

Vegetative cell and cyst assemblages of armored dinoflagellates in Onagawa Bay, northeast Japan

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Abstract: The vegetative cell and cyst assemblages of armored dinoflagellates were investigated in Onagawa Bay on the northeastern Pacific coast of Japan. In the water column of the bay, 82 vegetative species of armored dinoflagellates in total were identified throughout the whole study period from October 1992 to April 1994. Among the 82 species, 27 were known cyst-forming species. In the sediments, 28 distinctive cyst morphotypes were observed. The diverse cyst assemblage indicated the mixed characteristics of warm and cold waters in the bay. According to known linkages between vegetative cells and cysts, 24 vegetative species were assigned for the 28 cyst morphotypes. Among these 24, 21 vegetative species occurred in the water column of the bay. This number is 78 % of the cyst-forming species (27 species) observed in the water column. In both, vegetative cell and cyst assemblages, *Gonyaulax spinifera*, *Protoperidinium conicoides* and *Scrippsiella trochoidea* dominated. These results indicate that the cysts in the sediments may act as a seed population and play an important role in the population dynamics of dinoflagellates in the bay. Furthermore, this study reveals that the innermost part of the bay is a major site as a cyst depository.

Key words: dinoflagellates, vegetative cells, cysts, Onagawa Bay

Introduction

Among the dinoflagellates, many species produce resting cysts during their life cycles (cf. Dale 1983). Numerous studies have succeeded in taxonomically linking dinoflagellate cysts with their vegetative stages by laboratory incubation of the cysts (e.g. Wall & Dale 1966, 1968, 1971; Wall et al. 1967, 1970; Fukuyo et al. 1977; Matsuoka et al. 1982, 1988, 1990; Lewis et al. 1984; Matsuoka 1984, 1988; Kobayashi & Matsuoka 1984; Bolch & Hallegraeff 1990; Lewis 1990, 1991). Despite the recognition that may play an important role in bloom phenomena (Wall 1971, 1975; Anderson & Wall 1978; Dale 1983; Anderson 1984), few studies of the species composition and abundance of dinoflagellate cysts in bottom sediments have been carried out in Japanese coastal waters (Matsuoka 1976, 1982, 1985, 1987a; Kobayashi et al. 1986; Kobayashi & Yuki 1991; Kim & Matsuoka 1998). For improved understanding of population dynamics and species succession of dinoflagellates in a particular sea, it is necessary to examine not only their vegetative cell assemblage but also their cyst assem-

blage, which may play a role as “seed populations” in dinoflagellate population dynamics (Wall 1971; Steidinger 1975; Ishikawa & Taniguchi 1996).

Onagawa Bay (38° 25'N, 141° 30'E) is the southernmost embayment on the Pacific coast of Sanriku District, northeastern Honshu, Japan (Iwabuchi & Kikuchi 1985). The mouth of the bay is rather wide (ca. 4 km) and opens to the North Pacific Ocean. This topography allows water exchange between the inside and outside of the bay. It is known that, off Onagawa Bay, three major currents are present: the cold-water Oyashio Currents, the warm-water Kuroshio Current and the Tsugaru Warm Current (Taniguchi & Kawamura 1991). The last one originates from a branch of the Kuroshio or the Tsushima Warm Current in the Japan Sea. Water in the bay is affected directly and/or indirectly by these currents seasonally (Ishikawa 1992). No systematic investigation of the circulation system in the bay has been performed, but high species diversity in the diatom assemblage of the bay indicates their mixed influence (Inoue 1995). There have been few detailed studies of the species composition of vegetative populations of dinoflagellates in the bay and even fewer of the cysts.

In this paper, we report: (1) vegetative cell assemblage of

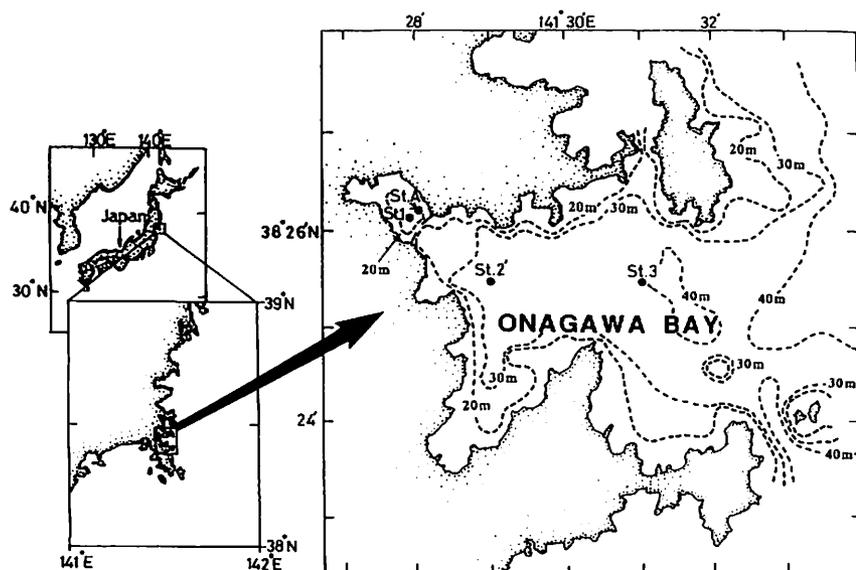


Fig. 1. Location of sampling stations in Onagawa Bay with bathymetric contours.

the armored dinoflagellates occurring in the water column in Onagawa Bay, (2) cyst assemblage of the armored dinoflagellates found in the surface sediments of the bay, (3) relationship between the cyst and the vegetative cell assemblages, and (4) abundance of cysts and their distribution. As a whole, this study was designed to evaluate the ecological function of seed population in naturally occurring armored dinoflagellate assemblages of vegetative cells in the water column in Onagawa Bay.

Materials and Methods

Study sites

In this study, 4 stations (Stns A, 1, 2' and 3) were sampled seasonally (Fig. 1). Stations A and 1 were located in the harbor, Stn 2' at the center of Onagawa Bay and Stn 3 at the mouth of the bay. Positions, average depths and sediment qualities at the stations are shown in Table 1.

