JARQ 52 (1), 77 - 89 (2018) https://www.jircas.go.jp

Palynomorph Assemblages Dominated by Heterotrophic Marine Palynomorphs in Tropical Coastal Shallow-water Sediments from the Southern Myanmar Coast

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Abstract

The goal of this study was to characterize palynomorph assemblages in tropical marine coastal shallow-water sediments collected from the southern coast of Myanmar, and possibly find them as useful tools for reconstructing changes in the tropical coastal environment. These sediment samples were dominated by heterotrophic marine palynomorphs, particularly in microforaminiferal linings and heterotrophic dinoflagellate cysts. In addition, these tropical marine palynomorph assemblages were characterized by low cell/grain concentrations, especially in photo/mixotrophic dinoflagellate cysts. These marine palynomorph characteristics are common to other tropical coastal surface sediments collected from Southeast Asia. These assemblages may reflect a diagnostic food web that characterizes tropical coastal shallow waters. For example, benthic foraminifers (microforaminiferal linings) that are always dominated usually consume prey organisms composed of bacteria, diatoms, dinoflagellates and amorphous organic substances. And bacteria can utilize dissolved organic matter delivered from terrestrial and marine environments via various organisms that inhabit water and sediment surfaces. The dominance of microforaminiferal linings appears to result from both microbial and grazing food webs in tropical coastal shallow-water sediments.

Discipline: Fisheries

Additional key words: coastal environment, dinoflagellate cyst, microbial loop, microforaminiferal lining, tinntinomorph

Introduction

Marine palynomorphs are microscopic organic-walled organism remains. These remains consist of different groups of planktonic and benthic microorganisms, such as the resting cysts of dinoflagellates, resting cysts and lorica of tintinids (tintinomorphs), organic linings of smaller benthic foraminifers (microforaminiferal linings), appendages, body and resting eggs of crustanceans (mainly copepods), and micro-remains of unknown organisms called acritarchs (Matsuoka et al. 2017). These organic-walled micro-remains preserved in sediments are regarded as a useful proxy of coastal environments and used in reconstructing coastal marine environmental history. In particular, dinoflagellate cysts are known as the most useful marine palynomorphs, typically employed for understanding eutrophication mainly in temperate to sub-boreal regions (Dale 2009, Matsuoka 2011, Pospelova 2005). Also along tropical Southeast Asian coasts, several studies have examined dinoflagellate cysts found in surface sediments of the Philippines (Baula et al. 2011, Furio et al. 2006), Myanmar (Srivilai et al. 2012, Su-Myat et al. 2012), the South China Sea (Kawamura 2004), the western Gulf of Thailand (Lirdwitayaprasit 1997), the southern Java Sea (Lirdwitayaprasit 1998), and the coast of

MEXT/JSPS-Grants-in-aid for Scientific Research (No: 26304031)
In cooperation with the Department of Fisheries Myanmar, Myeik University, and Myanmar Fisheries Federation near Myeik in the southern part of Myanmar, 2014-2016
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Received 30 November 2016; accepted 21 June 2017.

Selangor in Malaysia (Matsuoka et al. 2017). These studies concluded that the densities of dinoflagellate cysts preserved in surface sediments were lower in tropical regions than in temperate or sub-boreal regions (Furio et al. 2006, 2012). In addition, Baula et al. (2011) suggested that lower cyst density was due to high sedimentation rates accompanied by high precipitation and high fluvial sediment loads. Matsuoka et al. (2017) carefully observed the residues of sediments collected from the Selangor region of Malaysia and from Oman after palynological processing, and found that not only dinoflagellate cysts but also other palynomorphs such as tintinnomorphs, microforaminiferal linings, copepod eggs, bodies and appendages, scolecodonts and butterfly scales were preserved in these tropical surface sediments. Matsuoka et al. (2017) also found a relatively high proportion of heterotrophic dinoflagellate cysts and abundant occurrences of microforaminiferal linings, albeit with low photosynthetic dinoflagellate cysts. These findings were also supported by Su-Myat et al. (2012) as they reported relatively low cyst densities of modern dinoflagellates along the coast of Kadan Island in southern Myanmar, and by our subsequent study in the same areas that found an extreme abundance of microforaminiferal linings.

Palynomorph studies are useful to construct environmental shifts in past geologic times and current coastal areas. In the Arctic, palynomorphs consisting of dinoflagellate cysts, acritarchs, tintinnid remains, microforaminiferal linings, and pollen and fern spores preserved in sediments have been used to understand Holocene paleo-environmental change (Mudie 1992, Pienkowski et al. 2011, 2013). In temperate regions, Mudie et al. (2011) used non-pollen palynomorphs consisting of dinoflagellate cysts, acritarchs, colonial algae, cyanobacteria, zygnemataceaen remains, fungal spores, microforaminiferal linings, thecamoebians, copepod eggs, rotifers, scolecodonts and others to reconstruct salinity and environmental changes around the Caspian-Black Sea-Mediterranean corridor. In tropical regions, Kawamura (2004) observed a high density of microforaminiferal linings in surface sediments collected from the South China Sea, as well as *Cladopyxis* sp., *Halodinium majus*, *Pediastrum* spp. and *Cyclopsiella* spp. Limoges et al. (2010) also reported the abundant occurrence of foraminifera organic linings (hereafter referred to as microforaminiferal linings). Thakur et al. (2015) discussed the role of sedimentary marine/terrestrial palynomorphs from the standpoint of their distribution in tropical wetlands along the Kerala coast in India. However, the studies above paid little and/or different attention to marine palynomorphs other than dinoflagellate cysts in terms of ecosystems.

We have been conducting a study on marine palynomorphs by focusing on their ecological roles and trophic level positions in marine food webs, in order to reconstruct both historical and contemporary environmental changes (i.e., sea surface temperature, salinity and trophication levels). And as a part of this series, in this paper we describe and quantify the abundance of palynomorphs preserved in coastal marine sediments collected around Kadan Island in southern Myanmar, as the natural environments of both the coast and land around this area are still comparable with those of other tropical regions. Based on that data, together with previous works, we further discuss the ecological significance of their proportions in tropical marine palynomorph assemblages with a focus on marine food webs.

