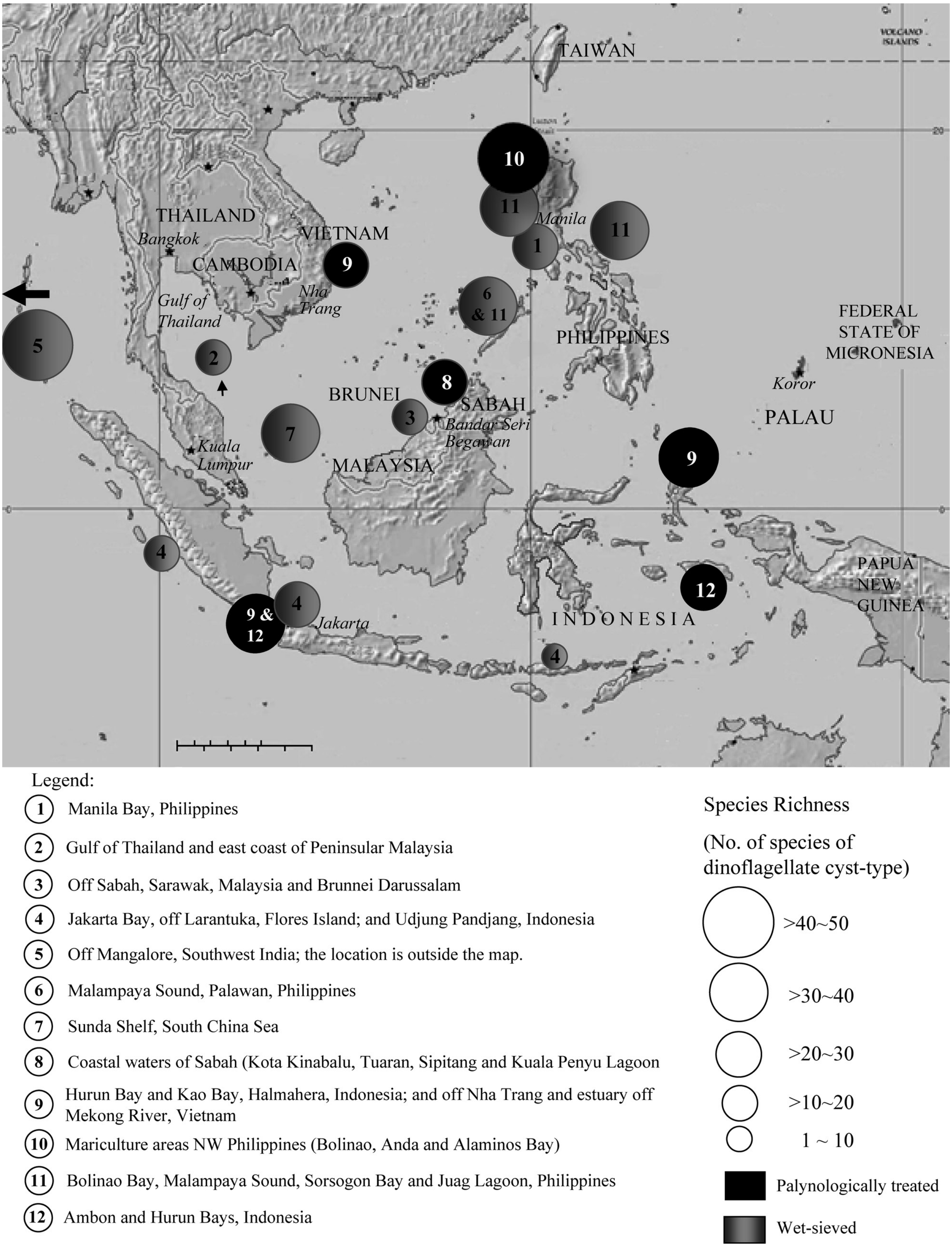


Fig. 3. Species richness of dinoflagellate cyst assemblage.

