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Dinoflagellate Cysts in Recent Sediments from Bahía Concepción, Gulf of California

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The composition, abundance, and distribution of dinoflagellate resting cysts in recent sediments were analyzed at 12 sites in Bahía Concepción in the subtropical Gulf of California. Calcareous and organic Peridiniales, Gonyaulacales, and Gymnodiniales were identified at species level (25 cyst types). Empty cysts constituted 75–90 % of cysts in the samples. Cyst assemblages were dominated by calcareous Peridiniales (30–70 %) and Gonyaulacales (13–44 %), represented mainly by *Scrippsiella trochoidea* and *Lingulodinium polyedrum*. In the first centimeter of sediment, cyst counts varied from 173 to 9, 933 cysts g^{-1} wet weight, and increased in abundance in the inner area of the bay. Cysts of the toxic species *Gymnodinium catenatum* were also detected, and successful cyst germination of *Alexandrium margalefii* is described. Cyst abundance and distribution patterns suggest that the bay acts as a cyst trap, and that the cyst assemblages reflect the local community of meroplanktonic dinoflagellates.

Introduction

About 260 of the 2000 identified living dinoflagellate species (Taylor 1987) are cyst-producers (Head 1996). Cysts are a resting stage during the life cycle of some dinoflagellates, and their formation is a protective mechanism against unfavorable conditions, such as nutrient depletion, grazing, competition, and high turbulence (Prakash 1967, Steidinger 1975, Dale 1983, Anderson 1998). Cysts act as seed stock, which supply the initial inoculum to form plankton blooms once favorable conditions (mainly temperature) are established, although endogenous (internal clock, growth factors) and exogenous variables (vitamins, humic acids) could be involved (Pfiester and Anderson 1987).

Distribution studies of cysts provide specialized information concerning the biogeography and ecology of living dinoflagellate species, and detect areas of accumulation of toxic species cysts (Wall *et al.* 1977, Dale 1983). Most investigations of cyst assemblages have been performed in subpolar and temperate areas of the Northern Hemisphere (e.g. Wall and Dale 1968, Matsuoka 1992, Matthiessen 1995, Nehring 1997, Persson *et al.* 2000). However, some have been conducted in the Southern Hemisphere (e.g. Bolch and Hallegraeff 1990, Sonneman and Hill 1997).

For deep basins in the Gulf of California, cyst assemblages and distribution in Holocene marine sediments were part of a major study by Martínez-Hernández and Hernández-Campos (1991). They concluded that local cyst assemblages have an affinity with cool, temperate, and tropical areas of the Atlantic Ocean and Caribbean Sea; most species are ubiquitous; some species become very abundant in certain areas.

Microphytoplankton in the Gulf of California includes 418 species of diatoms and 270 dinoflagellates (Hernández-Becerril 1987a, Licea *et al.* 1995, Moreno *et al.* 1996). Dinoflagellates are primarily holoplanktonic, and only 11 % are cyst producers. The latter includes toxic species such as *Gymnodinium catenatum* Graham, *Lingulodinium polyedra* (Stein) Dodge, and *Cochlodinium polykrikoides* Margalef (Mee *et al.* 1986, Hernández-Becerril 1987b, Cortés-Altamirano *et al.* 1995, Gárate-Lizárraga *et al.* 2000).

Bahía Concepción, one of the largest subtropical bays of the western Gulf of California (Fig. 1), has been examined for the presence of toxic dinoflagellates *Gymnodinium catenatum* and *Alexandrium* spp. and paralytic and diarrheic toxins in mollusks (Sierra-Beltrán *et al.* 1996, Lechuga-Devéze and Morquecho 1998). The origin of these potentially toxic dinoflagellates and their toxins has not been explained clearly. This paper presents a summary of distribution, abundance, and species composition of dinoflagellate cyst assemblages in Bahía Concepción. We also attempt to establish cyst-theca relationships among potentially toxic species and to identify species with heterospory.

Material and Methods

Sediment cores of 5–20 cm length and 1.3 cm diameter were collected with a gravity corer at 12 Bahía Concepción sites (Fig. 1) during September 1999. The
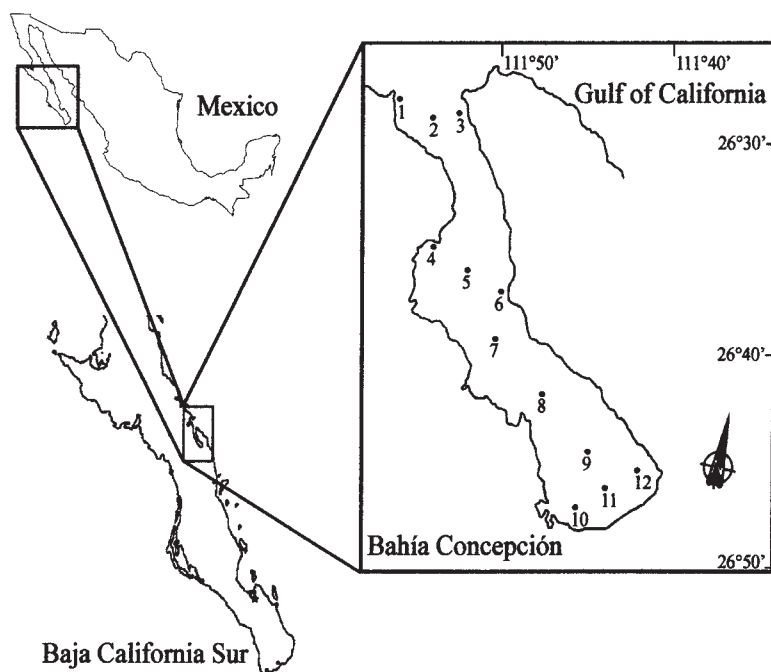
Fig. 1. Map of Bahía Concepción showing sites where sediment samples were collected.