Vegetative cell assemblage

Water samples were collected with a Van-Dorn sampler at depths of 0, 5 and 10 m and 0.5 m above the bottom at Stn A, 0 and 10 m at Stn 1, 0 and 15 m at Stn 2' and 0 and 20 m at Stn 3. The samplings were carried out 3 to 7 times a

Table 1. Position, average depth and sediment quality at 4 stations in Onagawa Bay.

Station	Position		Average depth (m)	Sediment quality
A	38°26.27'N	141°28.00'E	17	Mud
1	38°26.06'N	141°28.12'E	22	Mud
2'	38°25.50'N	141°29.00'E	33	Muddy sand
3	38°25.50'N	141°31.00'E	39	Sandy mud

month from October 1992 to January 1994 and once a month from February to April 1994 at Stn A, and once a month from September 1992 to October 1993, except for August 1993, at Stns 1, 2' and 3. Total number of sampling trips and water samples collected were 81 and 350, respectively. All the methods of sampling and fixation were kept unchanged throughout the study period. Water samples were fixed immediately after sampling by adding borax-buffered formaldehyde solution at a final concentration of 2%. Depending on the density of cells, 50- to 100-ml aliquot of the samples was settled in an Utermöhl chamber for at least 12 h and counting of armored dinoflagellate cells and identification of the species were done under an Olympus IMT-2 inverted microscope at 200 or 400 \times magnifications (usually 200 \times). In this study, density (cells l^{-1}) of the vegetative populations of armored dinoflagellates at the surface (0 m) of the 4 stations was determined monthly. In the case of Stn A, the cell densities were averaged for every month during the period from October 1992 to January 1994. Among the top five dominant species, cyst-forming ones were selected to determine the seasonal changes.

The identification of the species was made by referring to Abé (1981), Fukuyo (1981), Dodge (1982, 1989a), Fukuyo ex Fukuyo & Toriumi (1987), Toriumi ex Fukuyo & Toriumi (1987), Fukuyo et al. (1990) and Matsuoka et al. (1990). Species identified were rearranged on the basis of the recent taxonomic system employed by Steidinger (1997).

Cyst assemblage

Sediment samples were obtained at all the stations (Fig. 1) with a midget Smith-McIntyre grab sampler (bucket size: 26 cm long \times 23 cm wide \times 12.5 cm deep). Sampling was made once a month during the period of water sampling except at Stn A, where sediment was sampled for a

shorter period than water sampling, i.e., from October 1992 to January 1994. Four subcores were taken from the bucket, using polycarbonate tubes of 3.5 cm in diameter. The top 1 cm of each core was then sliced off and placed together into a sample bottle to allow for any small-scale heterogeneity in distribution within the sampled area (26×23 cm). For counting of cyst number in sediment, the sediment samples were treated according to a modification of the method described by Matsuoka et al. (1989). Namely, 2 g of wet sediment were suspended in ca. 50 ml of filtered sea water and sonicated for several seconds to release the cysts from aggregated materials. Then, the suspension was sieved through a 100- μm mesh onto a 20- μm mesh screen. The sieved fraction (20 to 100 μm) was resuspended in 20 ml of the filtered sea water. Thus, a final suspension at a concentration of 0.1 g ml⁻¹ of the original wet sediment was obtained. The suspensions made were fixed immediately by adding borax-buffered formaldehyde solution at a final concentration of 2%. From the fixed suspension a 0.25- or 0.5-ml (usually 0.25-ml) aliquot was spread over a slide glass to count dinoflagellate cysts by species under an Olympus BH-2 microscope at 100 or 200× magnifications (usually 100×). Living cysts which were filled with cytoplasm and empty cysts after germination were counted separately. The number of cysts was converted into density cm⁻³ of wet sediment by measuring the specific gravity of the original sediment. Finally, the number was averaged throughout the study period at each station. In total 55 sediment samples were examined in triplicate, giving 165 counts.

Identification of cysts was made by referring to Wall & Dale (1968), Harland (1982), Kobayashi & Matsuoka (1984), Lewis et al. (1984), Matsuoka (1982, 1985, 1987a, b), Fukuyo (1985), Bolch & Hallegraeff (1990), Matsuoka et al. (1990) and Lewis (1991). Since many cyst species of the armored dinoflagellates have long been named in paleontology, these are denoted with "†" marks in this paper. This description makes the present results comparable to previous reports which use mostly paleontological names.

Results

Vegetative populations

Over the course of this study, from October 1990 to April 1994, 82 species including 66 identified, 7 uncertain and 9 unidentified species with 4 groups of mixed unidentified species of armored dinoflagellates were observed in the water samples. On the basis of the taxonomic system of Steidinger (1997), these 82 species and 4 groups were classified into 18 genera of 11 families (Table 2). Among them, 27 species were reported to be cyst-forming. The rest 55 species have not been known to be cyst-forming so far, while more links of vegetative cells and cysts would possibly be found in future.

The abundance of the total vegetative populations at the surface was generally high, being 10⁴–10⁵ cells l⁻¹, during

the summer period from July to September but low, being 10²–10³ cells l⁻¹, during the winter and spring periods from November/December to April (Figs 2, 3). Thirteen out of 27 cyst-forming species dominated the populations (Figs 2, 3). Since *Alexandrium catenella* and *A. tamarense* were not distinguishable in routine work, they were counted as a single taxon (*Alexandrium* spp.) in the present analysis. The cells counted as *Scrippsiella trochoidea* might include a small amount of other 3 species, i.e. *S. crystallina*, *S. precaria* and *S. rotunda* (cf. Ishikawa 1992; cf. Ishikawa & Taniguchi 1993). Among these dominant species, *S. trochoidea* was almost always the most dominant at all the stations, occasionally occupying more than 50% of the total vegetative cells during the period from April to October. Following *S. trochoidea*, cyst-forming *Protoperidinium conicooides* and *Gonyaulax spinifera* were also dominant. In the cold season from December to April when *S. trochoidea* was less abundant, *P. conicooides* often appeared as a leading species. *Gonyaulax spinifera* was once the most dominant species occupying 69% of the total vegetative cells in December 1993 at Stn A.

