

**Dinoflagellate cyst
distribution in recent
sediments along the
south-east coast of India***

doi:10.5697/oc.55-4.979
OCEANOLOGIA, 55 (4), 2013.
pp. 979–1003.

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KEYWORDS

Dinoflagellate cysts
Heterotrophic
Phototrophic
South-east coast of India
Coastal sediments

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Received 2 January 2013, revised 2 August 2013, accepted 26 September 2013.

Abstract

The spatial variation in the dinoflagellate cyst assemblage from the south-east coast of India is presented along with a comparison of the cyst abundance from other regions of the world. Samples from 8 stations revealed the presence of 24 species from the genera *Protoperidinium*, *Zygabikodinium*, *Gonyaulax*, *Lingulodinium* and *Gyrodinium*. Cyst abundance was comparatively high at northern stations and was well correlated with the fine-grained (silt-clay dominated) sediments. In contrast, low cyst abundance was recorded in sandy sediments at southern stations. Fourteen cyst-forming dinoflagellate species previously unrecorded in planktonic samples were detected in the sediments. The cyst abundance recorded here is low (29–331 cysts g⁻¹ dry sediment) as compared to sub-tropical and temperate regions, but it is on a par with tropical regions, including the west coast of India.

* The financial support for this work was received from the Ministry of Earth Sciences (MoES) under the Indian XBT programme and the Ballast Water Management programme, funded by the Directorate General of Shipping, India.

The complete text of the paper is available at <http://www.iopan.gda.pl/oceanologia/>

Comparison of the cyst assemblage along the Indian coast revealed a smaller number of potentially harmful and red-tide-forming dinoflagellate species on the south-east coast (6 species) than on the west coast (10 species). Calcareous cysts of the genus *Scrippsiella* reported from the west coast and Visakhapatnam harbour (south-east coast) were not observed in this study although their planktonic cells have been reported.

1. Introduction

Dinoflagellates are a major component of the plankton community and play an important role in marine ecosystem dynamics. They are composed of phototrophic (autotrophic, mixotrophic) and heterotrophic species. Many species of dinoflagellates are known to produce toxins and form harmful algal blooms (HABs). As a consequence of the global increase in HAB events, the study of phytoplankton dynamics, including dinoflagellates and their cysts, has gained in importance. Dinoflagellates are amongst the most unwanted marine bioinvasers. Approximately 200 marine dinoflagellate species are known to form resting cysts (Head 1996) as part of their life cycle; these are known to be well preserved in sediments for several years (Dale 1983) and even for up to a century (Ribeiro et al. 2011). These cysts serve as potential seed banks that can be important to phytoplankton bloom dynamics and species dispersal (Anderson et al. 1995). They remain viable in a ship's ballast-tank sediment and biofilms, subsequently transported to different regions by shipping (Drake et al. 2005). Additionally, resting cysts may be introduced to new locations through shellfish transplantation (Anderson & Wall 1978). The sediments store resting stages produced by the planktonic species present in the region, thus providing a historical archive at different temporal resolutions (Dale 2001a). Cyst mapping of harmful dinoflagellate species assemblages can provide information about the mechanism of recurrence and spreading of HAB species. Moreover, by studying the cysts in a specific region, it is possible to record dinoflagellate species whose pelagic stages are rarely observed and difficult to identify (Hesse et al. 1996).

In spite of the importance of dinoflagellate cysts in understanding the population dynamics of vegetative stages, information from the seas around the Indian subcontinent is very limited and mainly restricted to the west coast of India (Godhe et al. 2000, D'Costa et al. 2008, D'Silva et al. 2011). In the Bay of Bengal, reports are available on cyst occurrence from Late Quaternary sediments (Naidu et al. 2012). Recently, a contemporary cyst assemblage has been studied from recent sediments of Visakhapatnam harbour (D'Silva et al. 2013). To date, information on modern cyst assemblages and their distributions from other parts of the western boundary of the Bay of Bengal is lacking.

This study of the dinoflagellate cyst distribution is the first of its kind from the south-east coast of India. Its aims are i) to evaluate the spatial variation of dinoflagellate cyst assemblages in the surface sediments along the south-east coast of India (western boundary of the Bay of Bengal), ii) to compare planktonic dinoflagellate records and dinoflagellate cyst data, iii) to compare the cyst abundance in the present study with that of other regions, and iv) to identify harmful and potentially harmful species.

2. Material and methods

2.1. Description of the study region

The sampling stations are located on the Indian continental shelf, in the vicinity of the western boundary of the Bay of Bengal (BOB). The physical oceanography of the area is controlled by the monsoon current system. Forming part of the seasonally reversing monsoon-current system, the East Indian Coastal Current (EICC) changes direction twice a year (Shankar et al. 2002). The summer monsoon (May–September) begins in May with strong winds blowing towards the south-west. The clockwise surface current develops in summer, flows in a south-westerly direction with a velocity of $\sim 0.2 \text{ m s}^{-1}$. During the winter monsoons (November–February), winds blow north-eastwards. The surface current flows in an anticlockwise (north-easterly) direction. The current velocity reaches 0.5 m s^{-1} .

The south-east continental shelf of India is a river-dominated shelf system characterized by inputs of fresh water, suspended sediment and nutrients from the Rivers Krishna-Godavari, Cauvery, Ponnaiyar and Penner. The surface water tends to be rich in silicate, supporting the predominance of diatoms throughout the year (Madhu et al. 2006). Weak, localized wind-driven upwelling has been reported in this area during the summer monsoon (Shetye et al. 1991). Oceanographic features like sea surface salinity (SSS) and sea surface temperature (SST) are influenced mainly by the reversing EICC and riverine runoff. The average SSS and SST respectively range from 27.3 to 30.0 PSU and from 25.6 to 34.5°C.

The characteristics of the shelf sediments vary from north to south. The south is dominated by silty-sand, whereas clayey-silt and silty-clay are present in the north (Musale & Desai 2010). The sediments along the continental shelf are thought to be fresh owing to the high sedimentation rate from riverine input.

2.2. Sediment sampling

Surface sediments were collected from 8 stations (covering a distance of 463 nautical miles) off the south-east coast of India (Figure 1, Table 1)

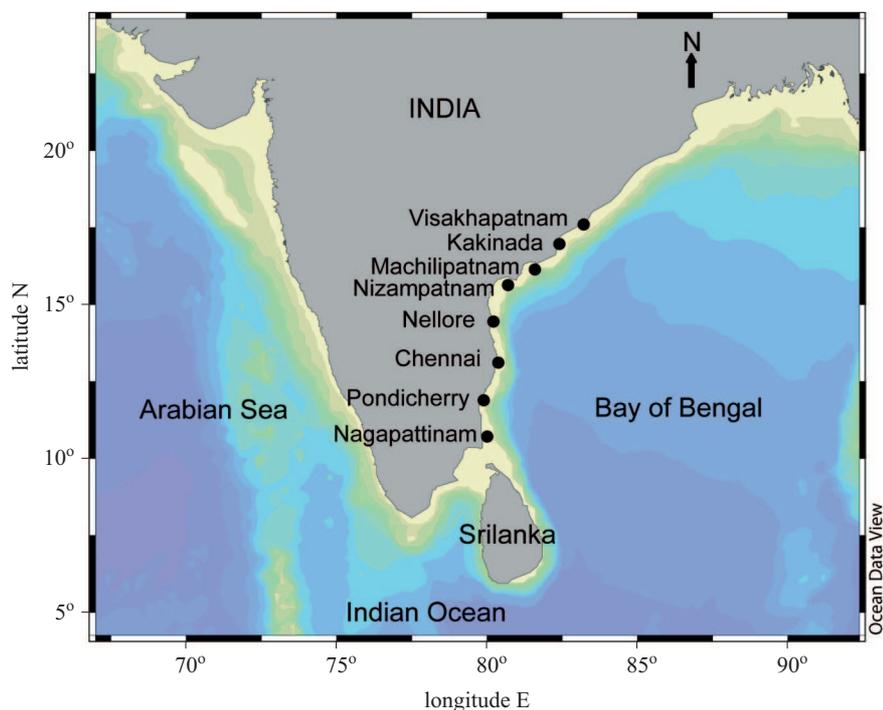


Figure 1. Location of sampling stations along the south-east coast of India

during the Sagar Sukti cruise (SASU 125) in the winter monsoon (December 2006). At each station (except Visakhapatnam) sediment sampling was carried out at 2–3 different sites at intervals of 2 nautical miles. Surface sediment samples were collected using a modified van Veen grab (grabbing area 0.04 m²) equipped with flaps on the top, enabling cores of surface sediments to be collected. Duplicate sediment cores (PVC cores, 25 cm long, inner diameter of 2.5 cm) were obtained with the grab. At Visakhapatnam, a sample was collected at only one position with a gravity corer (1 m length, inner diameter 5 cm). All sediment cores (PVC and gravity) were sectioned at 2 cm intervals, mixed well and stored in airtight plastic bags at 4°C in the dark.