Materials and methods

1. Environmental setting

The Tanintharyi Region in southern Myanmar has a tropical monsoon climate, with a rainy season extending from May to October, a dry season from November to February, and a post dry (hottest) season generally in March and April. Air temperature in this region ranges from 23.2°C to 30.2°C on average. Due to a relatively longer monsoon period, total precipitation in the Tanintharyi Region reaches approximately 3,800 mm per year (National Environmental Conservation Committee 2012).

Kadan Island and the small islands of Maingyi, Kala and Ma-aing are located west of Myeik City in the Tanintharyi coastal region (12°16'-13°40'N latitude, 98°13'-98°40'E longitude). Myeik City is one of the developing areas in southern Myanmar and its population is rapidly increasing (National Environmental Conservation Committee 2012). This city is also the fisheries center of the Tanintharyi Division. The area around Kadan Island, particularly along its eastern and southern coasts, is influenced primarily by the Tanintharyi River from the mainland, while its northern and western coasts are also affected by open ocean waters from the Andaman Sea. The eastern and southern coasts of Kadan Island and the area around Kara Island and Ma-aing Island are primarily characterized by natural mangrove forests. Consequently, only few people live in these areas. These environments are suitable for providing natural and tropical marine palynomorph assemblages.

2. Sediment sampling and palynomorph analysis

A total of nine surface sediment samples were collected from the area around the islands of Kadan, Maingyi, Kala and Ma-aing using a TFO gravity corer type II (Rigosha, Tokyo, Japan) in December 2014 (Fig. 1). The top 0-2 cm of all collected sediments was sub-sampled. After thorough mixing, sediment samples were provided for palynomorph analysis. The analytical method followed that of Matsuoka & Fukuyo (2000). After calcareous and silicate grains were removed using HCl and HF at room temperature, the remaining organic material was sieved using stainless-steel screens with opening-mesh sizes of 125 µm and 20 µm. The residue trapped in the 20-µm mesh was recovered and stored in a 7-ml plastic tube. One ml of an aliquot part was used for observations of palynomorphs under an Axio optical microscope (Carl Zeiss Co. Ltd. Jena, Germany). All marine palynomorph remains were represented as the numbers of cells, grains or pieces (for crustacean body remains) per dry weight of sediment.

The marine palynomorphs were classified into the following groupings: dinoflagellate cysts (dinoflagellate), tintinnomorphs (lorica and resting cysts), microforaminiferal linings (benthic foraminifera), testate amoeba (shell), and metazooplankton (resting eggs, body fragments and appendages of mainly copepods). We followed the palynomorph classification of Van Waveren (1993) and Matsuoka et al. (2017).

Results

After palynological treatment of the marine sediment samples, various microscopic organic substances (called palynodebris and palynomorphs) were observed. Most samples except from St. 5 and St. 9 contained large amounts of palynodebris consisting primarily of wood fragments, plant epidermises, invertebrate cuticles and other biotic remains. Palynomorphs consisted of terrestrial pollen, the spores of ferns and fungi, and other microscopic marine organic remains, as well as dinoflagellate cysts (Fig. 2a-h), acritarchs, tintinnomorphs (tintinnid lorica (Fig. 2r) and resting cysts (Fig. 2o, q)), chrysophycean statospores, amoeba testae (Fig. 2p), microforaminiferal linings (Fig. 2; s-w, small foraminiferal organic remains of less than 150 µm in total size), crustacean remains (primarily copepods) consisting of pseudochitinous body parts (Fig. 2k), appendages and resting eggs (Fig. 2i-j, l-n), scolecodonts, butterfly scales and other miscellaneous organic grains. Among these palynomorphs (excluding the pollen and fern spores), dinoflagellate cysts, tintinnomorphs, microforaminiferal linings and crustacean eggs, bodies and appendages occurred most abundantly. The marine palynomorph assemblage recovered from surface sediments around Kadan Island abundantly occurred at rather open sea sites instead of in mangrove canals and at the mouth of the river (Fig. 3).

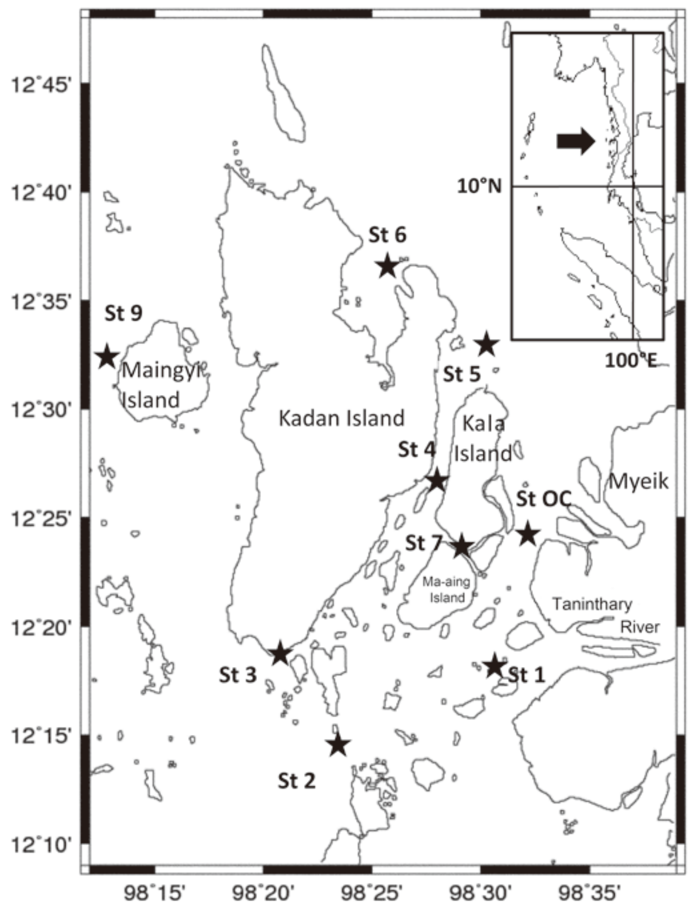

Fig. 1. Sampling locations around Kadan Island in southern Myanmar.