Cyst populations

Under the taxonomic system for vegetative cells (Steidinger 1997), the 28 cyst morphotypes of armored dinoflagellates found in cyst assemblage in Onagawa Bay are referable to five categories, i.e., Goniodomataceae, Gonyaulacaceae, Calciodinellaceae, Kolkwitzellaceae and Protoperidiniaceae. By current paleontological taxonomy (e.g. Matsuoka 1987b), while 17 of the 28 can be identified to the species of 8 genera, the rest 11 cyst morphotypes have not been named (Table 3). Light microphotographs of some of these cysts in the bay are shown in Fig. 4. Cysts of naked forms such as *Pheopolykrikos hartmannii* and *Polykrikos schwartzii* (Polykrikaceae), though commonly found, were not included in the present study.

Of the paleontologically named species, 3 morphotypes of †*Spiniferites* (†*S. membranaceus*, †*S. mirabilis*, †*S. ramosus*) are referable to a single vegetative species (*G. spinifera*) in modern taxonomy (cf. Matsuoka 1987b). In conclusion, all cyst morphotypes found in Onagawa Bay could be referable to 24 species and to 1 group of unidentified species of modern armored forms (Table 3). Among these species, *G. digitale* and *P. americanum* did not occur in vegetative populations. In addition, since cysts of *A. catenella* and *A. tamarense* were counted as a single taxon, 21 cyst species were confirmed to occur in vegetative populations in Onagawa Bay. This number represents 78% of the cyst-forming species (27 species) and 26% of 82 vegetative species found in the water samples during this study period from October 1990 to April 1994. On the other hand, while the vegetative cells of 4 species reported to be cyst-forming, *Heterocapsa triquetra*, *Oblea rotunda*, *P. minutum* and *Pyrophacus horologium*, were observed in the water column (Table 2), their cysts were not found in the sediments.

Table 2. List of species of armored dinoflagellates (vegetative cells) observed in Onagawa Bay during the period from October 1990 through April 1994.

Family Prorocentraceae	Family Pyrophacaceae
<i>Prorocentrum balticum</i> (Lohmann) Loeblich III	<i>Pyrophacus horologium</i> Stein*
<i>P. compressum</i> (Bailey) Abé ex Dodge	
<i>P. micans</i> Ehrenberg	Family Calciodinellaceae
<i>P. triestinum</i> Schiller	<i>Ensiculifera carinata</i> Matsuoka, Kobayashi & Gains*
Family Dinophysiaceae	<i>Scrippsiella crystallina</i> Lewis*
<i>Dinophysis acuminata</i> Claparède & Lachmann	<i>S. precaria</i> Montresor & Zingone*
<i>D. caudata</i> Saville-Kent	<i>S. rotunda</i> Lewis*
<i>D. fortii</i> Pavillard	<i>S. trochoidea</i> (Stein) Loeblich III*
<i>D. infundibulus</i> Schiller	
<i>D. norvegica</i> Claparède & Lachmann	Family Kolkwitziellaceae
<i>D. tripos</i> Gourret	<i>Diplopsalis lenticula</i> Bergh*
<i>D. spp.</i>	<i>Oblea rotunda</i> (Lebour) Balech ex Sournia*
<i>Phalacroma mitra</i> Schütt	<i>Preperidinium meunieri</i> (Pavillard) Elbrächter*
<i>P. rotundatum</i> (Claparède & Lachmann) Kofoid & Michener	
<i>P. sp. 1</i>	Family Peridiniaceae
Family Oxyphysaceae	<i>Heterocapsa triquetra</i> (Ehrenberg) Stein*
<i>Oxyphysis oxytoxoides</i> Kofoid	<i>Peridinium quiniuecorne</i> Abé
Family Ceratiaceae	Family Protoperidiniaceae
<i>Ceratium arietinum</i> Cleve	<i>Protoperidinium bipes</i> (Paulsen) Balech
<i>C. azoricum</i> Cleve	<i>P. brevipes</i> (Paulsen) Balech
<i>C. candelabrum</i> (Ehrenberg) Stein	<i>P. claudicans</i> (Paulsen) Balech*
<i>C. deflexum</i> (Kofoid) Jörgensen	<i>P. conicoides</i> (Paulsen) Balech*
<i>C. furca</i> (Ehrenberg) Claparède & Lachmann	<i>P. conicum</i> (Gran) Balech*
<i>C. fuscum</i> (Ehrenberg) Dujardin	<i>P. crassipes</i> (Kofoid) Balech
<i>C. gibberum</i> Gourret	<i>P. denticulatum</i> (Gran & Braarud) Balech*
<i>C. inflatum</i> (Kofoid) Jörgensen	<i>P. depressum</i> (Bailey) Balech
<i>C. kofoidii</i> Jörgensen	<i>P. divergens</i> (Ehrenberg) Balech
<i>C. macroceros</i> (Ehrenberg) Vanhöffen	<i>P. granii</i> (Ostenfeld) Balech
<i>C. tripos</i> (O. F. Müller) Nitzsch	<i>P. islandicum</i> (Paulsen) Balech
<i>C. sp. cf. horridum</i> (Cleve) Gran	<i>P. leonis</i> (Pavillard) Balech*
<i>C. sp. 1</i>	<i>P. minutum</i> (Kofoid) Loeblich III*
<i>C. sp. 2</i>	<i>P. mite</i> (Pavillard) Balech
<i>C. spp.</i>	<i>P. oblongum</i> (Aurivillius) Parke & Dodge*
Family Goniodomataceae	<i>P. ovatum</i> Pauchet
<i>Alexandrium catenella</i> (Whedon & Kofoid) Balech*	<i>P. pellucidum</i> Bergh
<i>A. tamarense</i> (Lebour) Balech*	<i>P. pentagonum</i> (Gran) Balech*
Family Gonyaulacaceae	<i>P. pyriforme</i> (Paulsen) Balech
<i>Amylax tracantha</i> (Jörgensen) Sournia	<i>P. roseum</i> (Paulsen) Balech
<i>Gonyaulax grindleyi</i> Reinecke*	<i>P. subpyriforme</i> (Dangeard) Balech
<i>G. polygramma</i> Stein	<i>P. sp. cf. cerasus</i> (Paulsen) Balech
<i>G. scrippsate</i> Kofoid*	<i>P. sp. cf. mariebouria</i> (Paulsen) Balech
<i>G. spinifera</i> (Claparède & Lachmann) Diesing*	<i>P. sp. cf. nipponicum</i> (Abé) Balech
<i>G. turbynei</i> Murray & Whitting	<i>P. sp. cf. pallidum</i> (Ostenfeld) Balech
<i>G. verior</i> Sournia*	<i>P. sp. cf. subinermis</i> (Paulsen) Loeblich III*
<i>G. spp.</i>	<i>P. sp. cf. thorianum</i> (Paulsen) Balech*
<i>Lingulodinium polyedrum</i> (Stein) Dodge*	<i>P. sp. 1</i>
	<i>P. sp. 2</i>
	<i>P. sp. 3</i>
	<i>P. sp. 4</i>
	<i>P. sp. 5</i>
	<i>P. sp. 6</i>
	<i>P. spp.</i>