2.3. Sediment preparation, processing and analysis

Sediment samples from the upper 0–2 cm sections of each sediment core were treated using a palynological method (Matsuoka & Fukuyo 2000) with some modifications (D'Costa et al. 2008). A known weight (2–3 g) of wet sediment was repeatedly washed with distilled water to remove salts. The salt-free sample was treated with 7 ml 10% HCl to dissolve calcareous minerals and then with 30% HF to dissolve silicate materials.

Table 1. Geographical coordinates and cyst abundance [cysts g⁻¹ dry sediment] at the sampling stations along the south-east coast of India. Note: data on sediment characteristics for the stations marked with an asterisk was obtained from Musale & Desai (2010)

Station Name	Latitude [°N]	Longitude [°E]	Water depth [m]	Samples analysed	Cyst abundance	Sediment characteristics [%]		
						Sand	Silt	Clay
Visakhapatnam	17.58	83.23	31	6	331	0.7	41.2	58.1
Kakinada*	16.95	82.41	30	10	128	0.8	42.5	56.7
Machilipatnam*	16.15	81.58	27	12	89	1.4	50.0	48.6
Nizampatnam*	15.61	80.66	20	10	59	1.6	67.5	30.9
Nellore*	14.45	80.23	24	8	83	61.5	19.3	19.1
Chennai	13.10	80.40	30	8	45	80.5	13.3	6.2
Pondicherry*	11.91	79.91	27	8	29	79.8	12.4	7.8
Nagapattinam*	10.70	80.03	25	4	63	81.8	11.7	6.5

Each chemically treated sample was rinsed 3–4 times with distilled water to remove acid. Subsequently, the acid-free slurry was sieved through a tier of two different meshes (120 and 20 μm) to remove coarse and fine material. The residue accumulated on the 20 μm mesh was then suspended in 10 ml distilled water and stored in a vial. For the quantification of calcareous cysts, 2–3 g of wet sediment samples were rinsed with distilled water only and sieved through 120 and 20 μm meshes without any acid treatment. The sieved sample (10 ml) was then stored in a vial until further analysis.

For the microscopic identification of dinoflagellate cysts, an aliquot of the processed sample was diluted to a total volume of 2 ml in a transparent Petri dish (3.8 cm diameter), mixed well and placed on the microscope stage. After the sample had settled, the entire Petri dish was scanned under an inverted microscope (Olympus IX 71) equipped with a digital camera (Olympus CAMEDIA C-4040ZOOM) at 100 and 400x magnifications. Depending on the volume of the aliquot, the processed sample was counted in duplicate or a higher number of replicates, such that a total of 2 ml was analysed. Dinoflagellate cysts were identified on the basis of the published literature (Wall & Dale 1968, Sonneman & Hill 1997, Matsuoka & Fukuyo 2000).

A known weight (1 g) of wet sediment sample was dried at 70°C for 24 h to estimate the water content (Matsuoka & Fukuyo 2000). Cyst concentration was calculated as the number of cysts per gram of dry sediment [cysts g^{-1} dry sediment] using the formula $N/W(1 - R)$, where N – number of cysts, W – weight of sediment and R – proportion of water in the sediment.

The percentage grain size composition of the sediment (sand, silt and clay) was determined by standard wet sieving (for sand) and pipette analysis (for silt and clay) (Buchanan 1984). In this study, sediment samples from three stations (Visakhapatnam, Chennai, Nagapattinam) were analysed for grain size composition, while data from other stations and the same period were obtained from Musale & Desai (2010). The size classification used was sand ($> 62 \mu\text{m}$), silt (62–3.9 μm) and clay ($< 3.9 \mu\text{m}$).

To assess the distribution of cyst-producing dinoflagellate species in the study area, the information collected from previous studies (Madhav & Kondalarao 2004) on the distribution of dinoflagellate planktonic cells during different seasons from the same study region is presented together with cyst data (present study; Table 2). Although several reports on phytoplankton distribution are available, we selected for comparison only those in which dinoflagellates from the sampling region (south-east coast of India) were identified down to species level.

Table 2. List of cyst-forming dinoflagellates from the south-east coast of India compiled from earlier published planktonic data (PSEC) and dinoflagellate cysts recorded previously along the west coast (DWC) and the south-east coast (DSEC) i.e. the present study (Pre Stu) and Visakhapatnam harbour (Vizag Har) (*continued on next page*)

Biological name	Palaeontological name	Species code	Planktonic dinoflagellate (PSEC)	Dinoflagellate cyst		
				DWC	DSEC	
					Pre Stu	Vizag Har ⁶
Phototrophic						
<i>Alexandrium affine</i> ^{††}	—			● ⁵		●
<i>Alexandrium cf. affine</i>	—			● ⁴		
<i>Alexandrium minutum</i> [†]	—			● ⁵		●
<i>Alexandrium cf. minutum</i>	—			● ^{3,4}		
<i>Alexandrium tamarense</i> [†]	—			● ⁵		
<i>Alexandrium cf. tamarense</i>	—			● ^{3,4}		
<i>Alexandrium cf. tamiyavanichi</i> [†]	—			● ³		
<i>Alexandrium sp.</i>	—			● ⁵		
<i>Cochlodinium cf. polykrikoides</i>	—			● ^{4,5}		
<i>Cochlodinium sp.</i>	—			● ⁵		●
<i>Gonyaulax diacantha</i>			● ¹			
<i>Gonyaulax digitalis</i>	<i>Spiniferites bentori</i>	GnxD	● ²	● ^{3,4,5}	●	●
<i>Gonyaulax scrippsae</i>	<i>Spiniferites bulloideus</i>	GnxS		● ^{3,4,5}	●	●
<i>Gonyaulax verior</i>	—			● ³		
<i>Gonyaulax spinifera</i> complex [†]	<i>Spiniferites miribilis</i>	GnxSp		● ^{3,4,5}	●	●
	<i>Spiniferites membranaceus</i>			● ^{3,4,5}	●	●
	<i>Spiniferites ramosus</i>			● ^{3,4,5}		
<i>Gonyaulax sp.</i>						●
<i>Gymnodinium catenatum</i> [†]	—			● ³		
<i>Gymnodinium cf. catenatum</i>	—			● ^{4,5}		
<i>Gyrodinium impudicum</i>	—	Gyrl		● ⁵	●	●
<i>Lingulodinium polyedrum</i> [†]	<i>Lingulodinium machaerophorum</i>	LngP		● ^{3,4,5}	●	●
<i>Pentapharsodinium dalei</i>	—			● ^{3,4,5}		●

Table 2. (continued)