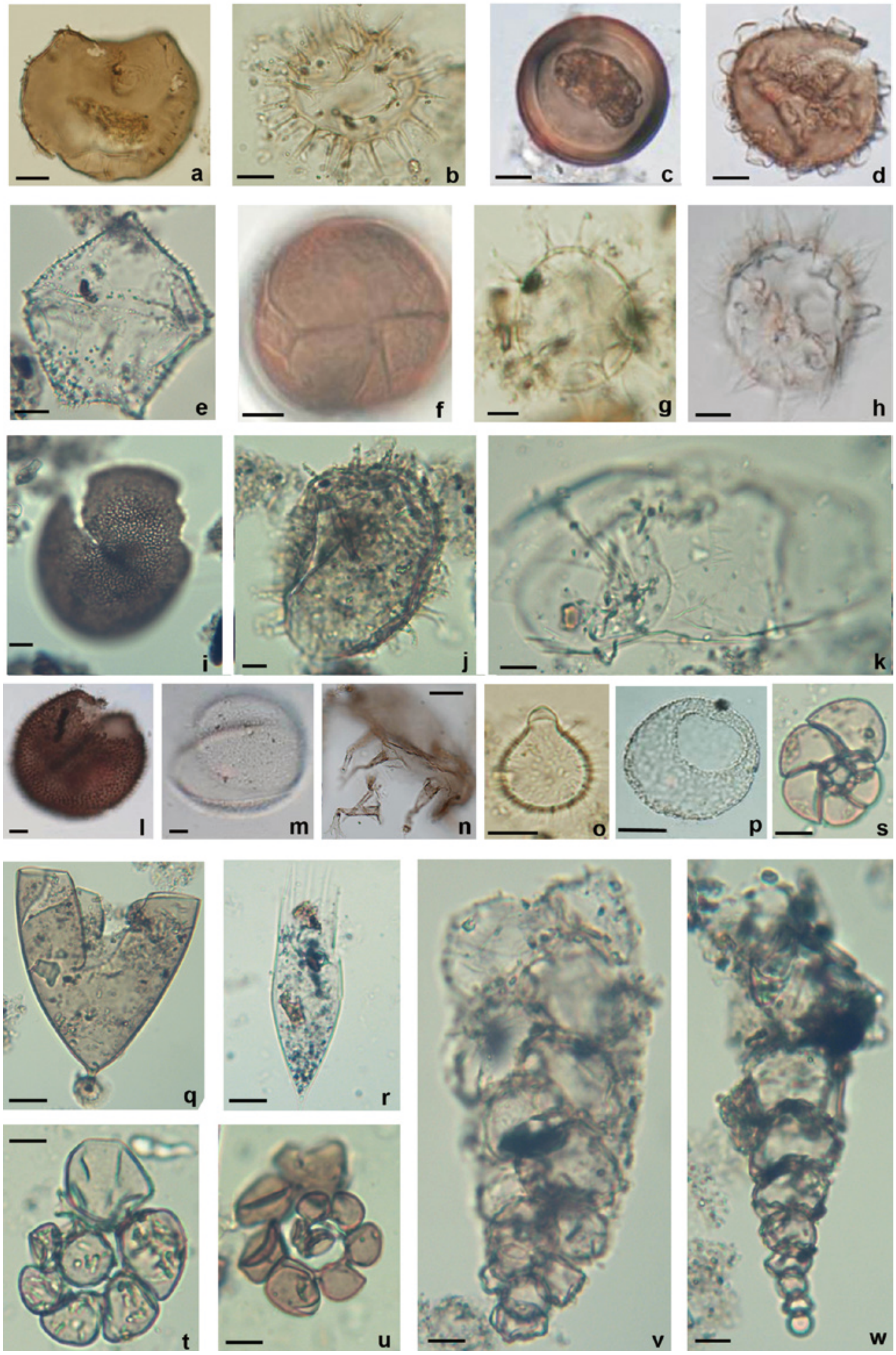

Fig. 2. Marine palynomorphs observed in surface sediments around Kadan Island in southern Myanmar. Scale bar is 10 µm.

a-f Heterotrophic dinoflagellate cysts, a: *Selenopemphix* sp., b: *Selenopemphix quanta*, c: *Brigantedinium* sp., d: *Echinidinium* sp. (spherical ornament), e: *Trinovantedinium applanatum*, f: *Dubridinium caperatum*; g-h Photo/mixotrophic dinoflagellate cysts, g: *Spiniferites ramosus*, h: *Dapsilidinium pastielsii*; i-n Crustacean remains, i: resting egg (reticulate type), j: resting egg (spinate type), k: body fragment, l: resting egg (spinate type), m: resting egg (granulate type), n: appendage; p: testate ameba shell; q-r Tintinnomorphs, o, q: resting cyst, r: lorica of *Dadayiella* sp.; s-w Microforaminifera linings, s-u: various forms of coiled type, v: biserial type, w: uniserial type.

The dinoflagellate cysts represented more than nine genera and 14 species. Cysts of photo/mixotrophic dinoflagellates (including only *Spiniferites bulloideus* and *S. ramosus*) were extremely rare. In contrast, heterotrophic dinoflagellate cysts were more diversified and composed of eight genera and at least 12 species, including *Brigantedinium* spp. (Protoperidiniacean spherical round brown cysts), *Lejeunecysta concreta*, *Lejeunecysta* sp., *Selenopemphix nephroides*, *Selenopemphix quanta*, *Stelladinium reidii* and *Trinovantedinium applanatum*, and cysts of *Protoperidinium* spp., *Niea acanthocysta* and *Echinidinium* spp. A conspicuous species characterized by a round brown cyst (tentatively identified as *Echinidinium* sp.) bearing spherical ornaments (Fig. 2d) also occurred frequently (Sts. 2, 3, 4, 6 and 9), but in low concentrations (Table 1). Acritachs, apparently the resting cells of micro algae and resting eggs of other protozoan organisms, and treated as an artificial taxonomic group, consisted of more than four genera and four species. Four morphologically different types of microforaminiferal linings (categorized as uniserial, biserial, coiled and compound types) were observed. Crustacean remains, mainly those of copepods and primarily consisting of two types of copepod resting eggs, fragment of body and appendages, were also encountered. It is difficult to count the numbers of these crustacean palynomorphs as application of the species concept to this group is often complex or infeasible.