* Known cyst-forming species.

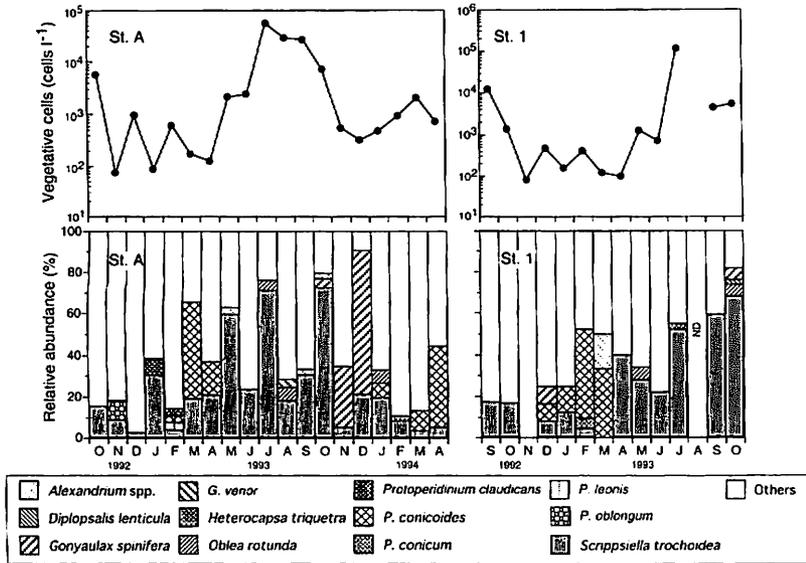


Fig. 2. Seasonal changes in density (upper panel) and in species composition (lower panel) of vegetative populations of armored dinoflagellates observed at the surface (0 m) at Stns A and I in Onagawa Bay during the period from October 1992 to April 1994 and from September 1992 to October 1993, respectively. At Stn A, the cell density was averaged monthly during the period from October 1992 to January 1994, since sampling was carried out 3 to 7 times a month. Of the top five dominant species in the vegetative populations, cyst-forming ones were selected and illustrated in the lower panel. *Alexandrium catenella* and *A. tamarense* were collected as a single taxon (*Alexandrium* spp.). Others include both cyst-forming species, which were not dominant, and non-cyst-forming species. ND denotes no data.

The total cyst abundance (including both living and empty cysts) in the top 1 cm of the sediment, averaged throughout the study period, decreased from the inner (2736, 3064 cysts cm^{-3}) to the outer parts (824 cysts cm^{-3}) of the bay (Table 4). In the cyst assemblage, Protoperidiniaceae was most dominant followed by the Calciodinellaceae and then followed by the Gonyaulacaceae at all stations. The Goniodomataceae and Kolkwitzellaceae were minor in the assemblage. Among the Protoperidiniaceae, *P. conicoides* (*†Brigantedinium simplex*) was the leading species in number, while its cysts were almost totally empty (Table 4). Among the living cysts of the Protoperidiniaceae, *Protoperidinium* spp. were the main component. In case of

the cysts of the Calciodinellaceae, *S. trochoidea* was predominant (75–90% of the Calciodinellaceae), while other *Scrippsiella* species were very rare. *Scrippsiella trochoidea* was also the most dominant species among total cyst species occupying 20–30% of the total number in the bay. The Gonyaulacaceae was dominated by *G. spinifera* (*†S. membranaceus*, *†S. mirabilis* and *†S. ramosus*) at Stns A, 1 and 2'.

Species composition and density of the cyst assemblage were rather stable throughout the year, relative to their vegetative populations (cf. Ishikawa 1995). Therefore, the data averaged throughout the study period (Table 4) represents the characteristic feature of the cyst assemblage in Onagawa Bay. Such average values can also reduce the technical variability of individual data, due to counting error.

Discussion

Vegetative cell assemblage of armored dinoflagellates

Ishikawa (1992) reported 62 of the 82 species from inner harbor of the bay during the period from October to November 1992, so this study records an additional 20 species found from November 1992 to April 1994. This means that more than 82 species may occur in Onagawa Bay on a longer term basis. In other areas, only a few studies dealt with dinoflagellate assemblages on more than an annual basis (Dale 1976; Dodge 1989b; Kobayashi & Yuki 1991). Comparing to these limited data, the number of armored species in Onagawa Bay exceeds the total number of species, including both armored and naked forms, in Trondheimsfjord, Norway (57 species, Dale 1976) and Matoya Bay, Japan (79 species, Kobayashi & Yuki 1991), and is comparable to the total number of species of both forms from North Sutherland, Scotland (85 species, Dodge 1989b). The complex hydrographic conditions in Onagawa