Biological name	Palaeontological name	Species code	Planktonic dinoflagellate (PSEC)	Dinoflagellate cyst		
				DWC	DSEC	
					Pre	Stu
<i>Pheopolykrikos hartmannii</i>	–			● ^{3,4,5}		
<i>Protoceratium reticulatum</i> [†]	<i>Operculodinium centrocarpum</i>	PcerR		● ^{3,4,5}	●	●
<i>Pyrodinium</i> cf. <i>bahamense</i>	–			● ⁴		
<i>Pyrodinium bahamense</i> var. <i>compressum</i> [†]	<i>Polysphaeridium zoharyi</i>			● ⁵		
<i>Pyrophacus steinii</i>	<i>Tuberculodinium vancampoae</i>		● ¹	● ^{4,5}		●
<i>Pyrophacus</i> sp.	–			● ⁵		
<i>Scrippsiella trifida</i> [#]	–			● ⁵		
<i>Scrippsiella trochoidea</i> ^{††, #}	–		● ¹	● ^{3,4,5}		●
<i>Scrippsiella</i> sp.	–			● ⁵	●	
Heterotrophic						
<i>Diplopelta parva</i>	–			● ^{3,5}		●
<i>Diplopsalis lenticula</i>	–		● ²	● ^{3,4,5}		
<i>Lebouraia minuta</i>	–			● ⁵		
<i>Lebouraia</i> cf. <i>minuta</i>	–			● ⁴		
<i>Polykrikos kofoidii</i>	–			● ⁵		
<i>Polykrikos</i> cf. <i>kofoidii</i>	–			● ⁴		
<i>Polykrikos schwartzii</i>	–			● ^{3,5}		
<i>Polykrikos</i> cf. <i>schwartzii</i>	–			● ⁴		
<i>Polykrikos</i> sp.	–			● ⁵		
<i>Protoperidinium americanum</i>	–			● ³		
<i>Protoperidinium avellana</i>	<i>Brigantedinium cariacense</i>	PpA		● ³	●	
<i>Protoperidinium</i> cf. <i>avellana</i>	–	PpAva		● ³	●	
<i>Protoperidinium brochii</i>	–		● ²			
<i>Protoperidinium claudicans</i>	<i>Votadinium spinosum</i>	PpCla	● ²	● ^{3,4,5}	●	●
<i>Protoperidinium compressum</i>	<i>Stelladinium stellatum</i>	PpCom		● ^{4,5}	●	●

Table 2. (continued)

Biological name	Palaeontological name	Species code	Planktonic dinoflagellate (PSEC)	Dinoflagellate cyst		
				DWC	DSEC	
					Pre Stu	Vizag Har ⁶
<i>Protoperidinium conicoides</i>	<i>Brigantedinium simplex</i>			● ^{4,5}		
<i>Protoperidinium conicum</i>	<i>Selenopemphix quanta</i>	PpC	● ²	● ^{4,5}	●	●
<i>Protoperidinium denticulatum</i>	<i>Brigantedinium irregulare</i>			● ⁵		●
<i>Protoperidinium divaricatum</i>	<i>Xandarodinium variable</i>			● ^{4,5}		
<i>Protoperidinium excentricum</i>	–		● ²	● ³		
<i>Protoperidinium grandii</i>			● ²			
<i>Protoperidinium latissimum</i>	–	PpLa		● ^{3,4,5}	●	
<i>Protoperidinium leonis</i>	<i>Quinquecuspis concreta</i>	PpL	● ²	● ^{4,5}	●	●
<i>Protoperidinium minutum</i>	–			● ³		
<i>Protoperidinium cf. minutum</i>	–			● ³		
<i>Protoperidinium nudum</i>	–	PpNu		● ³	●	
<i>Protoperidinium oblongum</i>	<i>Votadinium calvum</i>	PpO	● ²	● ^{3,5}	●	●
<i>Protoperidinium pentagonum</i>	<i>Trinovantedinium applanatum</i>	PpPn	● ²	● ^{4,5}	●	
<i>Protoperidinium cf. pentagonum</i>	<i>Trinovantedinium capitatum</i>			● ^{3,4,5}		●
	<i>Brigantedinium majusculum</i>			● ³		
<i>Protoperidinium stellatum</i>	–			● ³		
<i>Protoperidinium subinerme</i>	<i>Selenopemphix nephroides</i>		● ²	● ^{3,4,5}		●
<i>Protoperidinium thorianum</i>	–	PpThr			●	
<i>Protoperidinium sp.</i>	<i>Lejeunecysta sp.</i>	PpsLe		● ⁵	●	
<i>Protoperidinium sp.</i>	<i>Lejeunecysta concreta</i>					●
<i>Protoperidinium sp.</i>	<i>Stelladinium robustum</i>	PpSr		● ^{4,5}	●	
<i>Protoperidinium sp.</i>	<i>Peridinium cf. stellatum</i>					●
<i>Protoperidinium sp.</i>	<i>Trinovantedinium palidifluvium</i>			● ^{4,5}		
<i>Protoperidinium sp.</i>	<i>Brigantedinium sp.</i>					●
<i>Zygabikodinium lenticulatum</i>	<i>Dubridinium caperatum</i>	ZyLen		● ^{4,5}	●	●
<i>Protoperidinium sp. Type 1[§]</i>	–	PpS1			●	

Table 2. (*continued*)

Biological name	Palaeontological name	Species code	Planktonic dinoflagellate (PSEC)	Dinoflagellate cyst		
				DWC	DSEC	
					Pre Stu	Vizag Har ⁶
<i>Protoperidinium</i> sp. Type 2 ^s	–	PpS2		•		
Dinoflagellate cyst type 1 ^s	–	DS1		•		
Dinoflagellate cyst type 2 ^s	–	DS2		•		

References indicated as superscript numbers:

¹unpublished data,

²Madhav & Kondalarao 2004,

³Godhe et al. 2000,

⁴D'Costa et al. 2009,

⁵D'Silva et al. 2011,

⁶D'Silva et al. 2013;

†potentially harmful species;

††red-tide-forming species;

#calcareous cyst;

^sunidentified cyst recorded during present study. As they are not identified down to species level, they have not been considered in the comparison.

In order to evaluate the dinoflagellate cyst composition and identify the harmful and potentially harmful species in the Indian region, the cyst assemblage of the south-east coast of India (D'Silva et al. 2013, present study) is compared with that of the west coast of India (Godhe et al. 2000, D'Costa et al. 2008, D'Silva et al. 2011) and presented in Table 2. The dinoflagellate cyst species identified to species level are only considered for comparison.

2.4. Data analysis

The abundance of dinoflagellate cysts was converted into a lower triangular similarity matrix using the Bray-Curtis coefficient. This similarity matrix was then subjected to cluster analysis by the group average method to evaluate the spatial variation. All the analyses were carried using PRIMER software (version 5).

3. Results

3.1. Dinoflagellate cyst assemblage

A total of 24 dinoflagellate cyst morphotypes were recorded in the sediment samples collected along the south-east coast of India (Table 2; Figure 2). 20 of these 24 cyst types were identified to species level and 2 to genus level (*Protoperidinium* sp. type 1 (PpS1) and *Protoperidinium* sp. type 2 (PpS2); Table 2, Figures 3m–n). The remaining two cyst morphotypes (Figures 3o–p) could not be identified as they lacked identifying structures and germination efforts were not successful.

Hence, depending on their morphology, they are characterized as dinoflagellate cyst type 1 (DC1) or dinoflagellate cyst type 2 (DC2). Furthermore, cysts belonging to the *Gonyaulax spinifera* species complex, i.e. *Spiniferites mirabilis* and *S. membranaceus*, are recorded as *Gonyaulax*

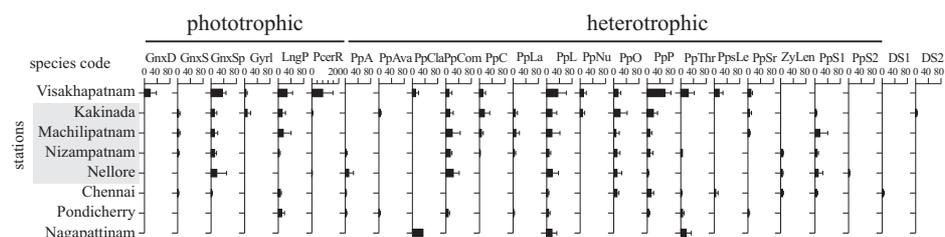


Figure 2. Dinoflagellate cyst abundance [cyst g^{-1} of dry sediment] of each species in the surface sediments at 8 sampling stations along the south-east coast of India. The error bar represents the standard deviation from the mean (for the species code, please refer to Table 2)

spinifera complex in this study. The light microscopy photomicrographs of the dinoflagellate cysts recorded are provided in Figure 3.