These marine palynomorph remains occurred at a density of 1,692-14,276 grains/g (6,154 grains/g on average). The highest palynomorph concentration in these samples was 14,276 grains/g in the samples from St. 9 west of Maingyi Island, and the lowest concentration was 1,692 grains/g in the sample from St. 4 in the channel between Kadan Island and Ma-aing Island (Fig. 3, Table 1). Microforaminiferal linings were the most abundant palynomorph in these samples, with concentrations ranging from 791 (St. 1) to 11,352 (St. 9) grains/g (3,224 grains/g on average). Among them, the coiled type was most dominant. Crustacean (mainly copepods) remains were the second most abundant group, ranging from 204 (St. 4) to 3,003 (St. 7) grains/g with an average of 1,482 grains/g. This group was primarily composed of reticulate and

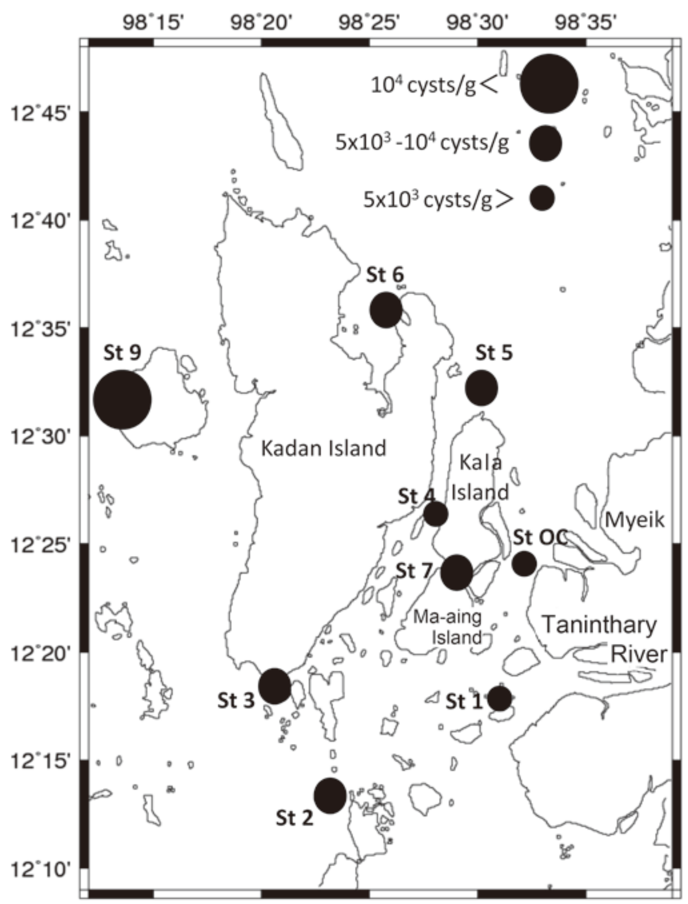

Fig. 3. Abundance of marine palynomorphs preserved in surface sediments around Kadan Island in southern Myanmar

Table 1. List and abundance of marine palynomorphs in surface sediments around Kadan Island in southern Myanmar

Palynomorph / Locality	St 0C		St 1		St 2		St 3		St 4		St 5		St 6		St 7		St 9	
	original	cells/g	original	cells/g	original	cells/g	original	cells/g	original	cells/g	original	cells/g	original	cells/g	original	cells/g	original	cells/g
DINOFLAGELLATA																		
GONYAULACALES																		
Spiniferites bulloideus	1	53																
Spiniferites ramosus																	1	71
PERIDINIALES																		
Brigantedinium spp.	4	213	4	151	5	168	11	1016	1	18	3	220	9	346	3	273	5	357
Lejeunecysta concreta					2	67	6	554										
Lejeunecysta sp.									1	18	1	73						
Selenopemphix nephroides															1	91		
Selenopemphix quanta L-type															1	91		
Selenopemphix quanta S-type													2	77				
Stelladinium reidii																	1	71
Trinnovantedinium applanatum	1	53			1	33												
Protoperidinium spp.	1	53									1	73						
Niea acanthocysta									1	18								
Echinidinium sp. (smal-type)	1	41			3	101			1	18					1	91		
Echinidinium sp. (spherical ornament type)		53			1	33	1	92	1	18			1	38			1	71
TOTAL DINOFLAGELLATES	8	466	4	151	12	402	18	1662	5	90	4	367	12	461	6	546	8	570
ACRITARCHA																		
Spherical type	1	53	3	113	3	101	6	554	2	37	2	147	3	115	4	364	3	214
Baltisphaeridinium sp.					1	33			1	18								
Concentricystes sp.					2	67												
Michystridium spp.	1	53			4	134							1	38			1	71
Halodinium minor							1	92	1	18								
TINTINNOMORPH																		
lorica					4	134	2	184	2	37	22	1617	8	308	5	455	2	142
cyst	10	533	2	75	7	235	4	369	6	111	2	147	6	231	7	637	3	214
AMOEBAE																		
Testae			1	37			1	92			1	73	3	115	3	273	1	71
FORAMINIFERA																		
Uniserial type	2	106	1	37	4	134			4	74	5	367	4	154	1	91	5	357
Biserial type	2	106							3	56	2	147	4	154	1	91	4	285
Coiled type	44	1409	17	642	70	2352	19	1755	56	1047	24	1764	101	3888	35	3185	150	10710
Compound type																		
TOTAL FORAMINIFERA	48	1621	17	791	70	2486	19	1755	63	1177	31	2278	109	4196	37	3367	159	11352
COPEPOD																		
Resting egg (reticulate type)	6	319	5	189	10	336	7	646	1	18	4	294	6	231	5	455	10	714
Resting egg(spinate type)	2	106	2	75	8	268	2	184	2	37	6	441	4	154	3	273	5	357
Body	9	479	12	453	29	974	16	1748	8	149	16	1176	12	422	25	2275	8	571
TOTAL COPEPOD	17	904	19	717	47	1578	25	2578	11	204	26	1911	22	807	31	3003	23	1642
TOTAL PALYNOMORPH	85	3630	46	1884	154	5170	76	7286	91	1692	89	6540	164	6271	95	8645	200	14276