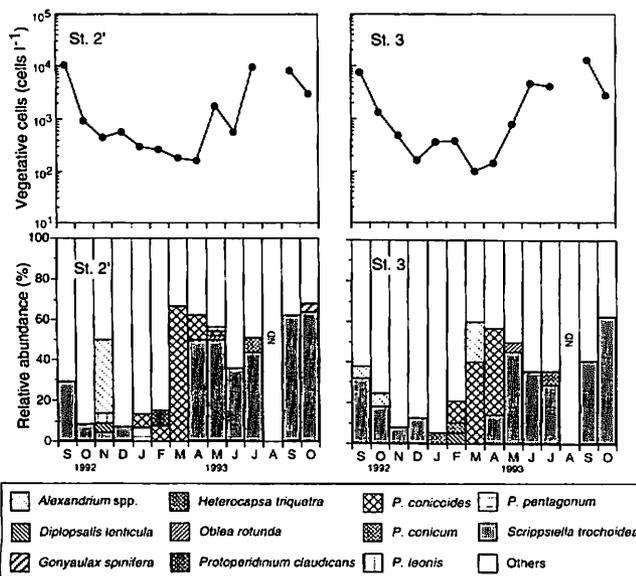


Fig. 3. As in Fig. 2, but at Stns 2' and 3 where water sampling was carried out during the period from September 1992 to October 1993.

Table 3. Vegetative cell–cyst links of armored dinoflagellates recovered from surface sediments of Onagawa Bay. NP: no photograph was taken.

Plankton name	Paleontological name	Microphotograph No. of the cyst	References ^d
Goniodomataceae			
<i>Alexandrium catenella</i> ^a and/or <i>A. tamarense</i> ^a	not named	Fig. 4A	1 2, 3
Gonyaulacaceae			
<i>Gonyaulax grindleyi</i>	not named	Fig. 4B	4
<i>G. digitale</i> ^b	<i>Spiniferites bentori</i>	NP	5
<i>G. scrippsae</i>	<i>S. bulloideus</i>	NP	5
<i>G. spinifera</i>	<i>S. membranaceus</i>	NP	6
	<i>S. mirabilis</i>	NP	5
	<i>S. ramosus</i>	NP	5
<i>G. verior</i>	not named	NP	7
<i>Lingulodinium polyedrum</i>	<i>Lingulodinium machaerophorum</i>	NP	5
Calciadinellaceae			
<i>Ensiculifera carinata</i>	not named	Fig. 4C	8
<i>Scrippsiella crystallina</i>	not named	Fig. 4D	9
<i>S. precaria</i>	not named	Fig. 4E	10
<i>S. rotunda</i>	not named	Fig. 4F	9
<i>S. trochoidea</i>	not named	Fig. 4G	11
Kolkwitzellaceae			
<i>Diplopsalis lenticula</i>	not named	NP	5
<i>Preperidinium meunieri</i>	<i>Dubridinium caperatum</i>	Fig. 4H	5
Protoperidiniaceae			
<i>Protoperidinium americanum</i> ^b	not named	Fig. 4I	6, 12, 13
<i>P. claudicans</i>	<i>Votadinium spinosum</i>	Fig. 4J	5
<i>P. conicoides</i>	<i>Brigantedinium simplex</i>	Fig. 4K, L	5
<i>P. conicum</i>	<i>Selenopemphix quanta</i>	Fig. 4M	5, 14
<i>P. denticulatum</i>	not named	Fig. 4N	15
<i>P. leonis</i>	<i>Quinquecuspsis concretum</i>	Fig. 4O	5
<i>P. oblongum</i>	<i>V. calvum</i>	NP	5
<i>P. pentagonum</i>	<i>Trinovantedinium capitatum</i>	Fig. 4P	5, 16
<i>P. subinerme</i>	<i>S. atlanticum</i>	NP	13, 17
<i>P. spp.</i>	<i>Brigantedinium</i> sp. 1 ^c	Fig. 4Q	
	<i>Selenopemphix</i> sp. ^c	NP	18
	<i>Votadinium</i> sp. ^c	NP	18

^a Could not distinguish cyst species between *A. catenella* and *A. tamarense*.

^b No vegetative cells were observed in water samples.

^c Vegetative cells is unknown.

^d 1, Yoshimatsu (1981); 2, Dale (1977); 3, Fukuyo (1985); 4, Matsuoka et al. (1997); 5, Wall & Dale (1968); 6, Dale (1976); 7, Matsuoka et al. (1988); 8, Matsuoka et al. (1990); 9, Lewis (1991); 10, Montresor & Zingone (1988); 11, Wall et al. (1970); 12, Matsuoka (1987a); 13, Bolch & Halegraef (1990); 14, Kobayashi & Matsuoka (1984); 15, Sonneman & Hill (1997); 16, Lewis et al. (1984); 17, Matsuoka (1982); 18, Matsuoka (1987b).

Bay influenced by three different currents, i.e., Oyashio Currents, Kuroshio Current and the Tsugaru Warm Current is likely to be the main reason for the higher species diversity, especially of non-cyst-forming dinoflagellates. Seasonal occurrences and alternation of distinctive indicator species of different water masses, such as *Chaetoceros mesanensis* (warm oceanic), *Thalassiosira nordenskiöldii* (cold oceanic), *C. curvisetus* (warm cosmopolitan) and *C. debilis* (cold cosmopolitan), were also recorded for the diatom assemblage in the bay (Inoue 1995).

