Botanica Marina 47 (2004): 184–201 © 2004 by Walter de Gruyter • Berlin • New York

Dinoflagellate cysts in recent marine sediments from the east coast of Russia

Tatiana Yu. Orlova[1,*], Tatiana V. Morozova[1], Kristin E. Gribble[2], David M. Kulis[2] and Donald M. Anderson[2]

[1] Institute of Marine Biology, Russian Academy of Science–Far East Branch, Vladivostok, 690041 Russia, e-mail: torlova@ibm.dvo.ru

[2] Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

*Corresponding author

Abstract

Forty-two different dinoflagellate cyst types were found in recent sediment samples collected between July 1999–September 2002 from 44 stations along the eastern coast of Russia. This represents the first survey of recent dinoflagellate cysts in Russian marine waters. Forty cysts were identified to the species level, representing 17 genera. The most common cysts were those of ellipsoidal *Alexandrium* spp., *Protoceratium reticulatum, Gonyaulax* spp.*, Polykrikos kofoidii, P. schwartzii*, *Protoperidinium americanum, P. minutum*, *P. conicoides*, *P. subinerme*, *P. conicum* and *Scrippsiella trochoidea*. Fifteen of the dinoflagellate species have not previously been recorded as motile cells in Russian marine waters: *Alexandrium* cf. *minutum*, *Cochlodinium* cf. *polykrikoides*, *Diplopsalis* cf. *lebourae*, *Fragilidium mexicanum, Gonyaulax elongata, G. membranaceae, Gymnodinium* cf. *catenatum*, *Pentapharsodinium dalei*, *P. tyrrhenicum*, *Protoperidinium americanum*, *P*. cf. *avellanum*, *Scrippsiella* cf. *lachrymosa*, *S*. cf. *precaria*, *S*. cf. *rotunda* and *Warnowia* cf. *rosea*. Cysts of the potentially toxic species *Alexandrium* cf. *minutum*, *A*. *tamarense* and *Gymnodinium* cf. *catenatum* were also found in this survey. Ellipsoidal *Alexandrium tamarense* type cysts were widely distributed and dominated many localities in the study area. These data suggest that additional cyst surveys should be conducted in areas of the eastern Russian coastline not yet investigated, and that the potential for paralytic shellfish poisoning toxicity as a result of blooms of toxic species may be more widespread than previously documented.

Keywords: *Alexandrium* spp.; cysts; dinoflagellates; toxic species.

Introduction

Reliance on a resting stage to withstand periods of unfavorable environmental conditions is a well-known life-history strategy in planktonic marine dinoflagellates. More than 200 species of marine dinoflagellates are known to form resting cysts (Head 1996). During the last four decades, dinoflagellate cysts from recent marine sediments have been studied in many areas of the world: on the east coast of the United States, in Japan, Australia and New Zealand, in Europe, China, India, among other locations (Wall and Dale 1968, Baldwin 1987, Bolch and Hallegraeff 1990, Ellegaard et al. 1994, Qi et al. 1996, Sonneman and Hill 1997, Nehring 1997a, Godhe et al. 2000, Persson et al. 2000). Such broad interest in this type of study indicates the importance of cysts as a component of coastal marine ecosystems. Dinoflagellate cysts can be useful indicators of the development or presence of eutrophication in recent marine environments (Harland 1983, Nehring 1995, Sætre et al. 1997, Matsuoka 1999, Dale et al. 1999). Cysts are also important in studies of dinoflagellate ecology and biogeography (Dale 1983). The distribution of cysts represents integrated records of the planktonic assemblage over time and space, and provides biogeographical information on a scale usually not attained by conventional plankton surveys (Dale 1983).

The cysts found in the sediment will indicate to some extent which species of motile dinoflagellate cells are present in the water column. Cyst surveys can thus give early warning of the presence and abundance of toxic species in a given area. It is well known that cyst germination provides an inoculum for blooms, and cyst formation can subsequently remove substantial numbers of cells as a major factor in bloom decline (Anderson and Wall 1978, Anderson 1984). The cyst survey reported here was prompted by questions about harmful algal blooms (HABs) previously recorded on the Russian Pacific coast (Konovalova 1995, 1999). The earliest documented case of paralytic shellfish poisoning (PSP) was in September 1945 when six people were poisoned, and two of them died after eating mussels collected in Pavla Bay on the west coast of the Bering Sea (Lebedev 1968, Konovalova 1999). Red tides caused by *Alexandrium tamarense* (Lebour) Balech were observed in Olyutorsky Bay in the Bering Sea in July 1986, 1988 and 1990 and were accompanied by mortalities of cetaceans, fish and birds (Konovalova 1999). Recent investigations of HAB events on the Russian Pacific coast have shown an increase in species diversity and expansion of potentially toxic species including *Alexandrium* spp. over the last several decades (Konovalova 1993, 1999, Orlova et al. 1998).

Knowledge of the composition and distribution of dinoflagellate cysts in the North Pacific area is limited and restricted mostly to the southwest Pacific coast. Cyst distribution has been studied in the coastal waters of Japan (Matsuoka 1985a,b, 1987, Kobayashi et al. 1986, Kobayashi and Yuki 1991), in the Chinese coastal areas of the South China Sea, in the East China Sea and Yellow Sea (Qi et al. 1996, Cho and Matsuoka 2001), and in

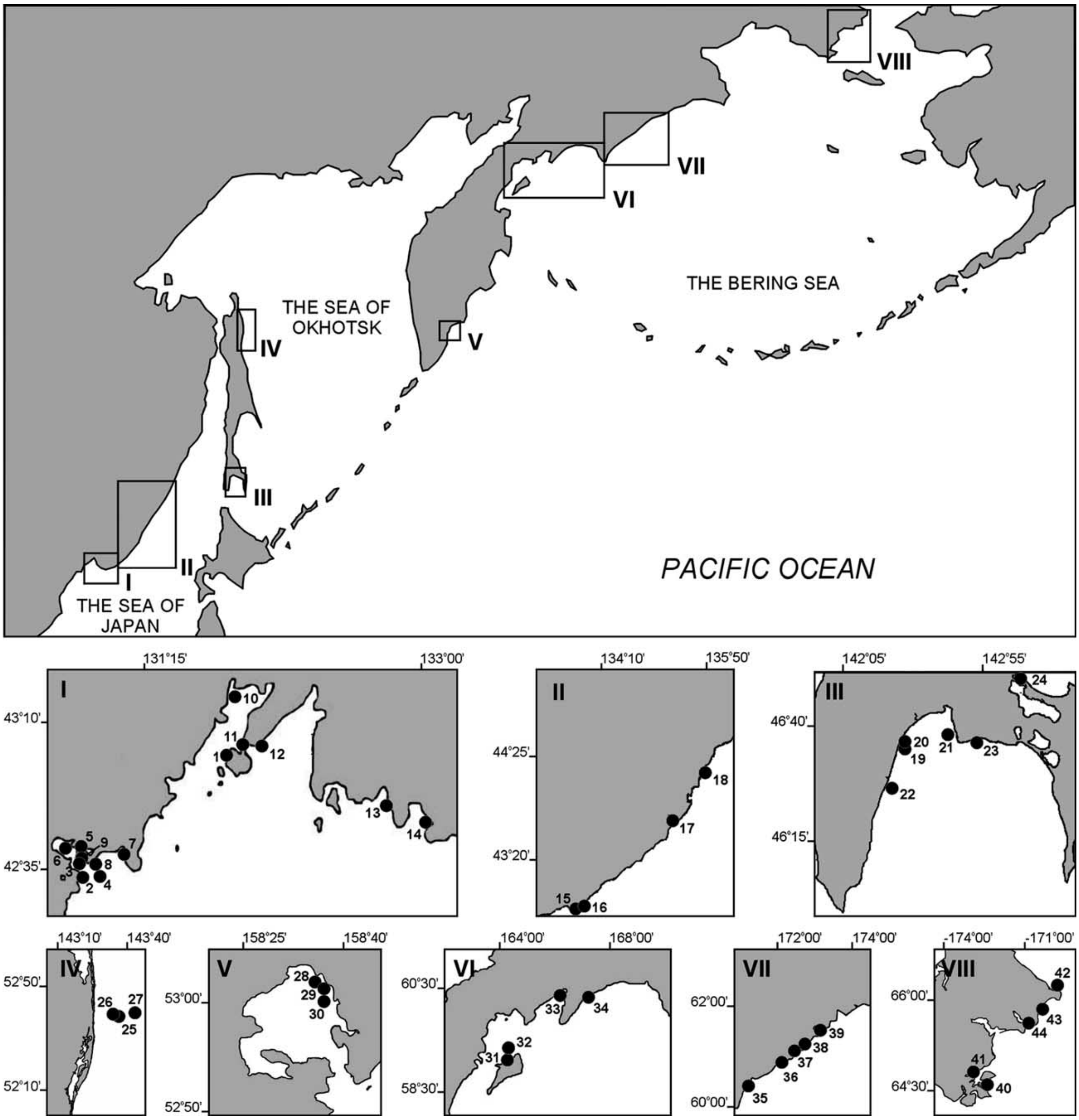


Figure 1 Map showing the sampling regions and stations on the Russian east coast.
(I) south Primorye, the Sea of Japan, (II) north east Primorye, the Sea of Japan, (III) Aniva Bay, Sakhalin Island, (IV) east coast of Sakhalin Island, the Sea of Okhotsk, (V) Avachinskaya Guba Inlet, Kamchatka, (VI) Olytorskii Gulf, the Bering Sea, (VII) the west coast of the Bering Sea and (VIII) Chukotka, the Bering Sea.

southern Korean waters (Lee and Matsuoka 1996). Surveys of fossil dinoflagellate cysts in sediments from the Bering Sea have been carried out by Bujak and Matsuoka (Bujak 1984, Bujak and Matsuoka 1986, Matsuoka and Bujak 1988). In contrast to adequate data on planktonic dinoflagellates in the Far Eastern Seas of Russia (Kisselev 1937, 1950, 1959, Gail 1950, Kuzmina 1962, Konovalova et al. 1989, Konovalova 1998), information on dinoflagellate cyst assemblages in recent marine sediments on the Russian Pacific coast is almost absent. Recently, resting cysts of *Gyrodinium instriatum* Freudenthal *et* Lee and *Scrippsiella crystallina* Lewis were described from Russian marine sediments (Orlova and Morozova 2003, Orlova et al. 2003). The objective of our study was to describe the species composition and distribution of dinoflagellate cysts in recent marine sediments from the Russian Pacific coast.

Materials and methods

Surface sediment samples were collected between September 1999 and October 2002 from 44 stations among 8 geographic regions along the Russian Pacific coast (Figure 1, Table 1). Samples were collected by divers using glass or aluminum coring tubes, or by grab. Samples were stored in the dark at 4°C. A total of 81 samples was analyzed and used for germination experiments within six months of collection. Sediment processing generally followed the methods of Anderson et al. (1982)

Table 1 Location on a map (Figure 1) latitude, longitude, water depth, and sediment characteristics of each sampling station on the east coast of Russia.