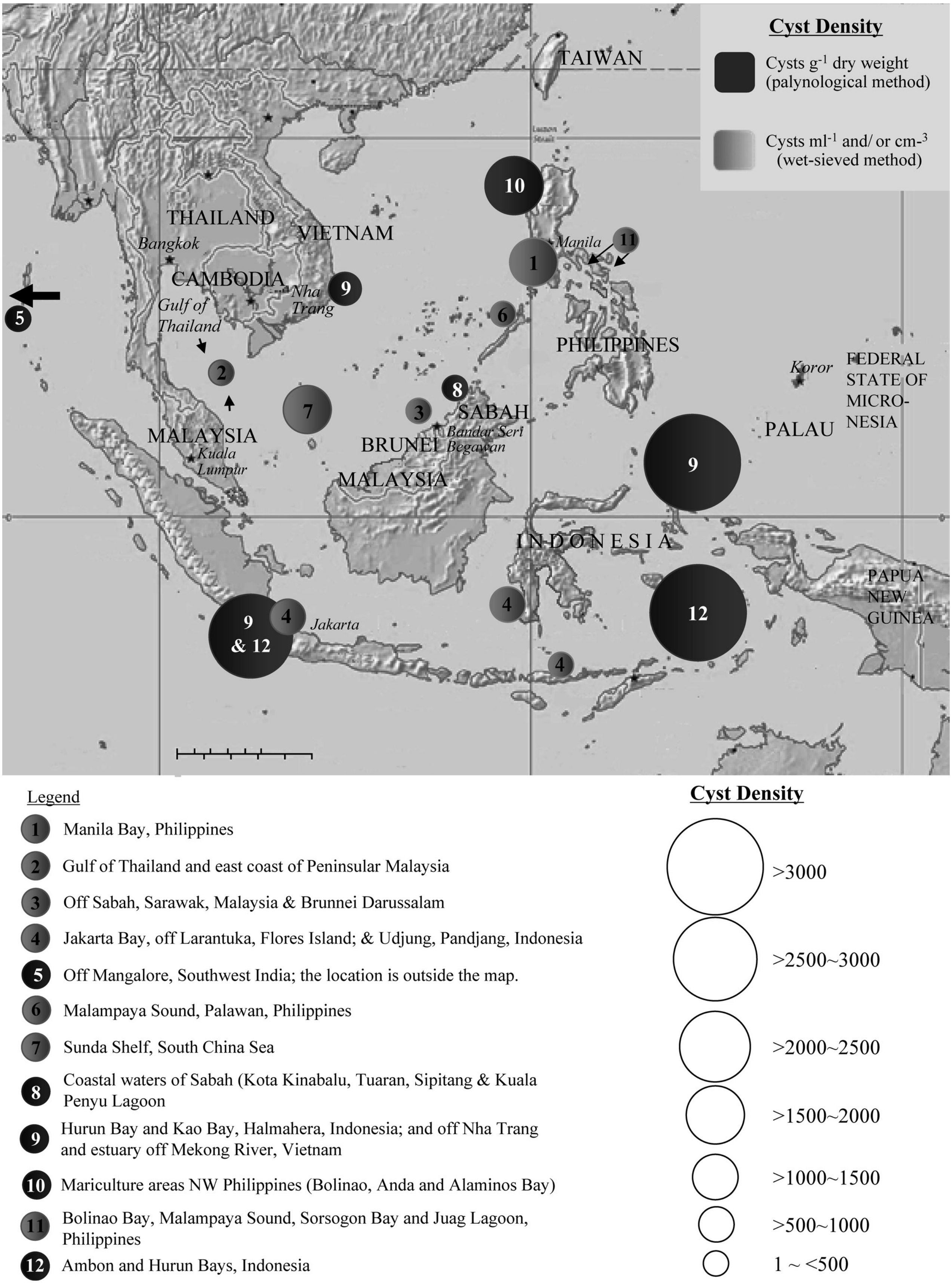


Fig. 4. Spatial variations of total cyst densities in recent surface sediments of Southeast Asian waters.