Cyst assemblage of armored dinoflagellates

There are several studies dealing with cyst assemblages in the sediments of Japanese coastal areas. According to Matsuoka (1976), in coastal area off Hachinohe, Japan, the cysts of Protoperidiniaceae dominate in near shore sediments, whereas the cysts of Gonyaulacaceae (*Spiniferites* spp.) and *Pyrophacus steinii* (*Tuberculodinium vancampoeae*) are very rare. The cysts of *G. grindleyi* (reported as *Operculodinium centrocarpum* in his paper: for taxonomy of these species, see Matsuoka et al., 1997, and Steidinger,

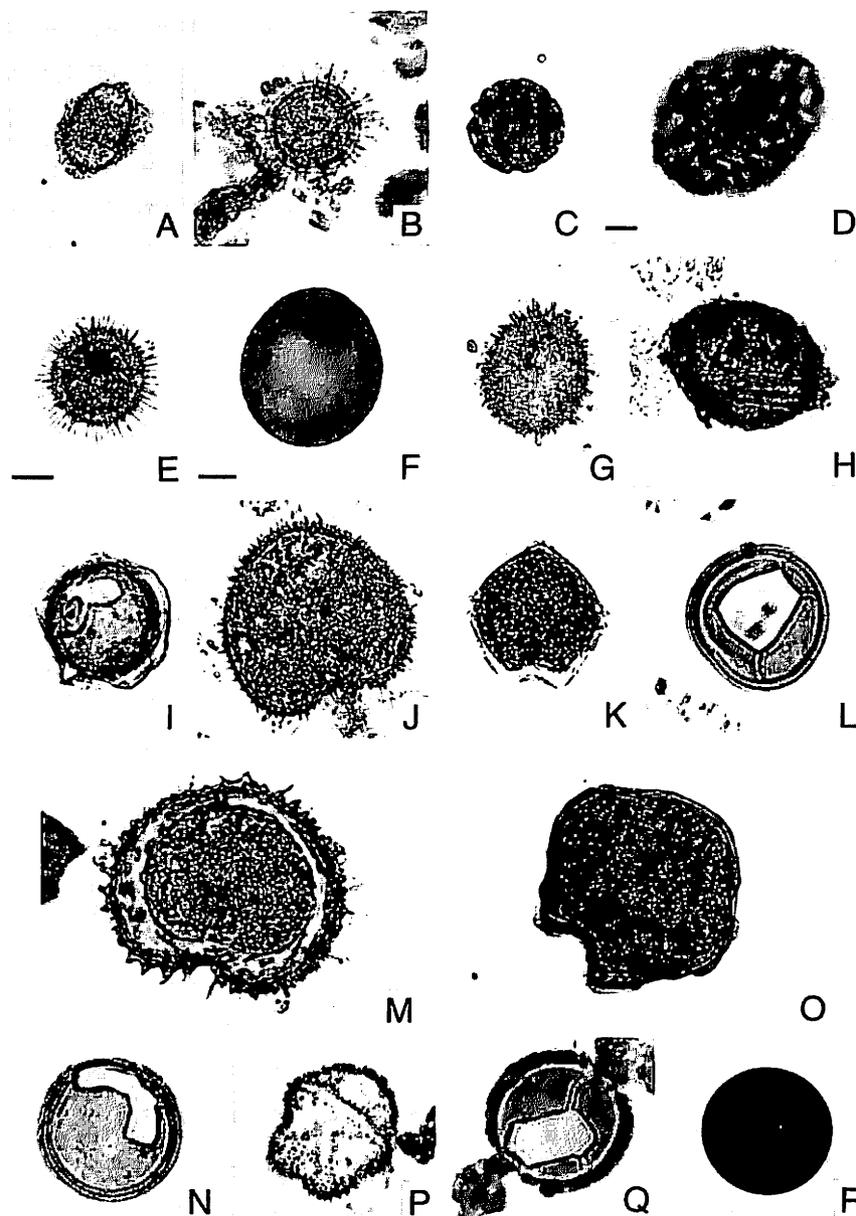


Fig. 4. Light microphotographs of armored dinoflagellate cysts in Onagawa Bay. A. Living cyst of *Alexandrium catenella* or *A. tamarensis* ($\times 320$). B. Living cyst of *Gonyaulax grindleyi* ($\times 480$). C. Living cyst of *Enciculifera carinata* ($\times 320$). D–G. Living cysts of *Scrippsiella* spp. D. *Scrippsiella crystallina*. E. *Scrippsiella precaria*. F. *Scrippsiella rotunda*. G. *Scrippsiella trochoidea* ($\times 480$). H. Living cyst of *Preperidinium meunieri* (\dagger *Dubridinium caperaria*) ($\times 480$). I. Empty cyst of *Protoperidinium americanum* ($\times 480$). J. Living cyst of *Protoperidinium claudicans* (\dagger *Votadinium spinosum*) ($\times 480$). K–L. Cyst of *Protoperidinium conicoides* (\dagger *Brigantedinium simplex*) ($\times 480$). K. Living cyst in theca. L. Empty cyst. M. Living cyst of *Protoperidinium conicum* (\dagger *Selenopemphix quanta*) ($\times 480$). N. Empty cyst of *Protoperidinium denticulatum* ($\times 480$). O. Living cyst of *Protoperidinium leonis* (\dagger *Quinquecuspis concretum*) ($\times 480$). P. Empty cyst of *Protoperidinium pentagonum* (\dagger *Trinovantedinium capitatum*) ($\times 480$). Q. One of the *Protoperidinium* spp. cysts (empty) (\dagger *Brigantedinium* sp. 1) ($\times 480$). R. One of the *Protoperidinium* spp. cysts (living) (\dagger *Brigantedinium* sp.) ($\times 320$).

\dagger Paleontological name. D–F. The same microphotographs shown in Ishikawa & Taniguchi (1993). Scale bars = 10 μ m.

1997) are abundant in offshore sediments. Matsuoka (1987a) reported abundant cysts of Protoperidiniaceae (mostly \dagger *Brigantedinium* spp.) with less abundant Gonyaulacaceae (\dagger *Spiniferites* spp.) and *Pyrophacus steinii* (\dagger *T. vancampoe*) from Lake Saroma, northeast Hokkaido,

Japan. He revealed that in Akkeshi Bay, east Hokkaido, the cysts of Protoperidiniaceae, especially of \dagger *Brigantedinium* spp., are also predominant and stated that the predominance of \dagger *Brigantedinium* spp. indicates the cold nature of the areas in Japanese waters. In contrast, Matsuoka (1982) re-

Table 4. Absolute and relative abundances of armored dinoflagellates in the total cyst populations in surface sediments of Onagawa Bay. The abundance of each species is the mean throughout the study period. Relative abundance of [†]*Brigantedinium* spp. ([†]*B. simplex*, [†]*B. sp. 1* and other [†]*Brigantedinium* species) in parenthesis.