Region	Station no.	Sampling date	No. samples	Latitude N	Longitude E	Depth (m)	Sediment characteristic
I	1	01 Nov 2000	1	43°02′	131°47′	25	sand
	2	16 Aug 2001	1	42°32.8′	130°50.5′	12	muddy sand
	3	28 Sep 2000	5	42°37′	130°49′	21	muddy sand
	4	11 Sep 1999	1	42°33′	130°56′	15	muddy sand
	5	10 Sep 1999	1	42°39′	130°50′	9	mud
	6	07 Sep 2001	1	42°40′	130°47′	6	mud
	7	05 Dec 2001	4	42°37.3′	131°07.5′	17	muddy sand
	8	15 Oct 2000	1	42°35.5′	130°55.5′	7	muddy sand
	9	28 Aug 2001	8	42°36.17′	130°51.5′	16	mud
	10	16 Aug 2000	4	43°15′	131°50′	11	mud
	11	11 Oct 2000	1	43°04.28′	131°52.3′	24	mud
	12	12 Oct 2000	2	43°04.559′	131°59.933′	30	mud
	13	15 Sep 2000	4	42°50′	132°46′	7	mud
	14	20 Sep 2000	3	42°45′	133°00′	10	mud
II	15	14 Oct 2000	1	42°49.341′	133°48.987′	86	mud
	16	14 Oct 2000	1	42°52.95′	133°51.55′	25	mud
	17	15 Oct 2000	1	43°40.308′	135°14.881′	26	mud
	18	17 Oct 2000	1	44°21′	135°50′	30	mud
III	19	17 Jun 2001	2	46°35.37′	142°25.645′	14	muddy sand
	20	17 Jun 2001	1	46°35.38′	142°25.645	14	mud
	21	17 Jun 2001	1	46°38.3′	142°41.8′E	15	mud
	22	17 Jun 2000	2	46°24.9′	142°23.3′E	15	sandy mud with pebbles
	23	02 Jul 2001	1	46°36.9′	142°52.1′E	10	sandy mud with pebbles
	24	08 Jul 2001	1	46°52′	143°07′	4	sandy mud with pebbles
IV	25	27 Sep 2001	1	52°42.821′	143°34.235′	31	sand
	26	28 Sep 2001	1	52°42.98′	143°33.8′	27	sand
	27	30 Sep 2001	1	52°43.6′	143°44′	25	sand
V	28	07 Sep 2001	1	53°02′	158°35′	2	volcanic muddy sand
	29	07 Sep 2001	1	53°01′	158°36′	2	volcanic muddy sand
	30	07 Sep 2001	1	53°00′	158°36′	1.5	volcanic muddy sand
VI	31	18 Jul 2002	4	59°06.53′	164°17.12′	3	mud
	32	19 Jul 2002	1	59°14.484′	164°17.12′	6	mud
	33	20 Jul 2002	2	60°13.33′	166°48.22′	6	mud
	34	20 Jul 2002	2	60°26.469′	167°03.915′	9	mud
VII	35	21 Jul 2002	3	60°21.236′	170°37.513′	12	muddy sand
	36	21 Jul 2002	1	60°26.25′	171°42.29′	21	muddy sand
	37	21 Jul 2002	2	61°01.187′	172°06.907′	24.4	mud
	38	22 Jul 2002	1	61°07.46′	172°15.63′	15.8	mud
	39	23 Jul 2002	3	61°26.694′	172°54.838′	8	mud
VIII	40	26 Jul 2002	2	64°38.8′	172°31.3′	38	mud
	41	26 Jul 2002	1	64°46.1′	173°09.2′	20	mud
	42	27 Jul 2002	1	66°10′	169°49′	10.5	muddy sand
	43	27 Jul 2002	2	65°51.23′	170°31.15′	15	mud
	44	27 Jul 2002	1	65°38.4′	170°52.6′	13.7	mud

and Matsuoka et al. (1989). Subsamples (1–2 ml) were diluted with filtered seawater and sonicated for 60 s using a Branson Sonifier 250 (Branson Ultrasonics Corp., Danbury, USA) with a 1.3 cm disrupter horn at a setting of 4 amperes. The sonicated suspension was sieved through Nitex screens to obtain a 20–80-μm size component. Sieved material was transferred to a polyethylene tube with filtered seawater and the final volume of this subsample adjusted to 15.0 ml. One-milliliter aliquots from this subsample were counted in Sedgwick-Rafter counting chambers using a Nikon Labophot (Tokyo, Japan) light microscope at a total magnification of 200×. Only live cysts were counted. The total numbers of cysts counted per 1 ml of subsample. Selected cysts were isolated by micropipette and placed on a microscopic slide, identified, and photographed with a Zeiss (Oberkochen, Germany) Axioskop light microscope, using bright field. Individual cysts were used for germination experiments in order to identify the species characteristics of both cyst and motile stages. If successful germination of cysts into thecate cells occurred, they were isolated, washed in filtered seawater and placed in separate wells of a 96-well tissue culture plate containing modified f/2 medium without silicate (Guillard and Ryther 1962), made up with filtered sea water (Millipore, 0.22 μm). The f/2 medium was modified by adding Na_2SeO_3 to 10^{-8} M and decreasing the concentration of $CuSO_4{\cdot}5H_2O$ to a final concentration of 10^{-8} M. The plates were sealed with tape to avoid evaporation and were incubated at 15°C on a 14:10 h light:dark cycle (ca. 200 μmol photons m^{-2} s^{-1} irradiance provided by cool white fluorescent bulbs). Cysts were monitored for germination for two weeks using an inverted Zeiss (Oberkochen, Germany) microscope, IM 35. Thecal plates of germinated cells were analyzed by staining with Calcofluor White and examining under epifluorescence, following the method of Fritz

Table 2 Names of dinoflagellate cyst types identified from the east coast of Russia.

Biological species name	Palaeontological species name	References	Number of germinated cysts	Figures (present paper)
Alexandrium cf. *minutum* (Lebour) Balech	None	Erard-Le Denn et al. 1993, p.110, fig. 2; Nehring 1997a, p. 308, figs 44–45	0	2
Alexandrium tamarense (Lebour) Balech	None	Dale 1977, p. 30, figs 1a–c; Anderson and Wall 1978, p. 226–227, figs 22–33	36	3–5
Cochlodinium cf. *polykrikoides* Margalef	None	Fukuyo 1982, as *Cochlodinium* sp. 1, p.207, pl. 2 figs 1–3; Matsuoka and Fukuyo 2000, as *Cochlodinium* sp. 1 (cf. *polykrikoides*), pl. 5	2	6, 7
Diplopelta cf. *parva* (Abé) Matsuoka	None	Matsuoka 1988, p. 100, pl. 1 figs G–K; Bolch and Hallegraeff 1990, p.186, figs 31 a–c; Hallegraeff and Bolch 1992, fig. 13	0	8, 9
Diplopsalis cf. *lebourae* (Nie) Balech	None	Matsuoka 1988, p. 101–105, pl. 2 figs G–L, fig. 3b	1	10, 11
Diplopsalis lenticula Bergh	None	Matsuoka 1988, p. 105, 107, pl. 3 figs E–K, pl. 7 figs C–E; Lewis 1990, p. 343–345, figs 12, 16, 17; Ellegaard *et al*. 1994, p. 184, figs 9–10	8	12
Fragilidium mexicanum Balech	None	Blanco 1989, p. 793–795, fig. 21 (as *Fragilidium* sp.1)	5	13–17
Gonyaulax digitalis (Pouchet) Kofoid	*Spiniferites bentori* (Rossignol) Wall *et* Dale	Wall and Dale 1968, p. 269, fig. 2; Dale 1983, fig. 5; Nehring, 1997a, p. 311, fig. 5	2	18, 19
Gonyaulax elongata (Reid) Ellegaard, Daugbjerg, Rochon, J. Lewis *et* I. Harding	*Spiniferites elongatus* Reid	Reid 1974, p. 602–603, pl. 3, 23,24; Nehring 1997a, p. 311, fig. 7; Ellegaard et al., 2003, 154–156, figs 4–30	0	20
Gonyaulax membranacea (Rossignol) Ellegaard, Daugbjerg, Rochon, J. Lewis *et* I. Harding	*Spiniferites membranaceus* (Rossignol) Sarjeant	Lewis et al. 1999, figs 1–19; Ellegaard et al. 2003, 157–158, figs 37–54	0	21
Gonyaulax cf. *scrippsae* Kofoid	*Spiniferites bulloideus* (Deflandre *et* Cookson) Sargeant	Wall and Dale 1968, p. 270–271, pl. 1 figs 13–15; Dale 1983, fig. 6; Matsuoka 1987, p. 42–44, pl. 2 figs 5–6; Qi et al. 1996, p. 91, pl. 1B; Nehring 1997a, p. 311, fig. 6	0	22, 23
Gonyaulax spinifera (Claparéde *et* Lachmann) Diesing Type *Spiniferites mirabilis*	*Spiniferites mirabilis* (Rossignol) Sarjeant	Wall and Dale 1968, pl. 1 fig. 10; Matsuoka 1985a, p. 36–37, pl. 3 figs 1–4; Bolch and Hallegraeff 1990, p. 175, figs 4a–c; Nehring 1997a, p.311, fig. 8		24, 25
Gonyaulax verior Sournia	None	Matsuoka et al. 1988, p. 313, figs 1–5; Ellegaard et al. 1994, p. 185–186, figs 17–18	4	26
Gonyaulax cf. *catenatum* Graham	None	Anderson et al. 1988, p. 259–261, figs 7–12, 14–16; Bolch and Hallegraeff 1990, p. 185, Figs 33 a–c; Matsuoka and Fukuyo 1994, p. 496, figs 2b–e	–	27
Gyrodinium instriatum Freudenthal *et* Lee	None	Fukuyo 1982, p. 206–207, pl. 1 figs 1–3; Kojima and Kobayashi 1992, p. 242–245, figs 1–7; Uchida et al. 1996, p. 121, figs 11–12	3	28
Lingulodinium polyedrum (Stein) Dodge	*Lingulodinium machaerophorum* (Deflandre *et* Cookson) Wall	Wall and Dale 1968, p. 271–272, pl. 1 fig. 18; Matsuoka 1985a, p. 40–41, pl. 8 figs 1–5; Ellegaard 2000, p. 75–78, pl. III fig. 1; Matsuoka and Fukuyo 2000, pl. 9	–	29
Pentapharsodinium dalei Indelicato *et* Loeblich III	None	Lewis 1991, p. 95–96, figs 10–11, 13–15; Godhe et al. 2000, p. 43, fig. 9	0	30
Pentapharsodinium tyrrhenicum (Balech)	*Calcicarpinum bivalvum* Versteegh	Montresor et al. 1993, p. 227, figs 16–21; Montresor et al. 1994, p. 51, pl. 1 fig. 6;	0	31, 32

(Table 2 continued)