spinate resting eggs. Dinoflagellate cysts were the third most abundant palynomorph, ranging from 90 (St. 4) to 1,662 (St. 3) grains/g with an average of 523 grains/g. The photo/mixotrophic dinoflagellate cysts and acritarchs were less abundant at all stations (Fig. 4).

Discussion

1. Low dinoflagellate cyst concentration in shallow-water sediments around Kadan Island

Generally, the marine palynomorph assemblage in surface sediments around Kadan Island abundantly occurred at rather open sea sites instead of in mangrove canals and at the mouth of the river, where the sedimentation rates are apparently very high as discussed later.

A low dinoflagellate cyst concentration is a characteristic feature of tropical dinoflagellate cyst assemblages. Over the last fifty years, many studies have been conducted on this feature of dinoflagellate cyst assemblages in tropical surface sediments, focusing primarily on higher sedimentation rates in tropical areas (Baula et al. 2011, Furio et al. (2006, 2012). Higher sedimentation rates, especially in comparison with temperate and boreal regions, may be a result of heavy soil erosion on land as suggested by Baula et al. (2011) and Furio et al. (2006, 2012). For example, the Tanintharyi Region receives more than 2,000 mm of precipitation during the rainy season, and huge amounts of fluvial organic and inorganic particles are transported from rivers and suspended in water, resulting in an extremely high diffuse attenuation coefficient that was recorded as 2.3 m^{-1} (on average) at the river mouth stations (Maung-Saw-Htoo-Thaw et al. 2017). Indeed, during the rainy season, thick and newly accumulated flocculent layers more than 2-cm thick were encountered in the bottom sediments. Such extensive sediment loads, mostly in the prolonged rainy season (lasting nearly six months), lead to unusual sedimentation rates in coastal bottom areas and thus result in lower palynomorph density. Therefore, a relatively high sedimentation rate is apparently an important factor related to relatively low cyst concentrations in tropical coastal areas.

Such extensive turbidity due to the fluvial sediment loads may also lead to palynomorph compositions. However, when the sedimentation rate is the primary driver, it is difficult to determine why the tropical shallow-water dinoflagellate cyst assemblage differs from that of temperate areas. Indeed, Matsuoka et al. (2017) suggested another factor of less light penetration relative to water column irradiance during the rainy season. Such attenuation of light due to rich suspended particles caused a low cell number of photosynthetic plankton, including cyst-forming dinoflagellates in tropical coastal areas. The lower abundance of photo/mixotrophic dinoflagellate cysts such as *Spiniferites* spp. revealed in this study that heterotrophic species cysts were rather abundant. A similar trend was also previously observed around Kadan Island (Su-Myat et al. 2013). During the rainy season, the lower abundance of photosynthetic plankton (mainly diatoms) in the Tanintharyi Region has also been recorded and discussed based on lower irradiance due to abundant sediments transported by the Tanintharyi River by Maung-Saw-Htoo-Thaw et al. (2017). Consequently, the rich

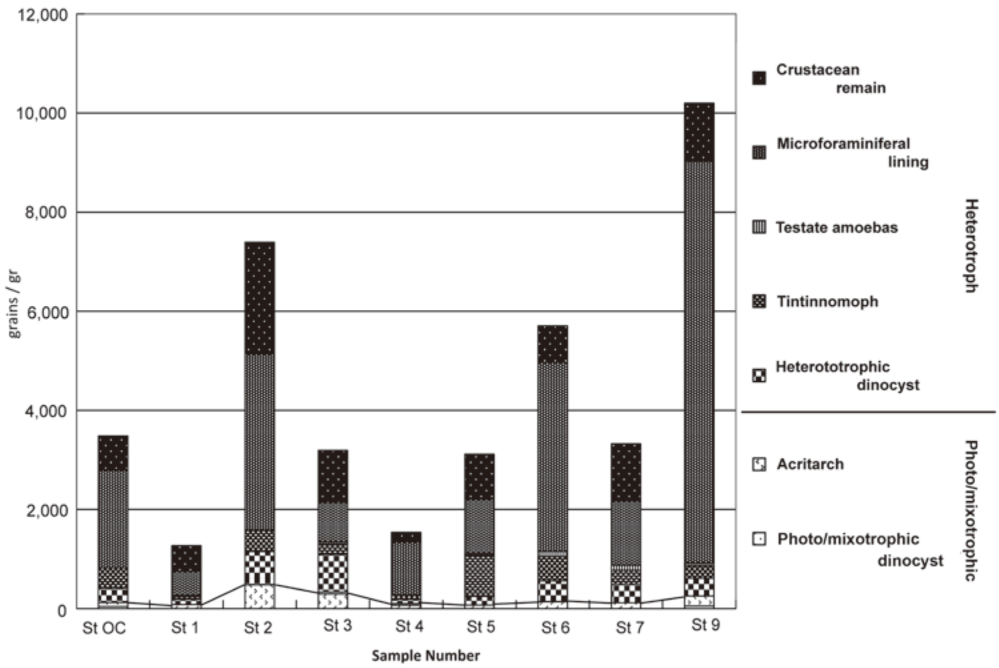

Fig. 4. Composition of marine palynomorphs around Kadan Island in southern Myanmar

suspended substances transported using rivers are another important reason for the less abundant photo/mixotrophic dinoflagellate cysts in the sediments of tropical coastal waters.