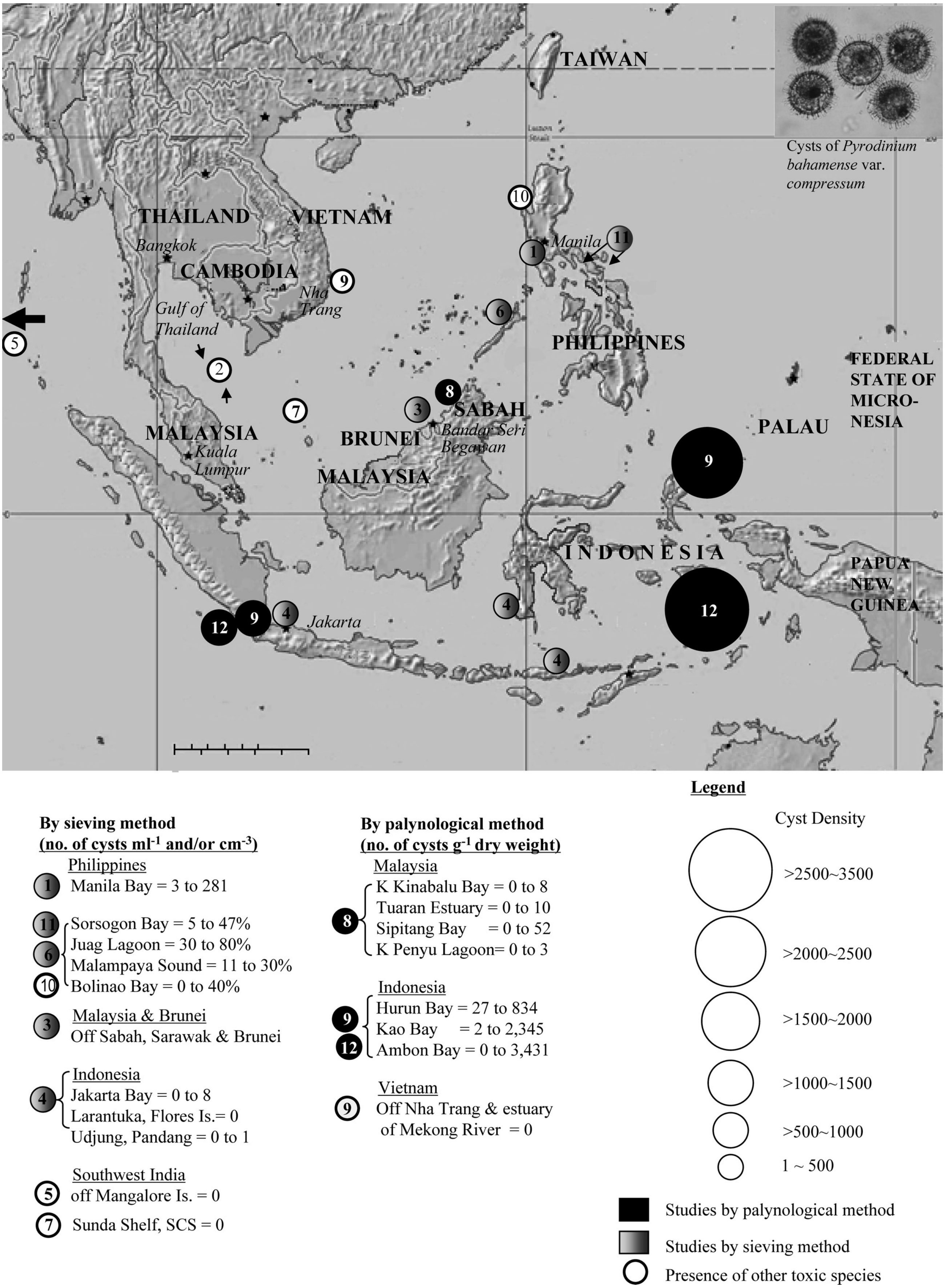


Fig. 5. Spatial distribution of total *Pyrodinium bahamense* var. *compressum* cyst densities.