Biological species name	Palaeontological species name	References	Number of germinated cysts	Figures (present paper)
Montresor, Zingone *et* Marino		Sonneman and Hill 1997, p. 158, figs 12a–d		
Polykrikos kofoidii Chatton	None	Matsuoka 1987, as *Polykrikos* sp. cf. *kofoidii*, p. 67–68, pl. 16 figs 1–9; Nehring 1997a, as, p. 312, figs 11–12	0	33, 34
Polykrikos schwartzii Bütschli	None	Matsuoka 1985a, p. 61–62, pl. 16 figs 4–10; Bolch and Hallegraeff 1990, p. 186, figs 32a–b; Nehring 1997a, p. 312, figs 13–14	0	35, 36
Preperidinium meunieri (Pavillard) Elbrächter	*Dubridinium caperatum* Reid	Wall and Dale 1968, p. 280, pl. 4 figs 21–22; Matsuoka 1988, p. 115–117, pl. 6 figs J–K, pl. 7 figs G–J, text-figs 8b–c	1	37, 38
Protoceratium reticulatum (Claparéde *et* Lachmann) Bütschli	*Operculodinium centrocarpum* (Deflandre *et* Cookson) Wall	Wall and Dale 1968, p. 272, pl. 1 fig. 20; Reid 1974, p. 594–595, pl. 2 figs 10–11; Matsuoka 1985a, p. 41–43, pl. 7 figs 1–6; Nehring 1997a, p. 312–313, figs 15, 38	6	39, 40
Protoperidinium americanum (Gran *et* Braarud)	None	Lewis and Dodge 1987, p. 114–115, pl. 1 figs. 1–4; Bolch and Hallegraeff 1990, p.184, figs 29 a–b; Ellegaard et al. 1994, figs 53–55; Nehring 1997a, p. 313, fig. 32	0	41, 42
Protoperidinium cf. *avellanum* (Meunier) Balech	*Brigantedinium cariacoense* (Wall) Reid	Wall and Dale 1968, p. 277, pl. 4 fig.2; Lewis et al. 1984, p. 26, fig. 2b; Matsuoka 1984, p. 38–39, pl. 2 figs 5–7, text-fig. 1; Ellegaard et al. 1994, fig. 44	–	43
Protoperidinium claudicans (Paulsen) Balech	*Votadinium spinosum* Reid	Wall and Dale 1968, p. 273, pl. 2 figs 1, 2; Matsuoka 1985a, p. 58–59, pl. 14 figs 1–6; Bolch and Hallegraeff 1990, p. 184, fig. 25; Nehring 1997a, p. 313, fig. 17	0	44–46
Protoperidinium conicoides (Paulsen) Balech	*Brigantedinium simplex* (Wall) Reid	Lewis et al. 1984, p. 26, fig. 2f; Matsuoka 1987, p. 54–55, pl. 6 figs 1–14; Ellegaard et al. 1994, p. 186, figs 36–40	0	47–49
Protoperidinium conicum (Gran) Balech	*Selenopemphix quanta* (Bradford) Matsuoka	Wall and Dale 1968, p. 273–274, pl. 2 figs 4–5; Kobayashi and Matsuoka 1984, figs. 1–15; Matsuoka 1985a, p. 51–52, pl. 11 figs 1–9	0	50–53
Protoperidinium leonis (Pavillard) Balech	*Quinquecuspis concreta* (Reid) Harland	Wall and Dale 1968, p. 276, pl. 2 figs 18–21; Lewis et al. 1984, p. 30–31, pl. 2, fig.3; Matsuoka 1985a, p. 56–57, pl. 3–8, pl. 13 figs 1–4	0	54, 55
Protoperidinium minutum (Kofoid) Loeblich	None	Wall and Dale 1968, p. 278; Fukuyo et al. 1977, p. 11, figs 2A, 3–4; Bolch and Hallegraeff 1990, p. 184, fig. 27; Nehring 1997a, p. 315, fig. 39; Godhe et al. 2000, p. 43, fig.13	0	56, 57
Protoperidinium oblongum (Aurivillius) Balech	*Votadinium calvum* Reid	Wall and Dale 1968, p. 272–273, pl. 1 figs 25–28; Baldwin 1987, p. 549, fig. 14; Bolch and Hallegraeff 1990, p. 182, fig. 19a; Nehring 1997a, p. 315, fig. 22	2	58
Protoperidinium pentagonum (Gran) Balech	*Trinovantedinium applanatum* (Bradford) Bujak *et* Davies	Wall and Dale 1968, p. 274, pl. 2 figs 11–12; Lewis et al. 1984, p. 31, pl. 2 fig. 1; Matsuoka 1985a, p.54–55, pl. 9 figs 1–6; pl. 10 figs 1–6	0	59, 60
Protoperidinium subinerme (Paulsen) Loeblich III	*Selenopemphix alticincta* (Bradford) Matsuoka	Wall and Dale 1968, p. 276, pl. 2 figs 22–24; Bolch and Hallegraeff 1990, p. 180, figs 16a–c; Baldwin 1987, p. 547, figs 9–11; Nehring 1997a, p. 317–318, fig. 25	0	61, 62
Pyrophacus horologium Stein	None	Wall and Dale 1971, p. 230–231, figs 34–36; Montresor and Marino 1994, p. 265, fig. 13	1	63
Pyrophacus steinii (Schiller) Wall *et* Dale	*Tuberculodinium vancampoae* (Rossignol) Wall	Wall and Dale 1971, p. 224–226, figs 19–23; Matsuoka 1985d, p. 252–254, plates 35–39	0	64, 66
Scrippsiella crystallina	None	Lewis 1991, p. 96–99, figs 17–29;	2	67

(Table 2 continued)

Biological species name	Palaeontological species name	References	Number of germinated cysts	Figures (present paper)
Lewis		Ishikawa and Taniguchi 1993, p. 2–3, pl. 1 figs 1–5		
Scrippsiella cf. *lachrymosa* Lewis	None	Lewis 1991, p. 98–99, figs 30–36; Montresor et al. 1994, p. 49; Nehring 1997a, p. 318, figs 26, 41, 58	0	68, 69
Scrippsiella cf. *precaria* Montresor *et* Zingone	None	Montresor and Zingone 1988, p. 391, figs 9–10; Ishikawa and Taniguchi 1993, p. 3, 6, pl. 1 figs 11–12	0	70
Scrippsiella cf. *rotunda* Lewis	None	Lewis 1991, p. 101–103, figs 49–52; Ishikawa and Taniguchi 1993, p. 3, pl. 1 figs 6–9	0	71
Scrippsiella trochoidea (Stein) Loeblich III	None	Bolch and Hallegraeff 1990, p. 177, figs 11a–f; Lewis 1991, p. 93–94, figs 1–7	8	72, 73
Scrippsiella sp.	None	Bolch and Hallegraeff 1990, p. 180, figs 13a–c	0	74
Warnowia cf. *rosea* (Pouchet) Kofoid *et* Swezy	None	Ellegaard et al. 2002, p. 543, figs 2–9	2	75–77
Unidentified cyst (cyst type A)			0	78

and Triemer (1985). The terminology used for describing the dinoflagellate cysts essentially follows the works of Wall and Dale (1968), Dale (1983), Matsuoka et al. (1989) and Matsuoka and Fukuyo (2000).

Results

A total of forty-two cyst types, representing 17 genera, was recorded in the sediment samples analyzed, of which forty-one types were identified to species level, and one to genus level. One cyst type could not be classified and is referred to as cyst type A. A list of the biological and palaeontological species names of the cysts is given in Table 2, together with reference to illustrations and descriptions in the literature. Cysts were found at all stations in the study area (Table 3). Most cysts were live and many of them were germinated for identification of the vegetative cell. The numbers of successful incubations for each cyst type are given in Table 2. Sampling sites from which cysts were successfully germinated into thecate cell are shown in Table 3. Since most of the species found are well described in the literature, we give a detailed description only of those of special interest, the potentially toxic species and cysts that are new or known as rare species and that differ in morphology from previously published reports .

***Alexandrium* cf. *minutum* (Lebour) Balech (Figure 2)**

The cyst is reniform in lateral view, 23–25 μm in diameter (number of specimens measured: 3). The wall is covered with an amorphous, transparent, mucilaginous material containing detritus. The living cyst contains numerous clear starch and lipid granules and a red accumulation body. This cyst type was found in Primorye (regions I and II) and Aniva Bay (region III). Motile cells of *A. minutum* have never been observed in plankton in Russian marine waters.

***Alexandrium tamarense* (Lebour) Balech (Figures 3–5)**

The elongated ellipsoidal cyst has rounded ends, is 42–62 μm long, and 32–42 μm wide (number of specimens measured: 45). The smooth wall is thick and covered by a mucoid layer containing detrital particles. The cyst contains numerous clear starch and lipid granules and one or two bright yellow-brown pigmented bodies. Ellipsoidal *Alexandrium* cysts were widely distributed and abundant in many localities in the study area (Table 2). All ellipsoidal *Alexandrium* cysts used for germination experiments produced motile cells (Figure 5), which were identified as *Alexandrium tamarense sensu* Balech (1995).

***Gymnodinium* cf. *catenatum* Graham (Figure 27)**

The cyst is dark reddish-brown, spherical, 51–55 μm in diameter (number of specimens measured: 4). The wall is covered by microreticulate surface ornamentation, with the paracingulum and parasulcus clearly delineated. The excystment opening is a slit (chasmic archeopyle *sensu* Matsuoka 1985c), usually following the paracingulum. Only empty cysts were found in south Primorye (region I), so germination experiments were impossible. Motile cells of *Gymnodinium catenatum* have never been observed in plankton in Russian marine waters.

***Fragilidium mexicanum* Balech (Figures 13–17)**

The cyst is spherical, 45–60 μm in diameter (number of specimens measured: 8), and contains a pale granular cytoplasm with small droplet inclusions and a bright yellow pigmentation body. The cyst wall is smooth and clear

Table 3 Distribution of dinoflagellate cysts at the sites investigated (% of total represented by each taxon).

Taxa / Stations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Alexandrium cf. *minutum*	2		2						1	1			1									1
Alexandrium tamarense	4		e		e	4	3	e	1	1	1	2	e	17*		e	3	e	11	12		20*
Cochlodinium cf. *polykrikoides*								e	1*	1	e											
Diplopelta cf. *parva*			2						1	1												
Diplopsalis cf. *lebourae*				4						1	e			e								
Diplopsalis lenticula	4	6*	2	e	6	8*	6*		3	3*	1	4	10	4*	5	3	3*	5	6	9	5	7*
Fragilidium mexicanum	8		4		2		3*	3		2*	3*	4	1	3			3*				5	
Gonyaulax digitalis		3	2		e			3	3*	2	1	2	3	3		3	6*	3		4		1
Gonyaulax elongata									1				e						3	4		1
Gonyaulax membranacea					6	e		3	3	1	1	e	1	3	e	3		e	3	e	5	
Gonyaulax cf. *scrippsae*				e		e	3	3	1	2	1	e	1	1	5	3	3		3	4		
Gonyaulax spinifera, type *Spiniferites mirabilis*	4		2	e	4	e	3		9	2	2	4	4	1	10	3	26	9	3	4	5	3
Gonyaulax verior							3*		1	2	1			1					6*	4*	5	3
Gymnodinium cf. *catenatum*				e	e			e	e				e				e					
Gyrodinium instriatum			2		2		6*		1	3*	1		1	1								
Lingulodinium polyedrum	e		e	e		e			e				e	e		e	e					e
Pentapharsodinium dalei																			3			3
Pentapharsodinium tyrrhenicum			2				2		1		1											
Polykrikos kofoidii	e		2	e	e	e	e	e	e	2	e	e	1	1		e	e		e	e	e	e
Polykrikos schwartzii			2	e	e	e			e	1	5	e	1	e	e		e				e	e
Preperidinium meunieri						4	3		1	1	1	2	1									1
Protoceratium reticulatum	12	18*	17	8	6	17	6	6*	7*	6	7	6	6	4	10	9	3	14	17*	7*	12	10
Protoperidinium americanum	4		2		3	4	3		3	1	1	4	1	1	e	e	e	5	3		e	3
Protoperidinium cf. *avellanum*	e	e	e		e	e	e		e	e	e	e			e					e		
Protoperidinium claudicans			2		6	8		3	1	1	1		3	1	e						5	1

(Table 3 continued)