2. High proportions of heterotrophic cysts in dinoflagellate cyst assemblages

In this study, it was observed that total dinoflagellate cyst concentrations around Kadan Island were very low and in particular, photo/mixotrophic species belonging to Gonyaulacales were relatively lower than heterotrophic dinoflagellate species. Only two species of photo/mixotrophic species cysts — *Spiniferites bulloideus* and *S. ramosus* — were observed in the present samples. Less abundant photo/mixotrophic dinoflagellate cysts are also known to exist along the coast of Selangor in Malaysia, where heterotrophic species cysts were rather abundant (Matsuoka et al. 2017) as confirmed in the previous study conducted around Kadan Island (Su-Myat et al. 2013). Species abundance of heterotrophic and less photo/mixotrophic dinoflagellate cysts are common traits relative to previous other studies in tropical coastal areas as summarized in Table 2, except for two cases observed along the coasts of Indonesia where a photo/mixotrophic *Pyrodinium bahamense* frequently formed red tides (Mizushima et al. 2007).

As mentioned above, diatoms were found to be less abundant around Kadan Island in the rainy season; this phenomenon is common in tropical coastal mangrove areas due to densely suspended inorganic matter near the mouth of a river (Maung-Saw-Htoo-Thaw et al. 2017). The dominant occurrence of heterotrophic dinoflagellate cysts seems to be a contradictory phenomenon in terms of the reproduction of heterotrophic dinoflagellates, because they need prey organisms. The following observation might be helpful for understanding abundant heterotrophic dinoflagellate cysts with less abundant prey organisms (e.g., diatoms) in the present study. Yurimoto et al. (2015) reported interesting red-tide blooms along the coast of the Gulf of Thailand, consisting of two ecologically different dinoflagellate species—photo/mixotrophic *Ceratium furca* and heterotrophic *Diplopsalis lenticula*. *C. furca* is a non-cyst producing gonyaulacacean dinoflagellate that may form dense blooms in coastal waters in the southern part of the Andaman Sea (Karthik et al. 2014) and in other areas. This species has usually been regarded as autotrophic because it possesses many chloroplasts. However, *C. furca* can also consume ciliates as prey organisms (Bockstahler & Coasts 1993, Smalley et al. 2003) and is thus a phagotrophic species (Stoecker 1999). *C. furca* can reproduce under non-photosynthetically suitable yet unfavorable environmental conditions, such as low light irradiance and nutrient depletion, by switching to an exordial nutrition ratio mixotrophic mode capability and preying on other organisms like bacteria (Stoecker 1999, Jeon et al. 2010). Another species causing dense blooms in the Gulf of Thailand was a cyst-forming heterotrophic species (*Diplopsalis lenticula* belonging to Protoperidiniaceae) that can consume other microorganisms such as diatoms like *Ditylum brightwellii* (Naustvoll 1998). However, according to Yurimoto et al. (2015), diatom densities were rather low when *D. lenticula* formed dense blooms. If preferable prey organisms like diatoms occurred at such low cell densities, *C. furca* at high cell densities could be a possible alternative prey organism for *D. lenticula*. However, there was no evidence that *D. lenticula* digested *C. furca* in the study observation by Yurimoto et al. (2015). This means that no microscopic organisms such as diatoms were present as prey for these two species. On the other hand, *D. lenticula* can also consume bacteria and possibly microflagellates instead of phytoplankton, which occur abundantly in tropical coastal waters (Gasol & Vaque 1993). Unfortunately, Yurimoto et al. (2015) did not report densities on bacteria when both species formed blooms in the Gulf of Thailand. *D. lenticula* cysts were observed around Kandan Island, as were other protoperidiniacean dinoflagellate cysts. The dominance of heterotrophic protoperidiniacean dinoflagellates in marine palynomorph assemblages was also recognized around Kadan Island (this study, Su-myat et al. 2012) and along the coast of Selangor in Malaysia (Matsuoka et al. 2017).

Two different dinoflagellate cyst assemblages are currently recognized from tropical surface sediments of Southeast Asia: one is dominated by photo/mixotrophic cyst species and the other is dominated by heterotrophic cyst species (Table 2). The first type has been observed on the Sunda Shelf in the South China Sea (Kawamura 2004), off South Kalimantan and East Java (Poliakova et al. 2017), and in the eastern Indian Ocean (Hesseler 2003) at sites that are somewhat offshore in deeper waters. In contrast, the second type has been observed in nearshore shallow waters less than 20 m in depth (Baula et al. 2011, Furio et al. 2006, Matsuoka et al. 2017, Mizushima et al. 2007, Su-Myat et al. 2012, this study). Heterotrophic dinoflagellate cysts often dominate nearshore areas even in temperate regions because prey organisms consisting primarily of diatoms are more abundant in these areas due to the nutrient-rich environment as suggested above. However, this is not the case in tropical coastal and nearshore shallow waters where phototrophic plankton is less abundant (Kathiresan & Bingham 2001); this paucity is particularly notable along the Myanmar coast during the rainy monsoon season, probably due to lower light penetration into the water column and unusual nutrient ratios (Maung-Saw-Htoo-Thaw et al. 2017). Thus, heterotrophic dinoflagellate cysts are dominant in nearshore mangroves to river mouth environments. Many possible prey organisms other than diatoms, such as other microorganisms for heterotrophic dinoflagellates including smaller organic particles, bacteria and heterotrophic microflagellates that inhabit such areas, have been observed in the case of *Protoperidinium crassipes* that can feed on rice four

Table 2. Species number of photo/mixotrophic and heterotrophic dinoflagellate cysts in surface sediments of Southeast Asia

Location	Environment	Photo/Mixotrophic species	Heterotrophic species	Reference
Kota Kinabalu Bay	Shallow & coast	12	15	Furio et al. 2006
Tuaran Estuary	Shallow & coast	6	7	
Sipitang Bay	Shallow & coast	12	12	
Kuala Penyu Lagoon	Shallow & coast	7	12	
Bolinao	Shallow & nearshore	12	23	Baula et al. 2012
Ambon Bay	Shallow & nearshore	13	11	Mizushima et al. 2007
Hurun Bay	Shallow & nearshore	14	12	
off Myeik	Shallow & coast	10	32	Su-Myat et al. 2012
Selangor	Shallow & coast	8	23	Matsuoka et al. 2017
Oman	Shallow & nearshore	6	16	
Gulf of Thailand	Shallow & nearshore	7 (11)	6 (10)	Lirdwitayap-rasit 1997
off Saba etc	Shallow & nearshore	7	9 (11)	Lirdwitaya-prasit 1998
Sunda Shelf	Deep & offshore	23	11	Kawamura 2004
Eastern Indian Ocean	Deep & offshore	31	20	Hesseler et al. 2003
Off Jelai River, Kalimantan	Shallow & offshore	13	13	Poliakova et al. 2017*

(Yamaguchi & Horiguchi 2008).