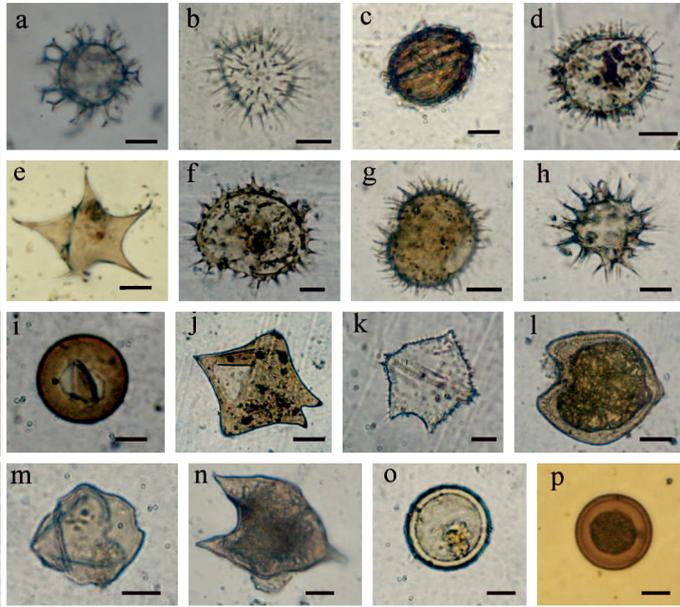


Figure 3. Photomicrographs of dinoflagellate cysts recorded from the recent sediments along the south-east coast of India: *Gonyaulax spinifera* complex (a), *Lingulodinium polyedrum* (b), *Zygabikodinium lenticulatum* (c), *Protoceratium reticulatum* (d), *Protoperidinium compressum* (e), *P. conicum* (f), *P. claudicans* (g), *P. nudum* (h), *P. avellana* (i), *P. latissimum* (j), *P. pentagonum* (k), *P. oblongum* (l), *Protoperidinium* sp. 1 (m), *Protoperidinium* sp. 2 (n), Dinoflagellate cyst type 1 (o), Dinoflagellate cyst type 2 (p). All scale bars 20 μm

The dinoflagellate cyst assemblage was dominated by heterotrophic dinoflagellates (Figures 4a,b,c) represented by 16 species (Figure 2) belonging to the genera *Protoperidinium* (15 species) and *Zygabikodinium* (1 species). Phototrophic dinoflagellates consisted of 6 species (Figure 2) representing four genera: *Gonyaulax* (3 species), *Lingulodinium* (1 species), *Protoceratium* (1 species) and *Gyrodinium* (1 species).

3.2. Dinoflagellate cyst distribution

The dinoflagellate cyst abundance ranged from 29 to 331 cysts g^{-1} dry sediment, and their numbers increased from southern (Nagapattinam) to northern (Visakhapatnam) stations (Figure 4a, Table 1). Cyst abundance

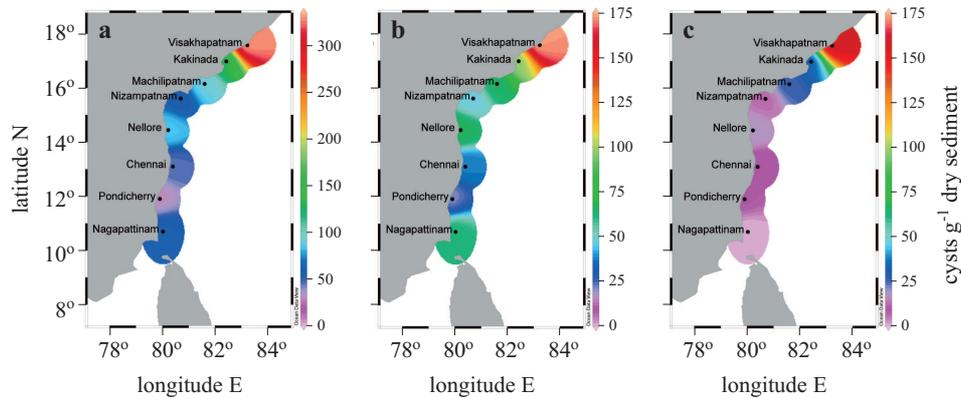


Figure 4. Spatial distribution of total dinoflagellate cysts (a), heterotrophic dinoflagellate cysts (b) and phototrophic dinoflagellate cysts (c)

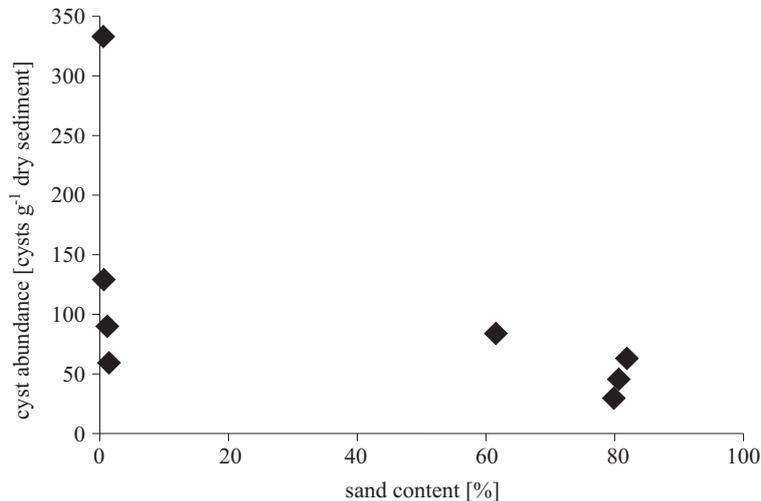


Figure 5. Dinoflagellate cyst abundance [cyst g⁻¹ dry sediment] versus sand content [%] in the surface sediment along the south-east coast of India

was influenced by the sediment characteristics. Cyst abundance was higher in the fine grained (silt-clay dominated) sediments than in the sandy sediments (Table 1, Figure 5). Cluster analysis of the sampling stations based on the dinoflagellate cyst assemblage at the 50% similarity level revealed one group of four stations (Machilipatnam, Kakinada, Nellore and Nizampatnam) and four ungrouped stations (Figure 6). The grouped stations had a higher cyst abundance (59 to 128 cysts g⁻¹ dry sediment). Among the four ungrouped stations, the cyst abundance (331 cysts g⁻¹ dry

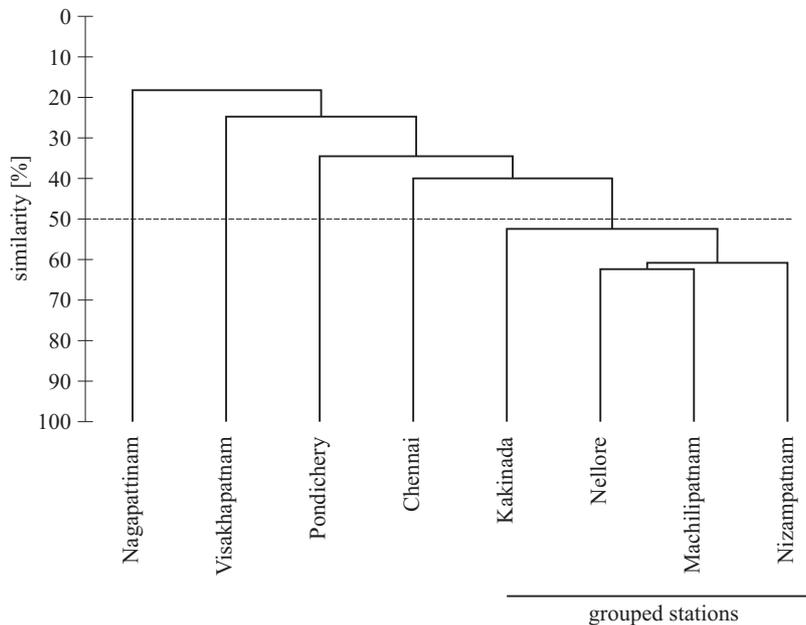


Figure 6. Cluster dendrogram of sampling stations relationship using the Bay-Curtis similarity coefficient and group average method

sediment) was the highest at Visakhapatnam and lower at the other three stations (Nagapattinam, Chennai and Pondicherry; Figure 4a, Table 1).

3.3. Comparison of dinoflagellate cysts and planktonic dinoflagellates

Comparison of the present data with the collated information on the cyst-forming species revealed that 14 cyst-producing dinoflagellate species present in the sediments (cysts) had not been previously identified in planktonic samples (Table 2). Among these, the *Gonyaulax spinifera* complex (2 subspecies), *Lingulodinium polyedrum* and *Protoperidinium compressum* dominated the cyst assemblage and had not been previously recorded in planktonic form. Furthermore, 8 cyst-producing dinoflagellate species previously recorded in the planktonic samples were not observed in their cyst forms (Table 2). Cysts of calcareous cyst-producing species were not observed in the sediment sample treated without acid.