Taxa / Stations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Protoperidinium conicoides	e	e	2	e	e	e	e	3	1	1	e	2	3	3		3	e		e	4	5	1
Protoperidinium conicum	e		2	4	3	4			1	5	4	6	1	4		6	3					
Protoperidinium leonis			e		3		e		1	1	3	e	e	e			e					
Protoperidinium minutum				e		4			1		1	2	1	e		3	3		e			1
Protoperidinium oblongum	4		2			4	6*	3	1	1	2	2	3*	1		3	e					
Protoperidinium pentagonum		3	2		6				e	1	e			3		e			3			3
Protoperidinium subinerme			2						1		1						e					
Pyrophacus horologium					3				1	1*												
Pyrophacus steinii	e		e			e	e		e	1	1	e										
Scrippsiella crystallina							3		1	5*	4		8*	1						7		6
Scrippsiella cf. *lachrymosa*																						1
Scrippsiella cf. *precaria*	4		2		9	4		6	3	2	1	6	3	4		3		4	3	4		3
Scrippsiella cf. *rotunda*					3				3	3	1	2	3	1		3		5				
Scrippsiella trochoidea	4	12	8	23	9	8	6*	9	11*	13	14	4	16*	2	10	12	3	14	3	4	5	7
Scrippsiella sp.	16	6	2	12	3	4	3	6	3	6	9	4	5	6			9		3	4		3
Warnowia cf. *rosea*							3*			1												1
Cyst type A																						
"Round brown" cysts*	20	20	17	27	14	14	21	28	16	12	19	28	12	14	21	22	13	14	17	14	17	10
Unidentified cysts*	14	32	18	22	12	13	17	24	17	13	13	16	10	20	39	21	22	27	13	15	31	10
Total number of cysts counted	70	65	100	45	90	60	65	65	156	136	220	108	154	144	40	68	62	45	72	52	40	140

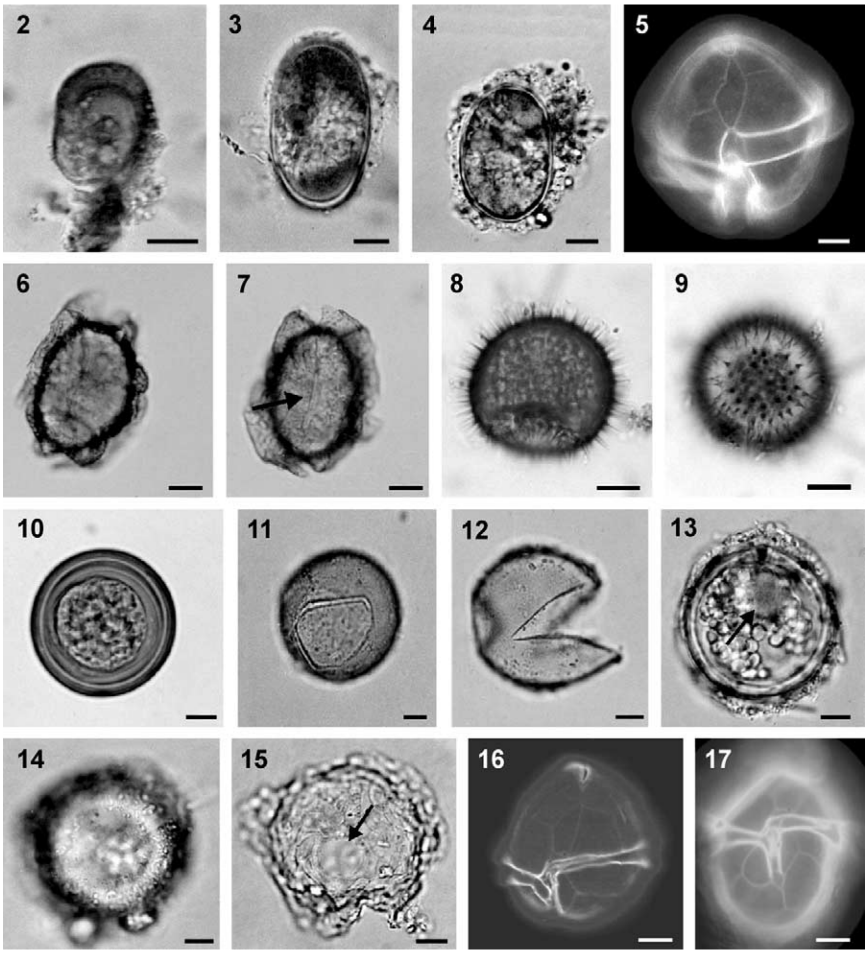
(Table 3 continued)

Taxa / Stations	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Alexandrium cf. *minutum*	1	2																				
Alexandrium tamarense		55*				92*	93	94	4	55	57*	90	56*	95	95	90*	47	14*	8	13	10	4
Cochlodinium cf. *polykrikoides*						0.1*		0.1														
Diplopelta cf. *parva*		1																				
Diplopsalis cf. *lebourae*						0.1*																
Diplopsalis lenticula	8	2	4	e	e	0.1	0.1	0.1		1	e		e		0.5							
Fragilidium mexicanum	1	1																				
Gonyaulax digitalis			1		e																	
Gonyaulax elongata	e	e	4	4	e	0.1		0.1	2	1	e	0.1	1	0.1		1	2	e	e	e		
Gonyaulax membranacea	1	e	e		e																	
Gonyaulax cf. *scrippsae*		1	3		2																	
Gonyaulax spinifera, type *Spiniferites mirabilis*	2	1	3		6																	
Gonyaulax verior	15*			5	3																	
Gymnodinium cf. *catenatum*																						
Gyrodinium instriatum										1	1											
Lingulodinium polyedrum	e		e	e																		
Pentapharsodinium dalei	2	1	5	8	6	1	0.2	0.3		5	6	1		1	0.5	1	2	24	35	5	8	28
Pentapharsodinium tyrrhenicum																						
Polykrikos kofoidii	e	e	e	e	e	0.1	e	0.1	e	e	e	e		e	e	e		e				
Polykrikos schwartzii			4	e	e	e			e		e	e				e						
Preperidinium meunieri		1	3	2	3*	0.1	0.1	0.3		1	e											
Protoceratium reticulatum	17	10*	22	10	12	1		0.3	6	8	2	0.4	8*		e	e	4	24	4	35*	15	
Protoperidinium americanum	2	e	3		3	0.1	0.1	0.1	2	1	3	0.1	1	0.1	e	e	2	4	4		5	4
Protoperidinium cf. *avellanum*	e		e							e			e		e			e				e
Protoperidinium claudicans	2								e	1	e			e								

(Table 3 continued)

Taxa / Stations	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Protoperidinium conicoides	2	e	e	4	3	0.1	e	0.1	e	e	1	e	e			e	e	e	4		e	4
Protoperidinium conicum			e							e	1											
Protoperidinium leonis														e		e		e	e			
Protoperidinium minutum	2		3	e	3	0.1	0.1	0.1	e		1											
Protoperidinium oblongum										1	e											
Protoperidinium pentagonum		e	e	e	e				e	e		e				e					e	e
Protoperidinium subinerme	2	1	e	4	3				2	1	e		2					2	e		5	4
Pyrophacus horologium																						
Pyrophacus steinii																						
Scrippsiella crystallina	2					1	1.4	0.2	3	3	6	0.3	2	0.5		e	15					20
Scrippsiella cf. *lachrymosa*						0.1		0.1	e	1		2										
Scrippsiella cf. *precaria*	2	3																				
Scrippsiella cf. *rotunda*																						
Scrippsiella trochoidea	5	1	4	5	3	1	2	3	70	9	4	4	4	1	1	5	4	4	8	4	12	4
Scrippsiella sp.	5	1	3	8	3	1	1	1	2	1	1	0.2									5	
Warnowia cf. *rosea*	2*																					
Cyst type A									2	6	7	1	2	0.1			2	2	7	4	5	4
"Round brown" cysts*	15	11	20	25	28	1	1	0.2	4	2	6	1	13	0.3	1	1	9	17	15	24	15	12
Unidentified cyst*	12	8	18	25	22	1	1	0.2	3	2	4	0.2	11	2	2	2	13	9	15	15	20	16
Total number of cysts counted	82	106	70	50	58	611	600	750	166	305	102	1200	92	585	306	1024	100	95	52	50	40	50

e: only empty cysts were observed; *: some cysts from this station were successfully germinated into thecate cell in the present study.



Figures 2–17 Dinoflagellate cysts isolated from recent sediments of the east coast of Russia.
(2) *Alexandrium* cf. *minutum*: median focus, contents. (3–5) *Alexandrium tamarense*: (3) ellipsoidal cyst, (4) elongated cyst, (5) theca of a motile cell, germinated from cyst of this type. (6–7) *Cochlodinium* cf. *polykrikoides*: (6) irregular labiate processes and folded membranous outer layer, (7) the germination opening split (arrow). (8–9) *Diplopelta* cf. *parva*: (8) median focus, contents, (9) surface ornamentation. (10–11) *Diplopsalis* cf. *lebourae*: (10) granular contents, (11) germinated cyst with hexagonal archeopyle. (12) *Diplopsalis lenticula*: empty cyst with theropylic archeopyle. (13–17) *Fragilidium mexicanum*: (13) median focus, contents and accumulation body (arrow), (14) surface view, granular wall, (15) circular archeopyle (arrow), (16, 17) theca of a motile cell, germinated from cyst of this type. – Figures 2–4, 6–15, light microscopy (bright field); Figures 5, 16, 17, light microscopy (epifluorescence using Calcofluor White). All scale bars 10 μm.

with varying amounts of mucilage and associated detrital particles attached. The excystment opening is circular. The wall of the empty cyst is colorless and slightly granular. This cyst type was common in Primorye (region I) and in Aniva Bay (region III). Six cysts were isolated and five of them were successfully germinated to produce motile cells after 3 days of incubation. The vegetative stage was identified in cell germination experiments from the thecal plate pattern (Figures 16, 17) as *Fragilidium mexicanum* (Balech 1988). Cysts are known for some species of the genus *Fragilidium* (Steidinger 1975, Owen and Norris 1985, Blanco 1989, Sonneman and Hill 1997). A red accumulation body is typical of *Fragilidium* spp. (Owen and Norris 1985, Sonneman and Hill 1997). All *Fragilidium* cysts that were used for germination experiments in this study contained a yellow-colored body. The cyst found in Russian waters is similar to a cyst of *Fragilidium* sp. described from European waters by Blanco (1989), showing the same size, shape, and a yellow-colored body. Motile cells of *F. mexicanum* have not been observed previously in Russian marine waters.

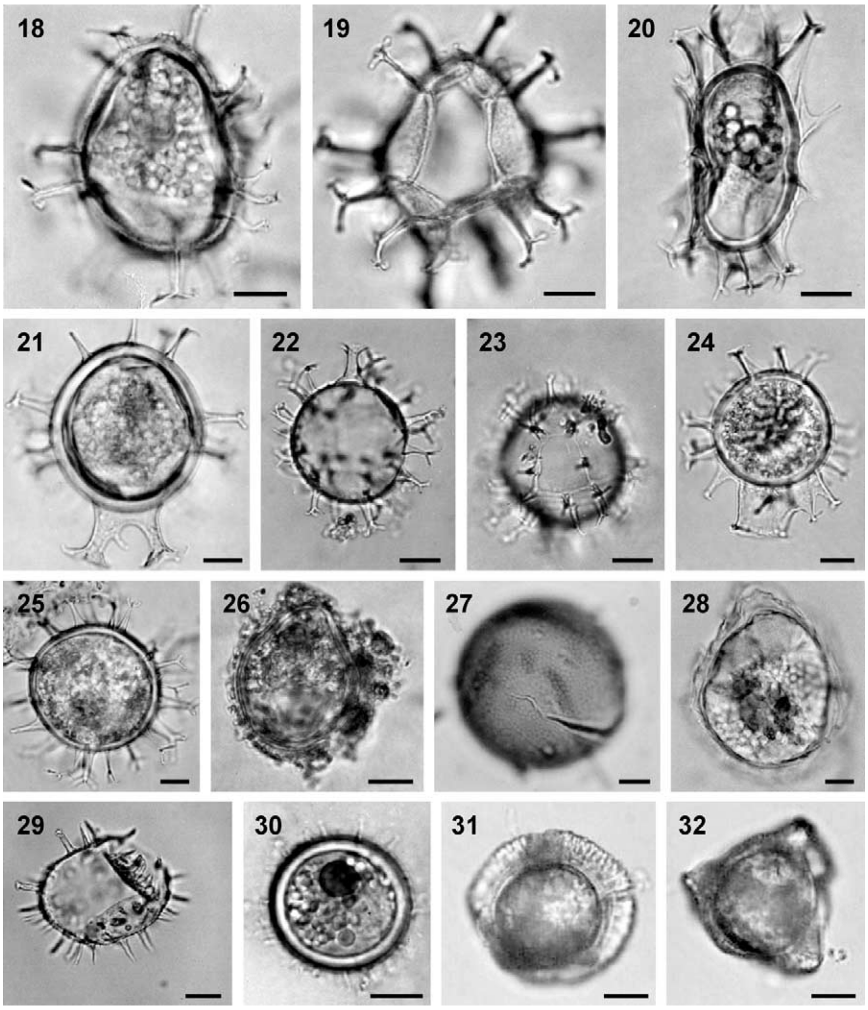
***Gonyaulax verior* Sournia (Figure 26)**

The cyst is ovoidal to ellipsoidal, 29–35 μm long, 25–30 μm wide (number of specimens measured: 11), with a clear yellow-pigmented body and many starch granules. The cyst is smooth or surrounded by gelatinous material containing detritus. The post-equatorial zone is the widest. The cyst wall is without tabulation, sometimes with small antapical boss. Russian cysts are slightly smaller in size than those reported for this cyst type in the references cited in Table 2.