3. Abundance of microforaminiferal linings, tintinnomorphs and crustacean remains

Among other marine palynomorphs, tintinnomorphs, microforaminiferal linings and crustacean (mainly copepods) remains were abundant in surface sediments around Kadan Island, as well as in other tropical shallow-water sediments. These palynomorphs occurred abundantly at Sts. 2, 3, 5, 6, 7 and 9 located offshore as compared with other stations except for St. 7 (Fig. 4). In these marine palynomorph assemblages, microforaminiferal linings should be noted. Around Kadan Island, the marine palynomorph assemblage was dominated by microforaminiferal linings, while dinoflagellate cysts, particularly photo/mixotrophic dinoflagellate cysts, were less abundant as mentioned above. Many articles dealing primarily with tropical dinoflagellate cysts have been published to date in Southeast Asia (Baula et al. 2011, Furio et al. 2006, Kawamura 2004, Lirdwitayaprasit 1997, 1998, Srivilai et al. 2012, Su-Myat et al. 2012). These studies reported lower abundances of dinoflagellate cysts in their samples, but did not quantify other marine palynomorphs. Matsuoka et al. (2017) found abundant microforaminiferal linings in shallow-water sediments along the coast of Selangor in Malaysia and along the coast of Oman. These marine palynomorph assemblages shared the common characteristics of those of Kadan Island. Consequently, fewer dinoflagellate cysts, particularly photo/mixotrophic species, and abundant microforaminiferal linings, tintinnomorphs and crustacean (particularly copepod resting eggs) remains characterize the marine palynomorph assemblage of the shallow mangrove sediments. Around Kadan Island, total marine palynomorphs were more abundant at Sts. 2, 3, 5, 6, 7 and 9, all of which face the open sea except for St. 7. In contrast, palynomorph density was lower at Sts. OC, 1 and 4. Sts. OC and 1 were positioned near the mouth of the Tanintharyi River and St. 4 was located in a mangrove channel. These features suggest that near Sts. OC, 1 and 4, the volumes of sediment particles provided by the Tanintharyi River were greater than that of Sts. 2, 3, 5, 6 and 9 as discussed above.

To understand the dominance of heterotrophic marine palynomorphs including heterotrophic dinoflagellates in tropical shallow-water coastal areas, it is important to know the prey-predator relationships (i.e., food web) in the characteristic coastal environment (i.e., mangroves) among these palynomorphs as discussed later.

4. Characteristics of food webs in mangrove coasts

A diverse variety of organisms (including the marine palynomorphs observed in this study) inhabits the coastal waters, sea floor and sediments in and around mangroves. These diverse organisms consist of viruses, bacteria, fungi, microalgae, macroalgae, sea grasses, protozoa, various metazoa and plants (Kathiresan & Bingham 2001). However, large amounts of organic substances also exist as dissolved and undissolved organic matter in seawater (Libes 1992, Ogawa 2000). In general, the primary producers in a food web consist of two different types. One group is comprised of photo/mixotrophic organisms that include photosynthetic planktonic, benthic and epiphytic microalgae that occur in coastal waters, on the surface of sediments in tidal flats and on submerged plants. More specifically, these organisms include prokaryotic cyanobacteria, eukaryotic diatoms, dinoflagellates, coccolithophorids and others (Fig. 5). However, in coastal mangroves, photosynthetic phytoplankton has less influence on primary production (Kathiresan & Bingham 2001, Maung-Saw-Htoo-Thaw et al. 2017). The other group consists of heterotrophic and chemoautotrophic bacteria that are also well known as important primary prey organisms (Pomeroy 1974). During the post-rainy season around tropical Kadan Island, dissolved organic carbon actually contributes to the reproduction of bacteria due to the extremely high concentration of dissolved organic carbon and high density of bacteria at 3.03-17.8 mg $C \cdot l^{-1}$ and 1.8×10^7 $cells \cdot ml^{-1}$, respectively (Maung-Saw-Htoo-Thaw et al. 2017) that suggest the preservation of abundant organic substances in the sediments.

In the conceptual tropical coastal marine food web shown in Fig. 5, various consumers graze on the primary producers as described above. These grazers include protists and heterotrophic benthic flagellates, such as smaller dinoflagellates, euglenids, cryptomonads, bicosoecids, kinetoplastids and others (Larsen & Patterson 1990). Grazers play an important role in decomposing organic cells and detritus, and in transferring energy from bacteria to metazoans (Sherr et al. 1982). Although not all these organisms can be preserved as remains (fossils) in sediments, several representative groups occurred as palynomorphs. Marine palynomorphs found in the surface sediments of tropical mangroves around Kandan Island included dinoflagellates (cysts), acritarchs, prasinophycean coenobia, tintinnomorphs, testate amoeba, microforaminiferal linings, various body parts from crustaceans (primarily copepods) and resting eggs. Among these palynomorphs, the abundant occurrence of microforaminiferal linings, tintinnomorphs and crustacean (mainly copepods) remains was one characteristic of marine palynomorph assemblages occurring in tropical shallow-water mangrove sediments as suggested by Matsuoka et al. (2017). In particular, low dinoflagellate cyst concentrations were associated with lower phytoplankton production and higher sedimentation rates as explained above, while microforaminiferal linings were more abundant and heterotrophic dinoflagellate cysts were dominant under those conditions (Matsuoka et al. 2017). However, no explanation for the extreme abundance of microforaminiferal linings in these sediments or any