3.4. Comparison of dinoflagellate cysts assemblage between the west and the south-east coasts of India

Taxonomic comparison of the dinoflagellate cyst data between the west and south-east coasts of India showed that although the cyst abundance

was comparable, the species composition was different (Table 2). Along both coasts, cysts belonging to the heterotrophic *Protoperidinium* species dominated the cyst assemblage over phototrophic species. However, the number of phototrophic species was higher along the west coast (26 species) than along the south-east coast (12 species). The number of cysts of potentially harmful and red-tide-forming dinoflagellates along the west coast (10 species) was also comparatively higher than along the south-east coast (6 species). A similar trend was also observed in the case of calcareous cysts between the two coasts. Calcareous cysts reported from the west coast were represented by 3 species belonging to the genus *Scrippsiella*, whereas a cyst of only one species (*S. trochoidea*) was reported from Visakhapatnam harbour on the south-east coast (Table 2). During the present study no calcareous cysts were observed along the south-east coast of India.

4. Discussion

4.1. Comparison of dinoflagellate cyst abundance with different regions

Zonneveld et al. (2013) summarized the global distribution of dinoflagellate cysts from recent sediments and their relationship with environmental conditions. The compilation presented here includes data sets on the dinoflagellate cyst distribution from this study region that were not published in any earlier compilation. The global distribution of dinoflagellate cyst abundance as collated from the literature and the present study is given in Table 3. For this comparison, studies that used similar sample processing (acid treatment) and cyst abundance presentation [cysts g⁻¹ dry sediment] methods are considered. The present compilation revealed that the cyst abundance recorded in this study was low (29 to 331 cysts g⁻¹ dry sediment) as compared to sub-tropical and temperate coastal regions (Table 3). However, the cyst abundance recorded is on a par with that of other tropical regions (Table 3), such as the coasts of south-east Asia (Furio et al. 2012) and the west coast of India (Godhe et al. 2000, D'Costa et al. 2008, D'Silva et al. 2011).

The abundance of dinoflagellate cysts (139 to 75 000 cysts g⁻¹ dry sediment) along the western boundaries of the African subcontinent (Table 3), has been related to intensive upwelling (Targarona et al. 1999, Sprangers et al. 2004, Holzwarth et al. 2007). A high dinoflagellate cyst abundance (100 to 25 000 cysts g⁻¹ dry sediment) is also recorded in the Arctic and Atlantic confluence (Table 3). In sub-polar regions with highly variable nutrient supplies and environmental conditions (Solignac et al. 2009), opportunistic species with higher growth rates are favoured, resulting in

Table 3. Records of dinoflagellate cysts abundance from different parts of the world

Study areas	Cyst abundances	References
a) off south-east Greenland	102–7920	Boessenkool et al. 2001
b) Mediterranean Sea	177–929	Elshanawany et al. 2010
Izmir Bay (Aegean Sea, Eastern Mediterranean)	41–3292	Aydin et al. 2011
c) North Canary Basin, NW Africa	192–13147	Targarona et al. 1999
Benguela upwelling, off SE Africa	139–38580	Holzwarth et al. 2007
Offshore NW Iberia	15000–>75000	Sprangers et al. 2004
d) Chinese Coastal waters	154–113483	Wang et al. 2004
Yellow China Sea	114–20828	Hwang et al. 2011
Geoje Island, Korea	528–2834	Shin et al. 2007
Tokyo Bay, Japan	240–8380	Matsuoka et al. 2003
e) Southern Ocean (eastern Atlantic sector)	74–8714	Esper & Zonneveld 2002
f) Eastern Australia	100–20000	McMinn 1990
g) Sabah, Malaysia	2–411	Furio et al. 2006*
North-western and central Philippines	30–580	Furio et al. (in press)*
North-western Philippines	43–1940	Baula et al. 2008*
h) MPT and JNPT Mumbai, India	36–262	D'Costa et al. 2008
Zuari estuary, India	150–750	Patil (unpublished)
West coast of India	6–1076	D'Silva et al. 2011
i) Visakhapatnam harbour, India	15–1218	D'Silva et al. 2012
South-east coast of India	29–331	present study

*obtained from Furio et al. 2012.

a lower species richness (Barton et al. 2010). In the Mediterranean Sea (Table 3) the high cyst abundance is influenced mainly by river plumes and eutrophic waters in coastal regions (Elshanawany et al. 2010, Aydin et al. 2011). Another region where high cyst numbers are reported embraces the waters around China, Korea and Japan (Table 3); this has been related to eutrophication (Matsuoka et al. 2003, Shin et al. 2007). Furthermore, a high abundance (in thousands) of dinoflagellate cysts has been recorded in sediment traps in the western Arabian Sea upwelling region (Zonneveld & Brummer 2000). Compared to these numbers, the dinoflagellate cyst

abundance reported along the coasts of India is low (Table 3), even though the west coast of this subcontinent is influenced by upwelling and the south-west monsoon. However, further intensive studies are needed to investigate the reason for the small numbers of dinoflagellate cysts in the region.

4.2. Cyst assemblages along the south-east coast of India

Along the south-east coast of India, the cyst abundance decreases from north to south (Figure 4a). It has been observed that the differences in cyst abundance and assemblage composition between areas are caused primarily by differences in the abundance of vegetative cells and their cyst production efficiencies, and/or by differences in the hydrology and the sedimentary regime (Dale 1983, Anderson et al. 1995, Joyce et al. 2005). Dinoflagellate cysts are believed to have the hydrodynamic characteristics of fine silt-sized particles (Dale 1983, Kawamura 2004) and can be transported by water currents. In the study area, the abundance of dinoflagellate cysts can be correlated with the texture of the sediment, i.e. silt and clayey sediment. A high cyst abundance was encountered in the fine-grained (silt and clayey) sediments as compared to the sandy sediments (Table 1, Figure 5). The southern stations (Chennai, Pondicherry and Nagapattinam, 3 ungrouped stations, Figure 6) contain a high percentage of sand, which is not suitable for cyst deposition (Dale 1983), while the sediments at the northern stations (Nellore, Nizampatnam, Machilipatnam, Kakinada and Visakhapatnam) are characterized by high percentage of silt-clay and a high cyst abundance (Table 1, Figure 5). These results indicate that sediment grain size plays a major role in determining the cyst distribution in this area.

Apart from this, other processes, like bio- and oxidative degradation, benthic predation and bioturbation, also influence the cyst assemblage and distribution in the sediments (Zonneveld et al. 1997, Persson & Rosenberg 2003). A contemporaneous study investigating the macrobenthic community along the south-east coast of India (Musale & Desai 2010) indicated the dominance of burrowing and subsurface deposit-feeding polychaetes (e.g. *Magelona cincta*, *Cirratulus* sp., *Capitella capitata* etc.), and bivalves in the silty-clayey sediments at the northern stations (Nellore, Nizampatnam, Machilipatnam and Kakinada), where cyst abundance was comparatively higher. At Pondicherry, the loose sandy sediment harboured only a few surface feeding polychaetes (*Prionospio* spp., *Amphiarete* sp.) and the cyst abundance was low. It has been reported that *Protooperidinium* cysts are more susceptible to degradation by the activity of deposit-feeding animals than the cysts of phototrophic species such as *P. reticulatum*, *L. polyedrum* and *Spiniferites* spp. (Persson & Rosenberg 2003). However, in this study, *Protooperidinium* cysts were dominant, indicating that bioturbation and

predation by benthic fauna are unlikely to be the major factors determining the composition of the cyst assemblages.

Another contemporaneous study from the west coast of India (D'Silva et al. 2011) reported the dominance of heterotrophic forms (*Protooperidinium* spp.). Their dominance is generally attributed to i) elevated nutrient concentrations and high productivity (Harland et al. 2006), ii) the availability of prey organisms such as diatoms (Matsuoka et al. 2003, Godhe & McQuoid 2003), iii) reduced light intensity (Dale 2001b) and iv) the smaller production of phototrophic dinoflagellates (Dale 2001b). As in any other tropical coastal environment, the high nutrient supply through riverine material, the dominance of diatoms (Madhu et al. 2006) and the low light penetration due to suspended riverine loads could be the governing factors ensuring the dominance of heterotrophic dinoflagellates over phototrophic dinoflagellates in this coastal region.