***Scrippsiella* sp. (Figure 74)**

The spherical cyst, 25–27 μm in diameter (number of specimens measured: 10), has clear contents and a bright, ruby-red accumulation body. The cyst wall is relatively thin and clear.

A similar taxon has been recorded in Tasmanian marine sediments (references in Table 2). This was a common and widespread cyst type in the study area. Germination experiments were unsuccessful.



Figures 18–32 Dinoflagellate cysts isolated from recent sediments of the east coast of Russia.
(18–19) *Gonyaulax digitalis*: (18) live cyst, median focus, granular contents, processes, (19) empty cyst, surface ornamentation, precingular archeopyle. (20) *Gonyaulax elongata*: live cyst, median focus, granular contents, processes. (21) *Gonyaulax membranacea*: live cyst, median focus, granular contents, processes. (22–23) *Gonyaulax* cf. *scrippsae*: (22) empty cyst, median focus, processes, (23) same cyst, surface ornamentation. (24–25) *Gonyaulax spinifera*: type *Spiniferites mirabilis,* live cyst, median focus, granular contents, processes. (26) *Gonyaulax verior*: live cyst with granular contents and accumulation body, median focus. (27) *Gymnodinium* cf. *catenatum*: cyst surface with ornamentation and archeopyle. (28) *Gyrodinium instriatum*: live cyst with granular contents and accumulation body. (29) *Lingulodinium polyedrum*: empty cyst with processes and archeopyle. (30) *Pentapharsodinium dalei*: live cyst, granular contents and accumulation body. (31–32) *Pentapharsodinium tyrrhenicum*: live cysts showing the outer calcareous ridges enclosing an inner spherical body. – Figures 18–32, light microscopy (bright field). All scale bars 10 μm.

Warnowia cf. *rosea* (Pouchet) Kofoid *et* Swezy (Figures 75–77)

The cyst is spherical, 32–37 μm in diameter excluding processes (number of specimens measured: 3), light brown in color with a central red-pigmented spot and globules. The cyst has irregular tufts of darker brown material and fused darker brown processes. The germination opening is a simple median split, identical to chasmic type openings. This cyst has the same size and morphology as specimens described from Portuguese waters (Ellegaard et al. 2002). Two cysts were germinated to produce a motile greenish cell. The motile cells were short-lived. After two days, cell division and swimming were not observed, so attempts to establish a culture were unsuccessful. The motile cell was similar to that of *W.* cf. *rosea*, described by Ellegaard et al. (2002), having the same size, shape, color and behavior in culture. Motile cells of *Warnowia* cf. *rosea* have not been observed in Russian marine waters.

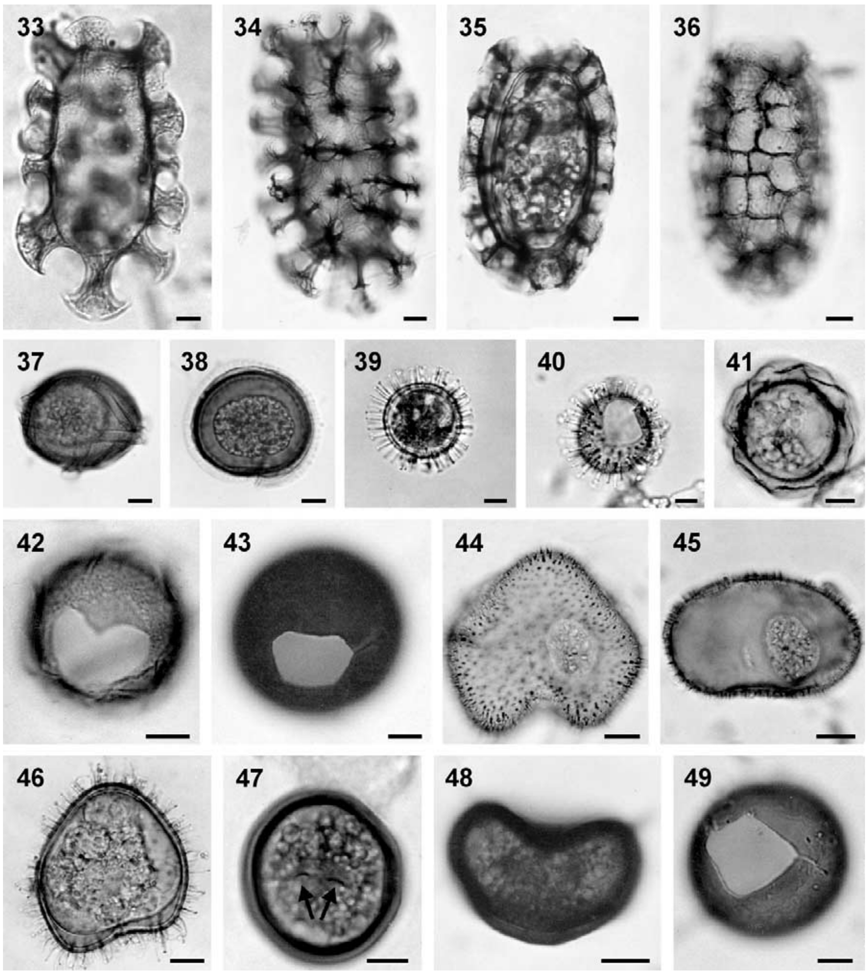
Cyst type A (Figure 78)

The one unidentifiable cyst type observed in the study area is termed type A. The sage-green cysts are round, 20–25 μm in diameter excluding spines (number of specimens measured: 6), with granular cell contents. The cyst surface is covered with numerous long spines (5–6 μm long), which are capitate at the apex. An encystment opening was not observed.

Discussion

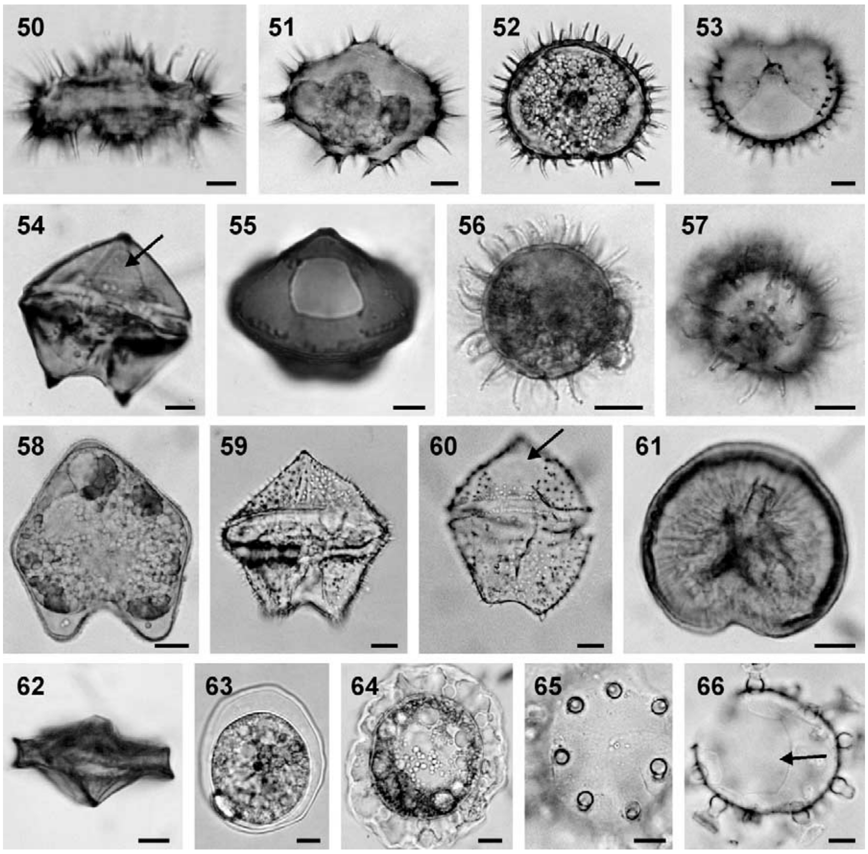
Distribution of cysts

This survey is the first record of dinoflagellate cysts in



Figures 33–49 Dinoflagellate cysts isolated from recent sediments of the east coast of Russia.
(33–34) *Polykrikos kofoidii*: (33) empty cyst, median focus, (34) same cyst, surface ornamentation. (35–36) *Polykrikos schwartzii*: (35) live cyst, median focus, (36) empty cyst, surface ornamentation. (37–38) *Preperidinium meunieri*: (37) live cyst, paracingulum, surface ornamentation, (38) same cyst, apical view. (39–40) *Protoceratium reticulatum*: (39) live cyst, contents, processes, median focus, (40) empty cyst, archeopyle. (41–42) *Protoperidinium americanum*: (41) live cyst, granular contents, folded membranous outer layer, (42) empty cyst, archeopyle. (43) *Protoperidinium* cf. *avellanum*: empty cyst, archeopyle. (44–46): *Protoperidinium claudicans*: (44) live cyst, dorsal view, spines, (45) same cyst, apical view, (46) live cyst, granular contents. (47–49) *Protoperidinium conicoides*: (47) live cyst, granular contents, para–flagellar pores (arrows), (48) live cyst in lateral view, (49) empty cyst, trapezoidal archeopyle. – Figures 33–49, light microscopy (bright field). All scale bars 10 μm.