Station	Λ				I				2'				3			
	Abundance (cysts cm ⁻³)				Abundance (cysts cm ⁻³)				Abundance (cysts cm ⁻³)				Abundance (cysts cm ⁻³)			
	Living	Empty	Total	%	Living	Empty	Total	%	Living	Empty	Total	%	Living	Empty	Total	%
Goniodomataceae			21.1	0.8			20.8	0.7			0.8	0.1			0	0
<i>Alexandrium catenella</i> and/or <i>tamarense</i>	12.1	9	21.1	0.8	16.9	3.9	20.8	0.7	0.8	0	0.8	0.1	0	0	0	0
Gonyaulacaceae			171.2	6.3			214.9	7			124.4	8.8			41.7	5.1
<i>Gonyaulax grindleyi</i>	6.1	6.7	12.8	0.5	15.8	12	27.8	0.9	4.4	7.2	11.6	0.8	1.9	6.2	8.1	1
<i>G. digitale</i> ^a	0	3.4	3.4	0.1	1.4	1.4	2.8	0.1	1.5	3.8	5.3	0.4	0	0	0	0
<i>G. scrippsae</i>	5.3	4.1	9.4	0.3	10.6	9.2	19.8	0.6	3.1	0	3.1	0.2	0	0	0	0
<i>G. spinifera</i> ^b	4.8	29.3	34.1	1.2	3.9	19.8	23.7	0.8	5.4	11.5	16.9	1.2	0	0	0	0
<i>G. verior</i>	5	10	15	0.5	10.2	14.1	24.3	0.8	1.6	15.1	16.7	1.2	0	1.9	1.9	0.2
<i>G. spp.</i> ^c	17.9	65.1	83	3	53.5	52.1	105.6	3.4	15	54.3	69.3	4.9	8.1	23.6	31.7	3.8
<i>Lingulodinium polyedrum</i>	5.3	8.2	13.5	0.5	1.4	9.5	10.9	0.4	0	1.5	1.5	0.1	0	0	0	0
Calciadinellaceae			912.6	33.4			1010.6	33			350.8	24.8			223.6	27.1
<i>Enciculifera carinata</i>	37.9	10.3	48.2	1.8	44.7	21.1	65.8	2.1	5.9	7	12.9	0.9	0.9	2.7	3.6	0.4
<i>Scripsiella crystallina</i>	7.4	3	10.4	0.4	13	6.6	19.6	0.6	0.8	1.5	2.3	0.2	0	3.7	3.7	0.4
<i>S. precaria</i>	8.1	0	8.1	0.3	1.3	0	1.3	0	1.4	0	1.4	0.1	0	0.9	0.9	0.1
<i>S. rotunda</i>	15.8	11	26.8	1	18.4	16.9	35.3	1.2	11.1	31.8	42.9	3	13.7	32.9	46.6	5.7
<i>S. trochoidea</i>	500.2	318.9	819.1	29.9	532.5	356.1	888.6	29	111.2	180.1	291.3	20.6	78.3	90.5	168.8	20.5
Kolkwitziellaceae			67.1	2.5			66.7	2.2			20.7	1.5			16.5	2
<i>Diplopsalis lenticula</i>	1.8	23	24.8	0.9	1.3	28.9	30.2	1	0	11.2	11.2	0.8	0	2.8	2.8	0.3
<i>Preperidinium meunieri</i>	2	40.3	42.3	1.5	0	36.5	36.5	1.2	0	9.5	9.5	0.7	0	13.7	13.7	1.7
Protoperidiniaceae			1564.1	57.2 (45.4)			1751.3	57.2 (43.3)			915.5	64.8 (49)			542.3	65.8 (47.1)
<i>Protoperidinium claudicans</i>	38.2	6.9	45.1	1.6	22.5	4	26.5	0.9	1.5	1.5	3	0.2	3.7	1.9	5.6	0.7
<i>P. conicoides</i>	6.1	438.9	445	16.3	1.3	466.3	467.6	15.3	0	300.4	300.4	21.3	0	160.8	160.8	19.5
<i>P. conicum</i>	8.6	24.2	32.8	1.2	9.2	15.9	25.1	0.8	3.1	8.3	11.4	0.8	2.8	18.1	20.9	2.5
<i>P. denticulatum</i>	0	10.2	10.2	0.4	0	14.5	14.5	0.5	0	9	9	0.6	0	7.3	7.3	0.9
<i>P. leonis</i>	16.5	66.4	82.9	3	17.2	100.7	117.9	3.8	0.8	102	102.8	7.3	3.6	68.5	72.1	8.7
<i>P. oblongum</i>	8.6	5.5	14.1	0.5	7.8	15.6	23.4	0.8	0	5.4	5.4	0.4	0	3.6	3.6	0.4
<i>P. pentagonum</i>	3	4.2	7.2	0.3	1.4	3.9	5.3	0.2	0	0.8	0.8	0.1	0	1.9	1.9	0.2
<i>P. subinermis</i>	2.1	2	4.1	0.1	0	0	0	0	0	1.5	1.5	0.1	0	0	0	0
<i>P. spp.</i> ^d	448.3	474.4	922.7	33.7	463.7	607.3	1071	35	128.1	353.1	481.2	34.1	76.6	193.5	270.1	32.8
Total living cysts	1161.1			42.4	1248			40.7	295.7			20.9	189.6			23
Total empty cysts		1575		57.6		1816.3		59.3		1116.5		79.1		634.5		77
Total cysts			2736.1				3064.3				1412.2				824.1	

^a No vegetative cells were observed in water column.

^b Sum of [†]*Spiniferites membranaceus*, [†]*Spiniferites mirabilis* and [†]*Spiniferites ramosus*.

^c *Spiniferites* spp.