At Visakhapatnam station, phototrophic species (*P. reticulatum*, *L. polyedrum* and *Gonyaulax* spp.) contributed significantly to the total cyst abundance (Figure 2). Earlier studies indicated that the dominance of phototrophic forms can be influenced by variable salinity regimes, nutrient inputs and sediment texture (Dale 2000, Godhe & McQuoid 2003, Kawamura 2004). The dominance of *P. reticulatum* in Visakhapatnam harbour has also been correlated with elevated nutrient inputs (D'Silva et al. 2013). The present sampling station at Visakhapatnam is part of the mesotrophic environment (Tripathy et al. 2005) in the vicinity of Visakhapatnam harbour and is influenced by a varying salinity (range 17 to 35 PSU) that is due to terrestrial runoff and the current circulation pattern (Vijaykumaran 2005). It is possible that a high nutrient input and varying salinity regimes could be the reason for the dominance of phototrophic forms. Cysts of *Alexandrium affine*, *A. minutum*, *Cochlodinium* sp., *Pentaparsodinium dalei*, *Pyrophacus steinii*, *Diplopelta parva*, *Protooperidinium denticulatum* and *P. subinermis*, reported from Visakhapatnam harbour (D'Silva et al. 2013), were not observed at this station, which is located approximately 4 km away from the harbour.

4.3. Comparison of dinoflagellate cysts and planktonic dinoflagellates

Analysis of planktonic and sediment samples enables identification of both motile and cyst stages, thus providing the best information on the dinoflagellate species composition (Dale 1983). Generally, the number of dinoflagellate species in a study area increases when information on cysts is included in the study (Persson & Rosenberg 2003, Orlova et al. 2004, Satta et al. 2010).

Fourteen cyst-forming dinoflagellate species not previously identified in planktonic samples were detected in the sediments analysed in this study (Table 2). This may be due to the sample preservation technique, which sometimes alters the morphology of planktonic cells. Particularly, the light microscopic identification of naked/unarmoured vegetative dinoflagellates is more difficult in the preserved state than of their cyst forms. The small size thecate *Gonyaulax* species like *G. spinifera*, *G. scrippsae* are very difficult to differentiate in poorly preserved samples. Apart from this, the identification of small thecate dinoflagellates is difficult without an exhaustive thecal plate analysis (Orlova et al. 2004). Consequently, some taxa of the genera *Protoperidinium*, *Gonyaulax*, *Gymnodinium* and *Gyrodinium* are usually identified only to generic level. These identification difficulties affect the comparative taxonomic analysis.

Seasonal cycles in the occurrence of vegetative cells and benthic cysts could be another factor for the mismatch.

On the other hand, the eight cyst-forming dinoflagellate species observed in planktonic form were previously not recorded in the recent sediments (Table 2). This may be attributed to i) the low production of cysts in the water column, which is insufficient to produce a detectable quantity of cysts; ii) the acids used in the palynological method of sediment preparation, which dissolve the calcareous cyst wall and/or cyst. Hence calcareous cyst-forming *S. trochoidea* and other *Scripsiella* spp. may be overlooked in such samples (Montresor et al. 1998). This could result in an underestimation of the total dinoflagellate cyst abundance. To resolve this, microscopic analysis of untreated, distilled water cleaned and sieved sediment samples was carried out. The absence of these species in an untreated sediment sample highlights the undetectable quantity of cyst production rather than the methodology used for sediment preparation.

4.4. Comparison of the dinoflagellate cyst assemblages along the west and the south-east coasts of India

Taxonomic comparison of the present data with the dinoflagellate cyst studies from the west coast of India (Godhe et al. 2000, D'Costa et al. 2008, D'Silva et al. 2011) indicates that the total number of cyst-forming species (26 phototrophic species and 33 heterotrophic species) is higher along the west coast than the south-east coast (12 phototrophs and 21 heterotrophs). Comparison of the data sets also showed that calcareous cysts of the genera *Scripsiella* reported from the west coast were not observed along the south-east coast in this study, even though their vegetative cells were reported in the planktonic samples (Table 2). However, the occurrence of these cysts has been reported from Visakhapatnam harbour (D'Silva et al. 2013).

The reason for the absence of calcareous cysts in the present sediment samples is not known and needs detailed investigation. Apart from that, cysts of eight potentially harmful dinoflagellate species, i.e. *A. minutum*, *A. tamarense*, *A. cf. tamiyavanichii*, *G. spinifera*, *Gymnodinium catenatum*, *L. polyedrum*, *P. reticulatum*, *Pyrodinium bahamense* var. *compressum* (IOC-UNESCO Taxonomic reference list of harmful micro algae, web: <http://www.marinespecies.org/HAB./dinoflag.php>, accessed 28 June 2013), and two red-tide-forming species, i.e. *A. affine* and *S. trochoidea* (Garate-Lizarraga et al. 2001, Su-Myat & Koike 2013) have been recorded from the surface sediments of the west coast of India (Table 2). Sediment core analyses from the west coast of India have reported the presence of *A. affine*, *A. minutum*, *G. spinifera*, *L. polyedrum*, *P. reticulatum* and *S. trochoidea* since the early 1900s (D'Silva et al. 2012). Incidences of HABs and outbreaks of paralytic shellfish poisoning (PSP) have also occurred along the west coast of India (Godhe et al. 2000). Compared to this, only three potentially toxic yessotoxin (YTX)-producing species *G. spinifera*, *P. reticulatum* and *L. polyedrum* have been reported from the surface sediments of the south-east coast of India. Moreover, the red-tide-forming species *A. affine* and *S. trochoidea*, as well as the potentially PSP producing species *A. minutum* have been reported from Visakhapatnam harbour (D'Silva et al. 2013). Oceanographic features like intensive coastal upwelling and anthropogenic input influence the dinoflagellate cyst composition along the west coast of India (D'Silva et al. 2011). Furthermore, D'Costa et al. (2008) observed the potential of the south-west monsoon to influence the seasonal cycling between planktonic dinoflagellates in the water column and cysts in the sediment.

In view of the influence of the south-west and north-east monsoons along the south-east coast of India, it is possible that the changes brought about by these events could affect the dinoflagellate cyst composition. This needs further elucidation.

5. Conclusion

The present study of the dinoflagellate cyst distribution along the south-east coast of India recorded a southward decrease in cyst abundance that was influenced mainly by sediment texture (a high cyst abundance in silt-clay and a low one in sandy sediments). Fourteen cyst-forming dinoflagellate species including three potentially harmful ones (*G. spinifera*, *P. reticulatum* and *L. polyedrum*), not previously reported in planktonic samples, were recorded for the first time. Cyst abundance along the south-east coast of India is low compared to subtropical and temperate coastal regions, but is similar to that in other tropical regions, including the west coast of India.

Comparatively, the number of potentially harmful cyst-forming species is less than that reported from the west coast.

Acknowledgements

We are grateful to Dr S.R. Shetye, Director, National Institute of Oceanography, Goa for his support. We acknowledge the crew and participants of the CRV *Sagar Sukti* for their valuable assistance. We thank Dr Ravidas Naik, Dr Shamina D'Silva, Mr Vinayak Kulkarni and Mr Rajath Chitari for their help. DDN is grateful to CSIR for being awarded the senior research fellowship (SRF). This is an NIO contribution (No. 5478).