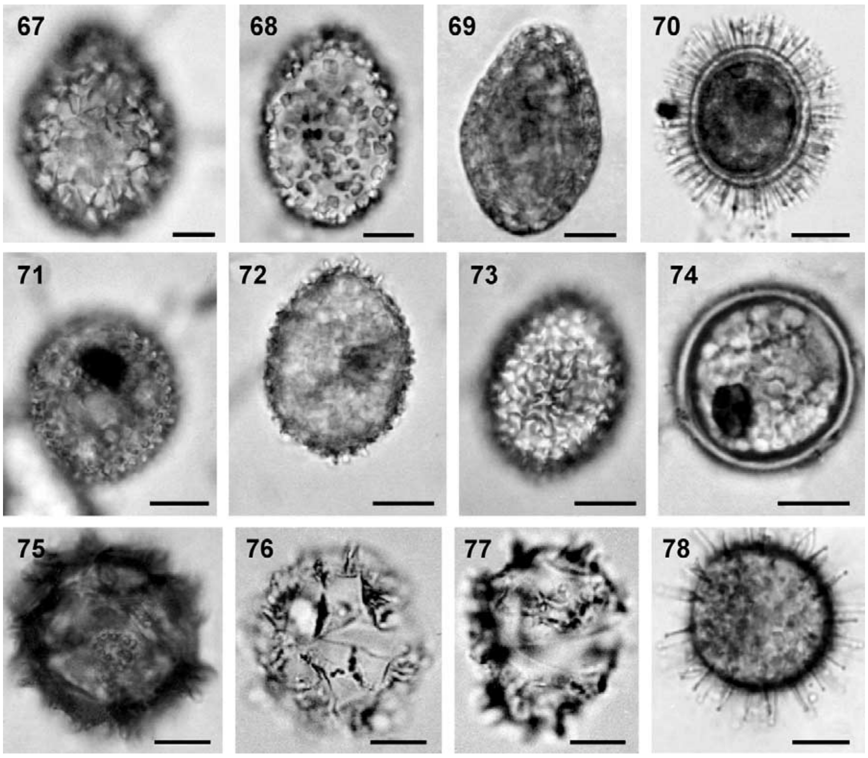
recent sediments from the Russian Pacific coast, and provides useful information on dinoflagellate species distribution in this area. It should be noted that this is the first study of its type, and is not intended to be comprehensive. Additional, more expansive and detailed studies are needed. Living dinoflagellate cysts were found at all forty-four stations. Dinoflagellate cysts were both diverse and abundant. The most common types were those of ellipsoidal *Alexandrium* sp., *Protoceratium reticulatum*, *Gonyaulax* spp., *Polykrikos kofoidii, P. schwartzii*, *Protoperidinium americanum*, *P. minutum*, *P. conicoides, P. conicum, P. subinerme* and *Scrippsiella trochoidea.* The study area covers more than 30 degrees of latitude and extends from the Arctic, in the northern Bering Sea, to the Southern Sakhalin and the Sea of Japan. Despite the difference in hydrographic conditions and number of sampling stations, we observed considerable similarity in cyst composition between different study locations (Table 3). More that 17% of cyst types were observed at all study locations. This may be explained by the high percentage of widely distributed and cosmopolitan dinoflagellate species, which can produce resting cysts in the plankton of the Far Eastern Seas of Russia (Konovalova 1998). The species composition of dinoflagellate cysts from recent marine sediments along the Russian Pacific coast is similar to that observed in Japanese, Korean and Chinese waters (Matsuoka 1985a,b, 1987, 1992, Qi et al. 1996, Lee and Matsuoka 1996, Cho and Matsuoka 2001). As this represents the first study of recent dinoflagellate cysts in Russian marine waters, comparison with nearby Russian localities is not possible. However, fossilized dinoflagellate cysts in sediments from the Bering Sea have been studied by Bujak and Matsuoka (Bujak 1984, Bujak and Matsuoka 1986, Matsuoka and Bujak 1988). Some of the species observed in the recent sediments in this study were also identified in sediment cores dated to the Upper Miocene and Pleistocene, e.g., *Protoperidinium conicoides* (=*Brigantedinium simplex*); *Protoceratium reticulatum* (=*Operculodinium centrocarpum*); *Gonyaulax spinifera* complex (=*Spiniferites frigidus*); *Protoperidinium leonis* (=*Quinquecuspis concreta*); *Pyrophacus steinii* (=*Tuberculodinium vancampoae*).



Figures 50–66 Dinoflagellate cysts isolated from recent sediments of the east coast of Russia.
(50–53) *Protoperidinium conicum*: (50, 51) live cysts, ventral view, (52) live cyst, apical view, granular contents and spines, (53) empty cyst, apical view, trapezoidal archeopyle. (54–55) *Protoperidinium leonis*: (54) live cyst, ventral view, trapezoidal archeopyle (arrow), (55) empty cyst, dorso-apical view, hexagonal archeopyle and paracingulum. (56–57) *Protoperidinium minutum*: (56) live cyst, median focus, contents, processes, (57) same cyst, surface ornamentation. (58) *Protoperidinium oblongum*: live cyst, median focus, contents. (59–60) *Protoperidinium pentagonum*: (59) live cyst, ventral view, (60) empty cyst, ventral view, paracingulum, hexagonal archeopyle (arrow). (61–62) *Protoperidinium subinerme*: (61) empty cyst, apical view, (62) same cyst, lateral view. (63) *Pyrophacus horologium*: live cyst, granular contents. (64–66) *Pyrophacus steinii*: (64) live cyst with granular contents and outer wall layer, (65) empty cyst, surface ornamentation, (66), same cyst, median focus, archeopyle. – Figures 50–66, light microscopy (bright field). All scale bars 10 μm.

Comparison between the species composition of planktonic dinoflagellates and the resting cysts in different study locations along the Russian east coast reveals similarity in distribution of species. Some dissimilarity may be noted, however. Cysts of *Gonyaulax* cf. *scrippsae* were common in sediments collected in study regions I and II (Primorye) and regions III and IV (Sakhalin Island) (Table 3). According to Konovalova (1998), motile cells of this species are known only in plankton of Peter the Great Bay (south Primorye). Cysts of *Protoperidinium oblongum* were found in coastal waters of Primorye (regions I and II), in Aniva Bay (region III) in the Bering sea (region VI) (Table 3). But distribution of this species in plankton is restricted to south Primorye coastal waters (Konovalova 1998). Species of *Preperidinium meunieri, Protoperidinium claudicans* and *P. leonis* have not been found previously as motile stages in the Bering Sea. Cysts of *Polykrikos kofoidii* and *P. schwartzii* were widespread and very common in the study area (Table 3). According to Matsuoka and Cho (2000), the cyst-motile form relationship in *P. schwartzii* and *P. kofoidii* must be reassessed, and they suggest that a separator based on the surface ornamentation of cysts is not effective for differentiating these two species. In this paper, we consider the cysts of *P. schwartzii* and *P. kofoidii* as two different species. No differences in the distribution of these species were observed in the study area. In surrounding waters, motile cells of *P. schwartzii* and *P. kofoidii* are known in the Avachinskaya Guba Inlet on Kamchatka and in coastal waters of south Primorye of the Sea of Japan (Konovalova 1998).

Primorye (region I) had the greatest diversity of species, with up to 90% of all cyst types found in the study area. In this region, the largest number of species was observed in samples collected at the seaport stations in Amurskii Bay (station 10), in Golden Horn Bay (station 11), in Nakhodka Bay (station 14) and in an area of aquaculture farms (stations 3, 7–9, 13). Plankton surveys have shown that this is an anthropogenically eutrophicated area, where massive blooms of phytoplankton occur annually (Stonik and Selina 1995, Stonik and Orlova 2002, Morozova et al. 2002). Cultural eutrophication can increase phytoplankton production including that of cyst-forming dinoflagellates (Dale and Fjellså 1994, Dale et al. 1999). Our results agree with data on dinoflagellate cyst assemblages in surrounding waters, which show the



Figures 67–78 Dinoflagellate cysts isolated from recent sediments of the east coast of Russia.
(67) *Scrippsiella crystallina*: live cyst, surface ornamentation. (68–69) *Scrippsiella* cf. *lachrymosa*: (68) live cyst, surface ornamentation, (69), live cyst, median focus. (70) *Scrippsiella* cf. *precaria*: live cyst, median focus, contents, processes. (71) *Scrippsiella* cf. *rotunda*: live cyst, median focus, contents. (72–73) *Scrippsiella trochoidea*: (72) live cyst, median focus, contents, (73) live cyst, surface ornamentation. (74) *Scrippsiella* sp.: live cyst, median focus. (75–77) *Warnowia* cf. *rosea*: (75) live cyst, median focus, granular contents and accumulation body, (76) germinated cyst, surface ornamentation, processes, (77) same cyst, archeopyle. (78) Cyst type A: live cyst, processes. – Figures 67–78, light microscopy (bright field). All scale bars 10 μm.

greatest abundance and diversity of cysts in sediments of eutrophic coastal waters of China, Korea and Japan (Lee and Matsuoka 1996, Qi et al. 1996, Matsuoka 1999).

Species previously unknown in Russian marine waters

Fifteen species observed in this study have not been found previously in Russian marine waters: *Alexandrium* cf. *minutum*, *Cochlodinium* cf. *polykrikoides*, *Diplopsalis* cf. *lebourae*, *Fragilidium mexicanum*, *Gonyaulax elongata*, *G. membranaceae*, *Gymnodinium* cf. *catenatum*, *Pentapharsodinium dalei*, *P. tyrrhenicum*, *Protoperidinium americanum*, *P.* cf. *avellanum*, *Scrippsiella* cf. *lachrymosa, S.* cf. *precaria*, *S.* cf. *rotunda* and *Warnowia* cf. *rosea*. Cysts of *Fragilidium mexicanum*, *Scrippsiella* cf. *precaria* and *Warnowia* cf. *rosea* were common (Table 3). Cysts of *Protoperidinium americanum* were viable in all study locations. Successful germination of *Cochlodinium* cf. *polykrikoides*, *Fragilidium mexicanum* and *Warnowia* cf. *rosea* suggests that these species may be common members of the phytoplankton community of the Far Eastern Seas of Russia. Almost all 'non-indigenous' species are difficult to identify as vegetative cells by light microscopy. Instead, most of these had an easily recognizable cyst stage. There are several possible explanations as to why the motile stages of these species have not been found previously in the plankton (Dale 1983, Ellegaard et al. 1994, Nehring 1994, 1996, 1997b, Sonneman and Hill 1997): the motile stage is difficult to identify, short-lived or rare, and hence overlooked in plankton surveys; the species may have been brought in to the new area as cysts by currents or ballast water and may not exist as a motile stage in the plankton; and empty cysts may be fossilized and originate from older sediments. *Cochlodinium* cf. *polykrikoides*, *Gymnodinium* cf. *catenatum* and *Warnowia* cf. *rosea* are known as naked dinoflagellates which are very difficult to identify live in plankton samples, and impossible in fixed samples. Small thecate dinoflagellates of both *Diplopsalis* and *Scrippsiella* are often recorded in phytoplankton surveys in the Far Eastern Seas of Russia but are difficult to identify without special treatment such as thecal plate analysis (G. Konovalova and M. Selina pers. comm.). Many *Scrippsiella* species were originally described on the basis of cultures obtained from germination of resting cysts (Montresor 1995, Lewis 1991).

Finding new species of dinoflagellates in Russian marine waters during the first cyst survey in the region, especially given the relatively limited sampling effort in comparison with the large existing phytoplankton data set, confirms the floristic and biogeographic importance of cyst (resting stage) research.

Cysts of toxic dinoflagellates

The cysts of potentially toxic species were found at all eight locations sampled in this study. *Alexandrium* cf. *minutum*, *A. tamarense* and *Gymnodinium* cf. *catenatum* are known as PSP producers. Ellipsoidal *Alexandrium* cysts were widely distributed and abundant in many localities in the study area. Shape, size and cyst contents varied greatly. The ellipsoidal *Alexandrium* cysts of the largest size (length) were observed in the coastal waters of the Bering Sea (regions 6–8) and near Sakhalin Island (regions 3 and 4). More elongated cysts of smaller size (length) were observed in the coastal waters of south Primorye (region 1). The yellow-brown accumulation body was the characteristic feature for all ellipsoidal *Alexandrium* cysts in this study area. A red accumulation body is typical of *Alexandrium* spp. cysts in some other locations (Anderson and Wall 1978). All ellipsoidal *Alexandrium* cysts used for germination experiments produced motile cells, which were identified as *Alexandrium tamarense sensu* Balech (1995). This cyst type was dominant in the coastal waters of the Bering Sea (regions 6 and 7), in the Anachinskaya Guba Inlet (region 5) and in Aniva Bay (region 3). This distribution is evidently consistent with the region in which toxic PSP events have been recorded (Lebedev 1968, Kurenkov 1973). The maximum density of *A. tamarense* cysts was recorded in Pavla Bay (region 7), the area where the earliest documented case of PSP in Russian waters was recorded in September 1945 (Lebedev 1968).