^d Sum of [†]*Selenopemphix* sp., [†]*Votadinium* sp. and cysts of *P. americanum*², [†]*Brigantedinium* sp. 1 and other unrecognizable spherical and brownish [†]*Brigantedinium* spp.

ported that Omura Bay, Nagasaki, southwest Japan, is dominated by the cysts of warm water species, such as Gonyaulacaceae [$\dagger S. bulloideus$, $\dagger S. mirabilis$, $\dagger S. bentori$, and $\dagger O. centrocarpum$ (=cyst of *G. grindleyi*)], *Pyrophacus steinii* ($\dagger T. vancampoae$), *P. hartmannii* and *P. schwartzii*. Matsuoka (1985) revealed, in Nagasaki and Senzaki Bays, southwest Japan, the dominance of the Gonyaulacaceae, especially of $\dagger S. bulloideus$, $\dagger S. hyperacanthus$ (vegetative cell is unknown) and $\dagger S. mirabilis$, indicating warm temperate to subtropical nature of dinoflagellate cyst assemblage. Kobayashi & Yuki (1991) reported the dominance of *G. spinifera* ($\dagger S. mirabilis$) and *S. trochoidea* followed by *Protoperidinium* spp. ($\dagger Brigantedinium$ spp.) in the cyst assemblage of Matoya Bay, central Japan.

In Onagawa Bay, $\dagger T. vancampoae$ and $\dagger S. hyperacanthus$ which have been reported to be warm water species were not found. Instead, abundant *Protoperidiniaceae* (57–66%), mainly $\dagger Brigantedinium$ spp., accompanied by lesser Gonyaulacaceae ($\dagger Spiniferites$ spp. and cyst of *G. grindleyi*) (5–9%) were recorded (Table 4). This composition is rather similar to that in Lake Saroma under the influence of both warm and cold currents (Matsuoka 1987a), as in Onagawa Bay. Mixed nature of the Onagawa Bay water is also supported by the occurrences of the cysts of *P. conicoides* ($\dagger B. simplex$) and *Lingulodinium polyedrum* ($\dagger Lingulodinium machaerophorum$), which have been recognized as polar/subpolar and equatorial/temperate species, respectively, in North Atlantic (Dale 1996).

Relationship between the cysts and the vegetative cells

In the cyst populations, Gonyaulacaceae, Calciodinellaceae and *Protoperidiniaceae* in Onagawa Bay were dominated respectively by *G. spinifera*, *S. trochoidea* and *P. conicoides* (Table 4). *Protoperidinium conicoides* ($\dagger B. simplex$) dominated the empty cysts of *Protoperidiniaceae* at 4 stations but not the living cysts. Since living cysts of all $\dagger Brigantedinium$ spp. are equally spherical and dark brownish in color, it is quite difficult to identify their species. They can be classified by their size and more accurately by the shape of archeopyle or opening for germination, which is left on the empty cyst walls. Therefore, species composition of $\dagger Brigantedinium$ spp. could be determined for the empty cyst populations. If the latter reflects on the living cyst populations, *P. conicoides* is most likely to be the leading species (Table 4).

The vegetative cells of *G. spinifera*, *S. trochoidea* and *P. conicoides* also dominated respectively Gonyaulacaceae, Calciodinellaceae and *Protoperidiniaceae* in surface water in the bay. It is known that they are major components among those germinating from in situ sediments in the bay (Ishikawa & Taniguchi 1997). Therefore, it can be said that the cyst assemblage in the sediments, as a whole, reflect the vegetative assemblage. The same trend was reported from Trondheimsfjord (Dale 1976) and Matoya Bay (Kobayashi & Yuki 1991), but the opposite was observed in Omura Bay

(Kobayashi et al. 1986) and Tasmanian waters, Australia (Bolch & Hallegraeff 1990).

Abundance of cysts and their distribution

Since the cysts of dinoflagellates are usually very small (15–70 μm), they are accumulated as fine silt particles or fine sand grains within the sedimentary regime by currents (Dale 1976, 1983; Wall et al. 1977; Lewis 1988; Kobayashi & Yuki 1991). Ishikawa (1992) investigated horizontal distributions of both sediment types and cysts of *Scrippsiella* spp. in the entire Onagawa Bay. The silt and clay (particle sizes less than 63 μm) fraction of the sediments generally decreases from inner (over than 90%) to the outer (almost 0%) parts of the bay. The abundance of the *Scrippsiella* cysts decreases in the same way (Table 4), indicating that the inner part of the bay acts as a cyst depository. Another depository of the cysts associated with a high silt and clay fraction (ca. 98%) was found in the central part of the mouth of the bay, where an eddy might be formed in the bottom layer. Such a condition would prevent outflow of cyst-forming species from the bay.

Different seed populations of cyst-forming and non-cyst-forming species

A naked dinoflagellate *Gymnodinium mikimotoi* (= *G. nagasakiense*) which produces no cysts has a strategy to survive winter by possessing broad temperature tolerance (Yamaguchi 1994). Its wintering cells, though very small in number, can grow rapidly when temperature becomes favorable (Yamaguchi 1994). These wintering cells were generally observed in semi-enclosed regions such as Omura Bay (Nakata & Iizuka 1987), Suo-Nada, Seto Inland Sea of Japan (Terada et al. 1987), Hiroshima Bay, Seto Inland Sea of Japan (Itakura et al. 1990), Tokyo Bay, central Japan (Hosaka 1990) and Uranouchi Inlet, Kochi, southwest Japan (Yamaguchi 1994). The same survival strategy, however, might not work well in Onagawa Bay, where exchange of waters of quite different natures often occurs. In other words, seasonal occurrence of the 55 non-cyst-species in the bay is possibly controlled by the water exchange, being transported into or from the bay. For such allochthonous species, transported vegetative cells from outside the bay seed blooms.

In contrast, the cyst-forming species are undoubtedly have an advantage for building larger vegetative populations in the bay (cf. Wall 1971). Many of the known cyst-forming species (78%) occurring in the water column of Onagawa Bay were confirmed to have seed populations in the sediments, and some of them, including *G. spinifera*, *P. conicoides* and *S. trochoidea*, were observed to be predominant among the vegetative assemblage. This strongly indicates the advantage of the autochthonous species, and the importance of their cyst populations in the population dynamics of the dinoflagellate assemblage in Onagawa Bay.

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