References

- Anderson D.M., Fukuyo Y., Matsuoka K., 1995, *Cyst methodologies*, [in:] *Manual on harmful marine microalgae*, G.M. Hallegraeff, D.M. Anderson & A.D. Cembella (eds.), IOC Manuals and Guides, Vol. 33, UNESCO, Paris, 229–245.
- Anderson D.M., Wall D., 1978, *The potential importance of benthic cysts of Gonyaulax tamarensis and Gonyaulax excavata in initiating toxic dinoflagellate blooms*, J. Phycol., 14 (2), 224–234, <http://dx.doi.org/10.1111/j.1529-8817.1978.tb02452.x>.
- Aydin H., Matsuoka K., Minareci E., 2011, *Distribution of dinoflagellate cysts in recent sediments from Izmir Bay (Aegean Sea, Eastern Mediterranean)*, Mar. Micropaleontol., 80 (1–2), 44–52, <http://dx.doi.org/10.1016/j.marmicro.2011.03.004>.
- Barton A.D., Dutkiewicz S., Flierl G., Bragg J., Follows M.J., 2010, *Patterns of diversity in marine phytoplankton*, Science, 327, 1509–1511, <http://dx.doi.org/10.1126/science.1184961>.
- Boessenkool K. P., Gelder M. V., Brinkhuis H., Troelstra S. R., 2001, *Distribution of organic-walled dinoflagellate cysts in surface sediments from transects across the Polar Front offshore southeast Greenland*, J. Quaternary Sci., 16 (7), 661–666, <http://dx.doi.org/10.1002/jqs.654>.
- Buchanan J.B., 1984, *Sediment analysis*, [in:] *Methods for the study of marine benthos*, N.A. Holme & A.D. McIntyre (eds.), Blackwell Sci. Publ., Oxford, 45–65.
- Dale B., 1983, *Dinoflagellate resting cysts: 'Benthic plankton'*, [in:] *Survival strategies of the algae*, G. A. Fryxell (ed.), Cambridge Univ. Press, Cambridge, 69–136.
- Dale B., 2000, *Dinoflagellate cysts as indicators of cultural eutrophication and industrial pollution in coastal sediments*, [in:] *The application of microfossils to environmental geology*, R.E. Martin (ed.), Kluwer Acad., Plenum Publ., New York, 305–321.
- Dale B., 2001a, *The sedimentary records of dinoflagellate cysts: Looking back into the future of phytoplankton blooms*, Sci. Mar., 65 (2), 257–272.

- Dale B., 2001b, *Marine dinoflagellate cysts as indicators of eutrophication and industrial pollution: A discussion*, *Sci. Total Environ.*, 264 (3), 235–240, [http://dx.doi.org/10.1016/S0048-9697\(00\)00719-1](http://dx.doi.org/10.1016/S0048-9697(00)00719-1).
- D'Costa P. M., Anil A. C., Patil J. S., Hegde S., D'Silva M. S., Chourasia M., 2008, *Dinoflagellates in a mesotrophic, tropical environment influenced by monsoon*, *Estuar. Coast. Shelf Sci.*, 77 (1), 77–90, <http://dx.doi.org/10.1016/j.ecss.2007.09.002>.
- Drake L. A., Meyer A. E., Forsberg R. L., Baier R. E., Doblin M. A., Heinemann S., Johnson W. P., Koch M., Rublee P. A., Dobbs F. C., 2005, *Potential invasion of microorganisms and pathogens via 'interior hull fouling': Biofilms inside ballast-water tanks*, *Biol. Invasions*, 7 (6), 969–982, <http://dx.doi.org/10.1007/s10530-004-3001-8>.
- D'Silva M. S., Anil A. C., D'Costa P. M., 2011, *An overview of dinoflagellate cysts in recent sediments along the west coast of India*, *Indian J. Geo.-Mar. Sci.*, 40 (5), 697–709.
- D'Silva M. S., Anil A. C., Borole D. V., Nath B. N., Singhal R. K., 2012, *Tracking the history of dinoflagellate cyst assemblages in sediments from the west coast of India*, *J. Sea Res.*, 73, 86–100, <http://dx.doi.org/10.1016/j.seares.2012.06.013>.
- D'Silva S. M., Anil A. C., Savant S. S., 2013, *Dinoflagellate cyst assemblages in recent sediments of Visakhapatnam harbour, east coast of India: Influence of environmental characteristics*, *Mar. Pollut. Bull.*, 66 (1–2), 59–72, <http://dx.doi.org/10.1016/j.marpolbul.2012.11.012>.
- Elshaniwany R., Zonneveld K., Ibrahim M. I., Kholeif S. E. A., 2010, *Distribution patterns of recent organic-walled dinoflagellate cysts in relation to environmental parameters in the Mediterranean Sea*, *Palynology*, 34 (2), 233–260, <http://dx.doi.org/10.1080/01916121003711665>.
- Esper O., Zonneveld K. A. F., 2002, *Distribution of organic-walled dinoflagellate cysts in surface sediments of the Southern Ocean (eastern Atlantic sector) between the Subtropical Front and the Weddell Gyre*, *Mar. Micropaleontol.*, 46 (1–2), 177–208, [http://dx.doi.org/10.1016/S0377-8398\(02\)00041-5](http://dx.doi.org/10.1016/S0377-8398(02)00041-5).
- Furio E. F., Azanza R. V., Fukuyo Y., Matsuoka K., 2012, *Review of geographical distribution of dinoflagellate cysts in Southeast Asian coasts*, *Coast. Mar. Sci.*, 35 (1), 20–33.
- Garate-Lizarraga I., Hernandez-Orozco M. L., Band-Schmidt C. J., Serrano-Casillas G., 2001, *Red tides along the coasts of the Baja California Sur, Mexico (1984 to 1999)*, *Oceanides*, 16 (2), 127–134.
- Godhe A., Karunasagar I., Karlson B., 2000, *Dinoflagellate cysts in recent marine sediments from SW India*, *Bot. Mar.*, 43 (1), 39–48, <http://dx.doi.org/10.1515/BOT.2000.004>.
- Godhe A., McQuoid M. R., 2003, *Influence of benthic and pelagic environmental factors on the distribution of dinoflagellate cysts in surface sediments along the Swedish west coast*, *Aquat. Microb. Ecol.*, 32, 185–201, <http://dx.doi.org/10.3354/ame032185>.

- Harland R., Nordberg K., Filipsson H.L., 2006, *Dinoflagellate cysts and hydrographical change in Gullmar Fjord, west coast of Sweden*, *Sci. Total Environ.*, 355(1–3), 204–231, <http://dx.doi.org/10.1016/j.scitotenv.2005.02.030>.
- Head M.J., 1996, *Modern dinoflagellate cysts and their biological affinities*, [in:] *Palynology principles and applications*, J. Janosnius & D.C. McGregor (eds.), AASP Foundation, Dallas, 1197–1248.
- Hesse K.J., Tillmann U., Nehring S., Brockmann U., 1996, *Factors controlling phytoplankton distribution in coastal waters of the German Bight North Sea*, [in:] *Biology and ecology of shallow Coastal waters*, A. Eleftheriou, A.D. Ansell & C.J. Smith (eds.), Olsen and Olsen, Fredensborg, 11–22.
- Holzwarth U., Esper O., Zonneveld K., 2007, *Distribution of organic-walled dinoflagellate cysts in shelf surface sediments of the Benguela upwelling system in relationship to environmental conditions*, *Mar. Micropaleontol.*, 64(1–2), 91–119, <http://dx.doi.org/10.1016/j.marmicro.2007.04.001>.
- Hwang C.-H., Kim K.-Y., Lee Y., Kim C.-H., 2011, *Spatial distribution of dinoflagellate resting cysts in Yellow Sea surface sediments*, *Algae*, 26(1), 41–50, <http://dx.doi.org/10.4490/algae.2011.26.1.041>.
- Joyce L.B., Pitcher G.C., du Randt A., Monteiro P.M.S., 2005, *Dinoflagellate cysts from surface sediments of Saldanha Bay, South Africa: an indication of the potential risk of harmful algal blooms*, *Harmful Algae*, 4(2), 309–318, <http://dx.doi.org/10.1016/j.hal.2004.08.001>.
- Kawamura H., 2004, *Dinoflagellate cyst distribution along a shelf to slope transect of an oligotrophic tropical sea (Sunda Shelf, South China Sea)*, *Phycol. Res.*, 52(4), 355–375, <http://dx.doi.org/10.1111/j.1440-1835.2004.tb00345.x>.
- Madhav V.G., Kondalarao B., 2004, *Distribution of phytoplankton in the coastal waters of east coast of India*, *Indian J. Geo.-Mar. Sci.*, 33(3), 262–268.
- Madhu N.V., Jyothibabu R., Maheswaran P.A., Gerson V.J., Gopalakrishnan T.C., Nair K.K.C., 2006, *Lack of seasonality in phytoplankton standing stock (chlorophyll a) and production in the western Bay of Bengal*, *Cont. Shelf Res.*, 26(16), 1868–1883, <http://dx.doi.org/10.1016/j.csr.2006.06.004>.
- Matsuoka K., Fukuyo Y., 2000, *Technical guide for modern dinoflagellate cyst study*, WESTPAC-HAB/WESTPAC/IOC, Japan Soc. Promotion Sci.
- Matsuoka K., Joyce L.B., Kotani Y., Matsuyama Y., 2003, *Modern dinoflagellate cysts in hypertrophic coastal waters of Tokyo Bay, Japan*, *J. Plankton Res.*, 25(12), 1461–1470, <http://dx.doi.org/10.1093/plankt/fbg111>.
- McMinn A., 1990, *Recent dinoflagellate cyst distribution in eastern Australia*, *Rev. Palaeobot. Palyno.*, 65(1–4), 305–310, [http://dx.doi.org/10.1016/0034-6667\(90\)90080-3](http://dx.doi.org/10.1016/0034-6667(90)90080-3).
- Moestrup Ø., Akselman R., Cronberg G., Elbraechter M., Fraga S., Halim Y., Hansen G., Hoppenrath M., Larsen J., Lundholm N., Nguyen L.N., Zingone A., (eds.), 2009 onwards, *IOC-UNESCO taxonomic reference list of harmful micro algae*, [available online at <http://www.marinespecies.org/HAB>], (accessed on 2013-6-28).