surface sediment off Mangalore coast, SW India (Godhe et al. 2000); *A.* cf. *minutum* in mariculture areas in Pangasinan, NW Philippines (Baula et al. 2008). *P. reticulatum* cyst is also present in the surface sediments of coastal waters of Sabah, Malaysia (Furio et al. 2006) and in other several basins in the Philippines (Reotita et al. 2008). The presence of cysts as enumerated above could well be a useful tool for explaining the population dynamics of these toxic species within the region as they could also pose potential risks for future bloom events.

Cyst seed beds

Results from various studies on the distribution of toxic dinoflagellate cysts in the tropics and/or SEA waters revealed highest concentrations in shallow areas (with depths shallower than 25 m) and associated with silt and sands (Azanza et al. 2004, Furio et al. 2006, Mizushima 2007). Most researchers had somehow provided their views or descriptions of these "discrete seed beds", indicating that local blooms of dinoflagellates were produced by autochthonous populations of resting cysts. Corrales and Crisostomo (1996) had suggested that the presence of cyst beds in the western part of Manila Bay coincided with the location (west coast of Bataan) of the highest live *P. bahamense* cyst densities. Bataan was the area where most blooms were initiated. They had confirmed that location of these suggested cyst beds agreed with observations that past blooms started in the west/north-west before spreading to other areas of Manila Bay. This was further validated from the Bureau of Fisheries and Aquatic Resources' HAB monitoring records (1992–1994 annual blooms) that *P. bahamense* cells first occurred on the western area of the Bay (off Bataan); after which the blooms spread to the north then to the east (Bajarias and Relox 1996).

A consideration on mechanism of the HAB dispersal and expansion in Southeast Asian region

The factors and mechanism of algal bloom expansion in the SEA region involving the resting cyst stage of causative HAB species were not well understood, though *P. bahamense* cysts had been documented to be widespread and abundant in most embayments in the region. The first documented *P. bahamense* bloom in the region was in Papua New Guinea in 1975 and then introduced in Sabah and Brunei waters in 1976 as had been confirmed from the first reported paralytic shellfish poisoning (PSP) episode in these areas (Maclean 1984). It had been suggested that this transport was via the Southern Equatorial Current, though there had been no study or little information about it to prove that there was such a true spreading event. The species bloom had been frequently recurring event since 1976 along the west coast of Sabah, particularly in Kimanis Bay. On the other hand, the first PSP outbreak associated with the species bloom in the Philippines in 1983, had been inferred as gradual HAB dispersal event within the region. PSP and blooms of *P. bahamense* have widely affected the Philippine coastline, causing extensive losses to the shellfish industry and human poisoning and fatalities. Apart from natural wind forces and water currents due to tropical cyclones, the movement of spat mussels and oysters from affected to unaffected areas was believed to be possible risk factor of transporting resting cysts in various coastal waters of the Philippines. Likewise, the PSP phenomenon in Kao Bay, Halmahera, East Indonesia, has been reported since 1977 (Praseno et al. 2003). But its causative species had been only identified as *P. bahamense* var. *compressum* in 1993 (Wiadnyana et al. 1994). Since then, occurrence of the species had been sporadically reported in Indonesian coastal waters such as Lampung Bay, Jakarta Bay, Hurun Bay and Ambon Bay (Praseno et al. 2003).

These observations clearly indicate that high priority should be given to continuing cyst mapping research in the entire SEA region as the information is so essential in describing HABs dispersal and occurrence in the region.

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