Gymnodinium cf. *catenatum* was found only in south Primorye (region 1). The morphology of this cyst is similar to the descriptions of the cysts of *Gymnodinium catenatum, G. microreticulatum* and *G. nolleri* (Ellegaard and Oshima 1998, Bolch et al. 1999). Differences among cysts of these species are mainly in size and color. Our cyst type resembles that of *G. catenatum* reported from Spain (Anderson et al. 1988), Tasmania (Bolch and Hallegraeff 1990) and Japan (Matsuoka and Fukuyo 1994). According to Matsuoka and Fukuyo (1994), both cysts and motile forms of *G. catenatum* are widely distributed in the plankton and surface sediments of the Japanese coast, including along the west coast of the Sea of Japan, where the maximum surface water temperature is above 25°C. The coastal waters of south Primorye (region 1) are characterized by summer surface water temperatures above 20°C. The presence of *G. catenatum* in the plankton of the study area is doubtful. It is quite possible that cysts observed in recent sediments are actually fossilized cysts.

Data on composition and distribution of dinoflagellate cysts showed that potentially toxic species were found at all study locations over a much wider area than was previously known from planktonic observations. These results suggest that additional cyst surveys should be conducted in areas of the eastern Russian coastline not yet investigated, and that the potential for PSP toxicity as a result of blooms of toxic species may be more widespread than previously documented.

Acknowledgments

The authors acknowledge Dr. G. Konovalova for critically reading the manuscript. We are grateful to anonymous reviewers for helpful comments on the manuscript. Also we express special gratitude to Mr. Gary Comer as, without his help, this publication would not have been possible. This research was supported by the Comer Science and Education Fund to D.M. Anderson, and partly supported by the Far Eastern Branch of the Russian Academy of Sciences (grant "Study of toxic species of phytoplankton in the Far Eastern Seas of Russia" and grant "Response of marine biota to the environmental and climate changes").

References

Anderson, D.M. 1984. The roles of dormant cysts in toxic dinoflagellate blooms and shellfish toxicity. *In*: (E. Ragelis, ed.). *Seafood toxins.* American Chemical Society Symposium series. American Chemical Society, Washington, D.C. pp. 125–138.

Anderson, D.M. and D. Wall. 1978. Potential importance of benthic cysts of *Gonyaulax tamarensis* and *G. excavata* in initiating toxic dinoflagellate blooms. *J. Phycol. 14*: 224–234.

Anderson, D.M., D.G. Aubrey, M.A. Tyler and D.W. Coats. 1982. Vertical and horizontal distributions of dinoflagellate cysts in sediments. *Limnol. Oceanogr. 27*: 757–765.

Anderson, D.M., D.M. Jacobson, I. Bravo and J.H. Wrenn. 1988. The unique microreticulate cyst of the naked dinoflagellate *Gymnodinium catenatum*. *J. Phycol. 24*: 255–262.

Baldwin, R.P. 1987. Dinoflagellate resting cysts isolated from sediments in Marlborough Sound, New Zealand. *N. Z. J. Mar. Freshwater Res. 21*: 543–553.

Balech, E. 1988. Una especie nueva del genero *Fragilidium* (Dinoflagellata) de la bahia de Chamela, Jalisco, Mexico. *Anales del Instituto Biologica UNAM, Series Zoologica 58*: 479–486.

Balech, E. 1995. *The genus Alexandrium Halim (Dinoflagellata).* Sherkin Island Marine Station, Sherkin Island, Co. Cork, Ireland. pp. 151.

Blanco, J. 1989. Quistes de Dinoflagelados de las costas de Galicia. I. Dinoflagelados gonyaulacoides. *Scient. Mar. 53*: 785–796.

Bolch, C.J. and G.M. Hallegraeff. 1990. Dinoflagellate cysts in recent marine sediments from Tasmania, Australia. *Bot. Mar. 33*: 173–192.

Bolch, C.J., A. Negri and G.M. Hallegraeff. 1999. *Gymnodinium microreticulatum* sp. nov. (Dinophyceae): a naked, microreticulate cyst-producing dinoflagellate, distinct from *Gymnodinium catenatum* and *Gymnodinium nolleri*. *Phycologia 38*: 301–313.

Bujak, J.P. 1984. Cenozoic dinoflagellate cysts and acritarchs from the Bering Sea and northern North Pacific. *Micropaleontology 30*: 180–212.

Bujak, J.P. and K. Matsuoka. 1986. Taxonomic reallocation of cenozoic dinoflagellate cysts from Japan and the Bering Sea. *Palynology 10*: 235–241.

Cho, H.-J. and K. Matsuoka. 2001. Distribution of dinoflagellate cysts in surface sediments from the Yellow Sea and East China Sea. *Mar. Micropaleontology 42*: 103–123.

Dale, B. 1977. Cysts of the toxic red-tide dinoflagellate *Gonyaulax excavata* (Braarud) Balech from Oslofjorden, Norway. *Sarsia 63*: 29–34.

Dale, B. 1983. Dinoflagellate resting cysts: 'benthic plankton'. *In*: (G.A. Fryxell, ed.) *Survival strategies of the algae*. Cambridge Univ. Press. pp. 69–136.

Dale, B. and A. Fjellså. 1994 Dinoflagellate cysts as paleoproductivity indicators: state of the art, potential, and limits. *In*: (R. Zahn, T.F. Pedersen, M.A. Kaminski and L. Labeyrie, eds) *Carbon cycling in the glacial ocean: constraints on the ocean's role in global change.* Springer-Verlag, Berlin. pp. 521–537.

Dale, B., T.A. Thorsen and A. Fjellså. 1999. Dinoflagellate cysts as indicators of cultural eutrophication in the Oslofjord, Norway. *Estuar. Coastal Shelf Sci. 48*: 371–382.

Ellegaard, M. 2000. Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years in the Limfjord, Denmark. *Rev. Paleobot. Palynol. 109*: 65–81.

Ellegaard, M. and Y. Oshima. 1998. *Gymnodinium nolleri* Ellegaard *et* Moestrup sp. ined. (Dinophyceae) from Danish waters, a new species producing *Gymnodinium catenatum*-like cysts: molecular and toxicological comparisons with Australian and Spanish strains of *Gymnodinium catenatum. Phycologia 37*: 369–378.

Ellegaard, M., N.F. Christensen and Ø. Moestrup. 1994. Dinoflagellate cysts from recent Danish marine sediments. *Eur. J. Phycol. 29*: 183–194.

Ellegaard, M., B. Dale and A. Amorim. 2002. The acritarchous resting cyst of the athecate dinoflagellate *Warnowia* cf. *rosea* (Dinophycea). *Phycologia 6*: 542–546.

Ellegaard, M., N. Daugbjerg, A. Rochon, J. Lewis and I. Harding. 2003. Morphological and LSU rDNA sequence variation within the *Gonyaulax spinifera-Spiniferites* group (Dinophyceae) and proposal of *G. elongata* comb. nov. and *G. membranacea* comb. nov. *Phycologia 42*: 151–164.

Erard-Le Denn, E., E. Desbruyeres and K. Olu. 1993. *Alexandrium minutum*: resting cyst distribution in the sediment collected along the Brittany coast, France. *In*: (T.J. Smayda and Y. Shimizu, eds) *Toxic phytoplankton blooms.* Developments in marine biology vol. 3. Elsevier, Amsterdam. pp. 109–114.

Fritz, L. and R.E. Triemer. 1985. A rapid simple technique utilizing calcofluor white M2R for the visualization of dinoflagellate thecal plates. *J. Phycol. 21*: 662–664.

Fukuyo, Y. 1982. Cysts of naked dinoflagellates. *In*: (T. Okaichi, ed.) *Fundamental studies of the effects of the marine environment on the outbreaks of red tides.* Reports of Environmental Sciences, B 148-R14-8. 1982. Monbusho, Tokyo. pp. 205–214.

Fukuyo, Y., J. Kittaka and R. Hirano. 1977. Studies on the cysts of marine dinoflagellates. 1. *Protoperidinium minutum* (Kofoid) Loeblich. *Bull. Plankton Soc. Japan 24*: 11–18.

Gail, G.I. 1950. A guide to phytoplankton of the Sea of Japan. *Izvestiya TINRO 33*: 3–177 (in Russian).

Godhe, A., I. Karunasagar and B. Karlson. 2000. Dinoflagellate cysts in recent marine sediments from SW India. *Bot. Mar. 43*: 39–48.

Guillard, R.R.L. and J.H. Ryther. 1962. Studies of marine planktonic diatoms I. *Cyclotella nana* Hustedt and *Detonula confervaceae* (Cleve) Gran. *Can. J. Microbiol. 8*: 229–239.

Hallegraeff, G.M. and C.J. Bolch. 1992. Transport of diatom and dinoflagellate resting spores in ship's ballast water: implications for plankton biogeography and aquaculture. *J. Plank. Res. 14*: 1067–1084.

Harland, R. 1983. Distribution map of recent dinoflagellate cysts in bottom sediments from the North Atlantic Ocean and adjacent seas. *Palaeontology 26*: 321–387.

Head, M.J. 1996. Modern dinoflagellate cysts and their biological affinities. *In*: (J. Jansonius and D.C. McGregor, eds) *Palynology: principles and applications.* American Association of Stratigraphic Palynologists Foundation. Dallas. pp. 1197–1248.

Ishikawa, A. and A. Taniguchi. 1993. Some cysts of the genus *Scrippsiella* (Dinophyceae) newly found in Japanese waters. *Bull. Plankton Soc. Japan 40*: 1–7.

Kisselev, I.A. 1937. Composition and distribution of phytoplankton in the north part of the Bering Sea and in the south part of the Chukcha Sea. *Issledovaniya Morei SSSR, 25*: 217–245 (in Russian).

Kisselev, I.A. 1950. *Thecate flagellates*. M.-L. Izdatelstvo AN SSSR. pp. 290 (in Russian).

Kisselev, I.A. 1959. Qualitative and quantitative composition of phytoplankton and its distribution in coastal waters of south Sakhalin Island and south Kuril Islands. *Issledovaniya Dalnevostochnih Morei SSSR, 6*: 58–77 (in Russian).

Kobayashi, S. and K. Matsuoka. 1984. Cyst and theca of *Protoperidinium conicum* (Gran) Balech, (Dinophyceae). *Jap. J. Phycol. (Sorui) 32*: 53–57.

Kobayashi, S. and K. Yuki. 1991. Distribution of dinoflagellate cysts in surface sediments of Japanese coastal waters II. Matoya Bay. *Bull. Plankt. Soc. Jap. 38*: 9–23.

Kobayashi, S., K. Matsuoka and S. Iisuka. 1986. Distribution of dinoflagellate cysts in surface sediments of Japanese coastal waters I. Omura Bay, Kyushu. *Bull. Plankt. Soc. Jap. 33*: 81–93.

Kojima, N. and S. Kobayashi. 1992. Motile cell-like cyst of *Gyrodinium instriatum* Freudenthal *et* Lee (Dinophyceae). *Rev. Palaeobot. Palynol. 74*: 239–247.

Konovalova, G.V. 1993. Toxic and potentially toxic dinoflagellates from the east coast waters of the USSR. *In*: (T. Smayda and Y. Shimizu, eds) *Toxic phytoplankton blooms in the Sea.* Elsevier, New York. pp. 169–174.

Konovalova, G.V. 1995. The dominant and potentially dangerous species of phytoflagellates in the coastal waters of east Kamchatka. *In*: (P. Lassus, G. Arzul, E. Erard, P. Gentien and C. Marcaillou, eds) *Harmful marine algal blooms*. Lavoisier, Paris. pp. 169–174.