- Montresor M., Zingone A., Sarno D., 1998, *Dinoflagellate cyst production at a coastal Mediterranean site*, J. Plankton Res., 20(12), 2291–2312, <http://dx.doi.org/10.1093/plankt/20.12.2291>.
- Musale A.S., Desai D.V., 2010, *Distribution and abundance of macrobenthic polychaetes along the South Indian coast*, Environ. Monit. Assess., 178(1–4), 423–436, <http://dx.doi.org/10.1007/s10661-010-1701-3>.
- Naidu P.D., Patil J.S., Narale D.D., Anil A.C., 2012, *A first look at the dinoflagellate cysts abundance in the Bay of Bengal: Implications on late quaternary productivity and climate change*, Curr. Sci., 102(3), 495–498.
- Orlova T. Y., Morozova T. V., Gribble K. E., Kulis D. M., Anderson D. M., 2004, *Dinoflagellate cysts in recent marine sediments from the east coast of Russia*, Bot. Mar., 47(3), 184–201, <http://dx.doi.org/10.1515/BOT.2004.019>.
- Persson A., Rosenberg R., 2003, *Impact of grazing and bioturbation of marine benthic deposit feeders on dinoflagellate cysts*, Harmful Algae, 2(1), 43–50, [http://dx.doi.org/10.1016/S1568-9883\(03\)00003-9](http://dx.doi.org/10.1016/S1568-9883(03)00003-9).
- Ribeiro S., Berge T., Lundholm N., Andersen T. J., Abrantes F., Ellegaard M., 2011, *Phytoplankton growth after a century of dormancy illuminates past resilience to catastrophic darkness*, Nat. Commun., 2, 311, <http://dx.doi.org/10.1038/ncomms1314>.
- Satta C.T., Angles S., Garce E., Lugli A., Padedda B.M., Sechi N., 2010, *Dinoflagellate cysts in recent sediments from two semi-enclosed areas of the Western Mediterranean Sea subject to high human impact*, Deep-Sea Res. Pt. II, 57(3–4), 256–267, <http://dx.doi.org/10.1016/j.dsr2.2009.09.013>.
- Shankar D., Vinayachandran P.N., Unnikrishnan A.S., 2002, *The monsoon currents in the north Indian Ocean*, Prog. Oceanogr., 52(1), 63–120, [http://dx.doi.org/10.1016/S0079-6611\(02\)00024-1](http://dx.doi.org/10.1016/S0079-6611(02)00024-1).
- Shetye S.R., Shenoi S.S.C., Gouveia A.D., Michael G.S., Sundar D., Nampoothiri G., 1991, *Wind-driven coastal upwelling along the eastern boundary of Bay of Bengal during southwest monsoon*, Cont. Shelf Res., 11(11), 1397–1408, [http://dx.doi.org/10.1016/0278-4343\(91\)90042-5](http://dx.doi.org/10.1016/0278-4343(91)90042-5).
- Shin H. H., Yoon Y. H., Matsuoka K., 2007, *Modern dinoflagellate cysts distribution off the eastern part of Geoje Island, Korea*, Ocean Sci. J., 42(1), 31–39, <http://dx.doi.org/10.1007/BF03020908>.
- Solignac S., Grosfeld K., Giraudeau J., de Vernal A., 2009, *Distribution of recent dinocyst assemblages in the western Barents Sea*, Norw. J. Geol., 89, 109–119.
- Sonneman J.A., Hill D.R.A., 1997, *A taxonomic survey of cyst-producing dinoflagellates from recent sediments of Victorian coastal waters, Australia*, Bot. Mar., 40(1–6), 149–178.
- Sprangers M., Dammers N., Brinkhuis H., van Weering T. C. E., Lotter A. F., 2004, *Modern organic-walled dinoflagellate cyst distribution offshore NW Iberia, tracing the upwelling system*, Rev. Palaeobot. Palyno., 128(1–2), 97–106, [http://dx.doi.org/10.1016/S0034-6667\(03\)00114-3](http://dx.doi.org/10.1016/S0034-6667(03)00114-3).

- Su-Myat, Koike K., 2013, *A red tide off the Myanmar coast: Morphological and genetic identification of the dinoflagellate composition*, *Harmful Algae*, 27 (7), 149–158, <http://dx.doi.org/10.1016/j.hal.2013.05.010>.
- Targarona J., Warnaar J., Boessenkool K. P., Brinkhuis H., Canals M., 1999, *Recent dinoflagellate cyst distribution in the North Canary Basin, NW Africa*, *Grana*, 38 (2–3), 170–178, <http://dx.doi.org/10.1080/00173139908559225>.
- Tripathy S. C., Kusumakimari B. A. V. L., Sarma V. V., Murty T. V. R., 2005, *Evaluation of trophic state and plankton abundance from the environmental parameters of Visakhapatnam Harbour and near-shore waters, east coast of India*, *Asian J. Microbiol. Biotech. Env. Sc.*, 7 (4), 831–838.
- Vijaykumaran K., 2005, *Productivity parameters in relation to hydrography of the inshore surface waters off Visakhapatnam*, *J. Mar. Biol. Ass. India*, 47 (2), 115–120.
- Wall D., Dale B., 1968, *Modern dinoflagellate cysts and evolution of the Peridinales*, *Micropaleontology*, 14 (3), 265–304, <http://dx.doi.org/10.2307/1484690>.
- Wang Z. H., Matsuoka K., Qi Y. Z., Chen J. F., Lu S. H., 2004, *Dinoflagellate cyst records in recent sediments from Daya Bay, South China Sea*, *Phycol. Res.*, 52 (4), 396–407, <http://dx.doi.org/10.1111/j.1440-1835.2004.tb00348.x>.
- Zonneveld K. A. F., Versteegh G. J. M., deLange G. J., 1997, *Preservation of organic-walled dinoflagellate cysts in different oxygen regimes: A 10 000 year natural experiment*, *Mar. Micropaleontol.*, 29 (3–4), 393–405, [http://dx.doi.org/10.1016/S0377-8398\(96\)00032-1](http://dx.doi.org/10.1016/S0377-8398(96)00032-1).
- Zonneveld K. A. F., Brummer G. J. A., 2000, *Palaeo-ecological significance, transport and preservation of organic walled dinoflagellate cysts in the Somali Basin, NW Arabian Sea*, *Deep-Sea Res. Pt. II*, 47 (9–11), 2229–2256, [http://dx.doi.org/10.1016/S0967-0645\(00\)00023-0](http://dx.doi.org/10.1016/S0967-0645(00)00023-0).
- Zonneveld K. A. F., Marret F., Versteegh G. J. M., Bogus K., Bouimetarhana I., Crouch E., de Vernal A., Elshanawany R., Esper O., Forke S., Grøsfjeld K., Henry M., Holzwarth U., Bonnet S., Edwards L., Kieft J.-F., Kim S.-Y., Ladouceur S., Ledu D., Chen L., Limoges A., Lu S.-H., Mahmoud M. S., Marino G., Matsuoka K., Londeix L., Matthiessen J., Mildenhall D. C., Mudie P., Neil H. L., Pospelova V., Qi Y., Radi T., Rochon A., Sangiorgi F., Solignac S., Turon J.-L., Wang Y., Wang Z., Young M., Richerol T., Verleye T., 2013, *Atlas of modern dinoflagellate cyst distribution based on 2405 datapoints*, *Rev. Palaeobot. Palyno.*, 191, 1–198, <http://dx.doi.org/10.1016/j.revpalbo.2012.08.003>.