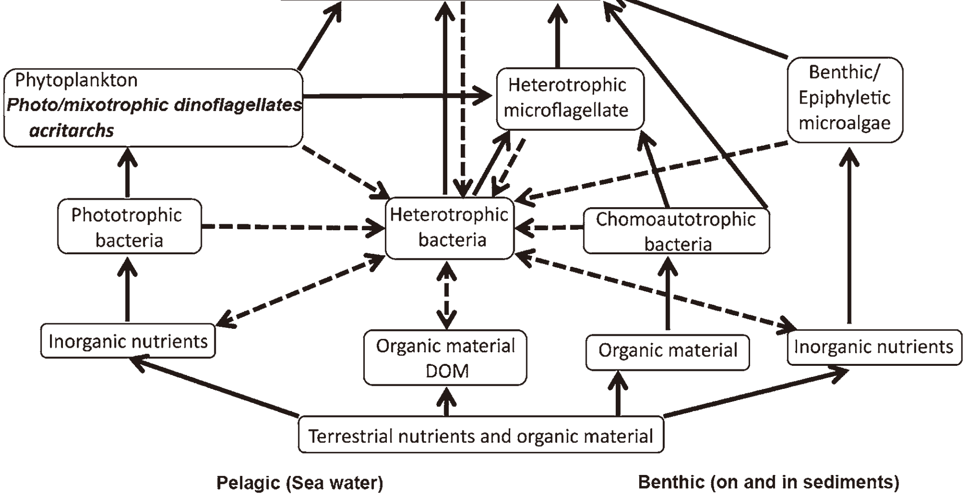

Fig. 5. Conceptual diagram of the ecosystem in lower levels of tropical shallow-water (mangrove) coastal areas.
Benthic foraminifera (microforaminiferal linings) occupy the position as a top predator in this ecosystem.

discussion of their ecological significance has been offered.

5. Significance of the dominance of heterotrophic marine palynomorphs in mangrove food webs

Marine palynomorphs found in tropical mangrove sediments consisted of two ecological types: mixotrophs and heterotrophs (photosynthesizers). In the palynomorph assemblage around Kadan Island, photosynthetic organisms included the gonyaulacoid dinoflagellates *Spiniferites* spp., some acritarchs, and chrysophycean stomatocysts, which were less abundant. All other marine palynomorphs were heterotrophic. The photo/mixotrophic dinoflagellates and acritarchs are primarily planktonic and, along with diatoms, are important primary producers in marine coastal waters. The other marine palynomorph members of Protoctista are planktonic tintinnids and benthic foraminiferans (i.e., organisms originating the microforaminiferal linings), and grazers. Mesozooplankton such as copepods, which have both planktonic and benthic forms, are also consumers. The heterotrophic dinoflagellates are omnivorous and their food sources include bacteria, diatoms, photo/mixotrophic dinoflagellates, ciliates, nanoflagellates and colorless organic detritus particles (Hansen 1991, Jacobson & Anderson 1986). Tintinnids are omnivorous and consume bacteria, diatoms, dinoflagellates, microflagellates (e.g., chlorophytes, chrysophytes, pelagophytes, prasiophytes, pyrenomonadaceae), raphidophytes, other ciliates and small organic particles (Dolan 2013, Montagnes 2013). Benthic foraminiferans are also omnivorous and consume bacteria, pennate diatoms, micro-algae, other protozoans and dead organic material (Armstrong and Braseir 2005, Topping et al. 2006). And the coiled type of microforaminiferal linings (benthic foraminiferans) primarily inhabits shallow coastal areas (e. g. Kitazato 1981). Thus, the remarkable dominance of microforaminiferal linings in sediments along tropical mangrove coasts may be due to abundant bacteria and organic particles preserved in the water and sediments. Copepods are omnivorous and consume diatoms, dinoflagellates, ciliates, fecal pellets and organic detritus (Sherr & Sherr 1988, Taniguchi 1975). Interestingly, these marine palynomorphs are not simple herbivores but are omnivorous. Thus, in tropical mangroves, organic and inorganic substances provided by various organisms form the base of the food web, with complex predator-prey relationships that may support remarkable production and species diversity. Marine palynomorph assemblages observed in the sediments of Kandan Island in southern Myanmar and along the coast of Selangor in Malaysia suggest that the high proportion of heterotrophic microforaminiferal linings and other marine palynomorphs in tropical coastal sediments may be a result of the dominance of microbial loops that start from bacteria and dissolved organic matter. In order to better understand this complex food web in tropical coastal waters and sediments, the coupling biotopes of water and sediment must be further investigated.

Summary

1. Marine palynomorphs found in surface sediments around Kandan Island consisted of dinoflagellate cysts, acritarchs, tintinnomorphs, amoeba testate, microforaminiferal linings and crustacean (mainly copepods) remains.
2. The marine palynomorph assemblages were characterized by the dominance of heterotrophic organisms, especially microforaminiferal linings, and the low abundance of dinoflagellate cysts, especially from photo/mixotrophic species.
3. The abundance of microforaminiferal linings among marine palynomorphs may be due to rich organic and inorganic particles in surface sediments.
4. The extreme dominance of heterotrophic organisms was the result of a significant microbial food web based on the large amount of dissolved and undissolved organic matter and bacteria in the coastal mangrove waters around Kadan Island.

Acknowledgments

The authors wish to express deep appreciation to officials of the Department of Fisheries (Myeik) and the staff from Myeik University in Myanmar for their assistance in our field work. The authors also wish to thank Myanmar Fisheries Federation (MFF) for their kind support of our visit to Myanmar. Finally, the authors wish to thank the two anonymous reviewers for their constructive and helpful comments toward improving this article. This work was partially supported by MEXT/JSPS-Grants-in-aid for Scientific Research (No: 26304031).

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