Konovalova, G.V. 1998. *Dinoflagellatae (Dinophyta) of the Far Eastern Seas of Russia and adjacent waters of the Pacific Ocean.* Dalnauka, Vladivostok. pp. 300 (in Russian).

Konovalova, G.V. 1999. Red tides and blooms of waters in the Far Eastern Seas of Russia and adjacent waters of the Pacific Ocean. *Russian J. Mar. Biol. (Biologiya Morya) 25*: 295–304.

Konovalova, G.V., T.Yu. Orlova and L.A. Pautova. 1989. *Atlas fitoplanktona Yaponskogo morya*. Nauka, Leningrad. pp. 169 (in Russian).

Kurenkov, I.I. 1973. *Krasnii priliv v Avachinskoi Gube.* Otchet 6294818. Arhiv KamchatNIRO, Petropavlosk-Kamchatskii. pp. 23 (in Russian).

Kuzmina, A.I. 1962. Phytoplankton of Kuril Straits as indicator of different water masses. *Issledovaniya Dalnevostochnih Morei SSSR 8*: 6–90 (in Russian).

Lebedev, S.P. 1968. Caution: red tides. *Rybnoe Khozyaistvo 5*: 19–20 (in Russian).

Lee, J.B. and K. Matsuoka. 1996. Dinoflagellate cysts in surface sediments of southern Korean waters. *In*: (T. Yasumoto, Y. Oshima and Y. Fukuyo, eds) *Harmful and toxic algal blooms*. Intergovernmental Oceanographic Commission of UNECSO, Japan. pp. 173–176.

Lewis, J. 1990. The cyst-theca relationship of *Oblea rotunda* (Diplopsalidaceae, Dinophyceae). *Brit. Phycol. J. 25*: 339–351.

Lewis, J. 1991. Cyst-theca relationships in *Scrippsiella* (Dinophyceae) and related orthoperidinoid genera. *Bot. Mar. 34*: 91–106.

Lewis, J. and J.D. Dodge. 1987. The cyst-theca relationship of *Protoperidinium americanum* (Gran & Braarud) Balech. *J. Micropalaeontol. 6*: 113–121.

Lewis, J., J.D. Dodge and P. Tett. 1984. Cyst-theca relationships in some *Protoperidinium* species (Peridiniales) from Scottish sea lochs. *J. Micropalaeontol. 3*: 25–34.

Lewis, J., A. Rochon and I. Harding. 1999. Preliminary observations of cyst-theca relationships in *Spiniferites ramosus* and *Spiniferites membranaceus* (Dinophyceae). *Grana 38*: 113–124.

Matsuoka, K. 1984. Cyst and theca of *Protoperidinium avellana* (Meunier) Balech (Dinophyceae). *Bull. Fac. Lib. Arts, Nagasaki Univ., Nat. Sci. 25*: 34–47.

Matsuoka, K. 1985a. Organic-walled dinoflagellate cysts from surface sediments of Nagasaki Bay and Senzaki Bay, West Japan. *Bull. Fac. Lib. Arts, Nagasaki Univ., Nat. Sci. 25(2)*: 21–115.

Matsuoka, K. 1985b. Distribution of the dinoflagellate cyst in surface sediment of the Tsushima Warm Current. *Quaternary Res. 24*: 1–12.

Matsuoka, K. 1985c. Archeopyle structure in modern gymnodinialean dinoflagellate cysts. *Rev. Paleobot. Palynol. 44*: 217–231.

Matsuoka, K. 1985d. Cyst and thecate forms of *Pyrophacus steinii* (Schiller) Wall *et* Dale, 1971. *Trans. Proc. Palaeont. Soc. Japan, N. S. 140*: 240–262.

Matsuoka, K. 1987. Organic-walled dinoflagellate cysts from surface sediments of Akkeshi Bay and Lake Saroma, North Japan. *Bull. Fac. Lib. Arts, Nagasaki Univ., Nat. Sci. 28*: 35–123.

Matsuoka, K. 1988. Cyst-theca relationships in the diplopsalid group (Peridiniales, Dinophyceae). *Rev. Paleobot. Palynol. 56*: 95–122.

Matsuoka, K. 1992. Species diversity of modern dinoflagellate cysts in surface sediments around the Japanese islands. *In*: (M.J. Head and J.H. Wrenn, eds) *Neogene and Quaternary dinoflagellate cysts and acritarchs*. American Association of Stratigraphic Palynologists Foundation, Dallas. pp. 33–53.

Matsuoka, K. 1999. Eutrophication process recorded in dinoflagellate cyst assemblages – a case of Yokohama Port, Tokyo bay, Japan. *Sci. Total Environ. 231*: 17–35.

Matsuoka, K. and J.P. Bujak. 1988. Cenozoic dinoflagellate cysts from the Navarin Basin, Norton Sound and St. George Basin, Bering Sea. *Bull. Fac. Lib. Arts, Nagasaki Univ., Nat. Sci. 29*: 1–147.

Matsuoka, K. and H.-J. Cho. 2000. Morphological variation in cysts of the gymnodinialean dinoflagellate *Polykrikos*. *Micropaleontology 46*: 360–364.

Matsuoka, K. and Y. Fukuyo. 1994. Geographical distribution of the toxic dinoflagellate *Gymnodinium catenatum* Graham in Japanese coastal waters. *Bot. Mar. 37*: 495–503.

Matsuoka, K. and Y. Fukuyo. 2000. *Technical guide for modern dinoflagellate cyst study*. WESTPAC-HAB/WESTPAC/IOC. pp. 29.

Matsuoka, K., Y. Fukuyo and D.M. Anderson. 1988. The cyst and theca of *Gonyaulax verior* Sournia (Dinophyceae) and their implication for the systematics of the genus *Gonyaulax*. *Jap. J. Phycol. (Sorui) 36*: 311–320.

Matsuoka, K., Y. Fukuyo and D.M. Anderson. 1989. Methods for modern dinoflagellate cyst studies. *In*: (T.Okaichi, D.M. Anderson and T. Nemoto, eds) *Red tides: biology, environmental science and toxicology*. Elsevier, Amsterdam. pp. 461–479.

Montresor, M. 1995. *Scrippsiella ramonii* sp. nov. (Peridiniales, Dinophyceae), a marine dinoflagellate producing a calcareous resting cyst. *Phycologia 34*: 87–91.

Montresor, M. and D. Marino. 1994. New observations on the life cycle of *Pyrophacus horologium* Stein (Dinophyceae). *Bollettino Della Società Adriatica di Scienze 75*: 261–268.

Montresor, M. and A. Zingone. 1988. *Scrippsiella precaria* sp. nov. (Dinophyceae), a marine dinoflagellate from the Gulf of Naples. *Phycologia 27*: 387–394.

Montresor, M., A. Zingone and D. Marino. 1993. The calcareous resting cyst of *Pentapharsodinium tyrrhenicum* comb. nov. (Dinophyceae). *J. Phycol*. *29*: 223–230.

Montresor, M., E. Montesarchio, D. Marino and A. Zingone. 1994. Calcareous dinoflagellate cysts in marine sediments of the Gulf of Naples (Mediterranean Sea). *Rev. Paleobot. Palynol. 84*: 45–56.

Morozova, T., T. Orlova and M. Selina. 2002. Phytoplankton in the scallop culture area in Minonosok Bight (Pos'eta Bay, Sea of Japan). *Russian J. Mar. Biol. 2*: 94–99.

Nehring, S. 1994. *Scrippsiella* spp. resting cysts from the German Bight (North Sea): a tool for more complete checklists of dinoflagellates. *Nethl. J. Res. 33*: 57–63.

Nehring, S. 1995. Dinoflagellate resting cysts as factors in phytoplankton ecology of the North Sea. *Helgoländer Meeresunters. 49*: 375–392.

Nehring, S. 1996. Recruitment of planktonic dinoflagellates: importance of benthic resting cysts and resuspension events. *Int. Revue ges. Hydrobiol. 81*: 513–527.

Nehring, S. 1997a. Dinoflagellate resting cysts from recent German coastal sediments. *Bot. Mar. 40*: 307–324.

Nehring, S. 1997b. Dinoflagellate resting cysts from recent sediments of the Western Baltic as indicators for the occurrence of "non-indigenous" species in the water column. *In*: (A. Andrusaitis, ed.) *Proceedings of the 13th Symposium of the Baltic Marine Biologists*. Institute of Aquatic Ecology, University of Latvia. pp. 79–85.

Orlova, T.Yu. and T.V. Morozova. 2003. On morphology of cysts and vegetative cells of *Scrippsiella crystallina* Lewis (Dinophyta) from the Far Eastern seas of Russia. *Algologia. 4*: 411–416

Orlova, T.Yu., M.S. Selina and I.V. Stonik. 1998. Distribution of harmful microalgae in Peter the Great Bay, the Sea of Japan, Russia. *In*: (B. Reguera, J. Blanco, M.L. Fernández and T. Wyatt, eds) *Harmful algae.* Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO. pp. 86–87.

Orlova, T.Yu., M.S. Selina and O.G. Shevchenko. 2003. The morphology of cysts and motile cells of *Gyrodinium instriatum* (Dinophyta), a species new to the seas of Russia. *Russian J. Mar. Biol. 2*: 120–122.

Owen, K.C. and D.R. Norris. 1985. Cysts and life cycle considerations of the thecate dinoflagellate *Fragilidium. J. Coast. Res. 1*: 263–266.

Persson, A., A. Godhe and B. Karlson. 2000. Dinoflagellate cysts in recent sediments from the west coast of Sweden. *Bot. Mar. 43*: 69–79.

Qi, Y.-z., H. Ying, Zh. Lei, D.M. Kulis and D.M. Anderson. 1996. Dinoflagellate cysts from recent marine sediments of the South and East China seas. *Asian Mar. Biol. 13*: 87–103.

Reid, P.C. 1974. Gonyaulacaceae dinoflagellate cysts from the British Isles. *Nova Hedwigia 25*: 579–637.

Sætre, M.M.L., B. Dale, M.I. Abdullah and G.-P. Sætre. 1997. Dinoflagellate cysts as potential indicators of industrial pollution in a Norwegian fjord. *Mar. Environ. Res. 44*: 167–189.

Sonneman, J.A. and D.R.A. Hill. 1997. A taxonomic survey of cyst-producing dinoflagellates from recent sediments of Victorian coastal waters, Australia. *Bot. Mar. 40*: 149–177.

Steidinger, K. 1975. Implications of dinoflagellate life cycles on initiation of *Gymnodinium breve* red tide. *Envir. Letters 9*: 129–139.

Stonik, I.V. and M.S. Selina. 1995. Phytoplankton as indicator of trophic level of phytoplankton in Peter the Great Bay, the Sea of Japan. *Russian J. Mar. Biol. (Biologiya Morya) 21*: 403–406.

Stonik, I.V. and T.Yu. Orlova. 2002. Phytoplankton of the coastal waters off Vladivostok city (the north-western part of the East Sea) under eutrophic conditions. *Ocean and Polar Res. 24*: 359–365.

Uchida, T., Y. Matsuyama, M. Yamaguchi and T. Honjo. 1996. The life cycle of *Gyrodinium instriatum* (Dinophyceae) in culture. *Phycol. Res. 44*: 119–123.

Wall, D. and B. Dale. 1968. Modern dinoflagellate cysts and evolution of the Peridiniales. *Micropaleontology 14*: 265–304.

Wall, D. and B. Dale. 1971. A reconsideration of living and fossil *Pyrophacus* Stein, 1883 (Dinophyceae)*. J. Phycol. 7*: 221–235.

Received 23 May, 2003; accepted 16 April, 2004