cores were wrapped in aluminum foil and stored in the dark at 4 °C. For identification and enumeration of the samples, the undisturbed first centimeter of each sample (cm 0–1) was processed using a biological method for cleaning and concentrating cysts (Matsuoka *et al.* 1989, Matsuoka and Fukuyo 2000). This first centimeter was weighed and mixed with filtered seawater. The suspension was treated with an ultrasonic cleaner (Bransonic 200, Branson Ultrasonics Corp., Danburg, CT, USA) for 5 min, filtered through a 100-μm sieve, and concentrated on a 20-μm sieve. The residue on the 20-μm sieve was washed continuously with filtered seawater until the wash water remained clear. Samples were stored in 10-mL vials. Aliquots (0.5–1 mL) from each vial were examined with an inverted microscope at 40× magnification (Carl Zeiss Axiovert 100, Oberkochen, Germany), by scanning 100 % of the Utermöhl chamber bottom. Most cysts were identified from descriptions in the literature on cysts. Data on each group was expressed by relative abundance (%) and total abundance (cysts g^{-1} wet sediment). To compare counts between sampling stations and to define the most suitable area for cyst deposition and accumulation, the Bray-Curtis coefficient (Bray and Curtis 1957) was applied. A hierarchical cluster was constructed using a group average linkage.

To define cyst-theca relationships, germination experiments were performed after isolating living cysts with a micropipette. Specimens were incubated on 24-well culture plates filled with GSe medium (Blackburn *et al.* 1989) in a culture room (12:12 h dark:light, 65 μE m^{-2} s^{-1} light intensity, 20±1 °C) and examined regularly for germination. Experiments in which cysts did not germinate within 15 days were discarded. Photographic records of the cysts were made (Carl Zeiss MC80, Oberkochen, Germany). Different theca staining methods, such as Trypan Blue (Graham 1942), iodine-containing stains (Imamura and Fukuyo 1987), and Calcofluor White (Fritz and Triemer 1985) were used to identify dinoflagellates obtained from cyst germination. Selected samples were fixed with 0.2 % glutaraldehyde, dehydrated in increasing concentrations of ethanol, collected on nucleopore filters (2 μm), and dried at critical point with liquid CO_2. Filters were mounted on aluminum stubs, sputter coated with platinum, and examined with a scanning electron microscope (JEOL JSM-840, JEOL Inc., Peabody, MA, USA).

Results

Species composition

In this survey, 25 cyst types belonging to 4 groups were associated with their vegetative cells at species level (Table I). The systematic account is in accordance with the classification of Sournia (Chrétiennot-Dinet *et al.* 1993). Calcareous Peridiniales (Figs 7–8) and Gonyaulacales (Figs 12–15) cysts were the most representative morphotypes (Fig. 31B). Calcareous cysts were represented mainly by *Scrippsiella trochoidea* (30–69 %); *Scrippsiella precaria* was found sporadically. Among Gonyaulacales, *Lingulodinium polyedrum* was the most representative morphotype (4–17 %), but the cysts of *Gonyaulax spinifera*,

Table I. Occurrence and abundance of dinoflagellate cysts in Bahía Concepción. From the spherical *Alexandrium* spp. cysts, *A. margalefii* was successfully germinated.

Resting cyst species	Abundance (cysts g^{-1} wet weight)											
	Sampling stations											
	1	2	3	4	5	6	7	8	9	10	11	12
Gonyaulacales												
Alexandrium spp. (spherical)	18	30	16	139	174	627	752	391	654	642	764	312
Gonyaulax scrippsae Kofoid	2	50	100	30	3	100	200	100	100	80	200	100
Gonyaulax spinifera (Claparède *et* Lachmann) Diesing	5	35	46	11	4	50	56	120	26	69	33	49
Lingulodinium polyedrum (Stein) Dodge	7	122	478	104	72	1304	992	1038	755	1179	1294	907
Protoceratium reticulatum (Claparède *et* Lachmann) Bütschli	2	0	0	6	0	25	16	0	0	0	52	89
Pyrophacus steinii (Schiller) Wall *et* Dale	2	79	113	35	130	414	336	241	277	328	298	342
Gymnodiniales												
Cochlodinium sp.	0	0	0	0	0	0	0	0	0	0	39	0
Gymnodinium catenatum Graham	7	6	49	41	58	88	48	75	101	104	129	59
Phepolykrikos hartamannii (Zimmermann) Matsuoka *et* Fukuyo	5	12	16	0	7	125	96	15	25	15	26	74
Polykrikos kofoidii Chatton	0	12	32	58	51	163	112	105	101	119	117	74
Polykrikos schwartzii Bütschli	0	0	49	6	14	88	48	105	50	75	52	74
Calcareous Peridiniales												
Scrippsiella trochoidea (Stein) Loeblich III	53	280	1215	678	2014	6056	5104	5669	5358	4000	6356	4431
Scrippsiella precaria Montresor *et* Zingone	0	18	146	46	43	88	0	0	0	0	0	0
Organic Peridiniales												
Diplopsalis sp.	1	0	0	0	0	3	0	0	0	1	0	1
Protoperidinium americanum (Gran *et* Braarud) Balech	0	0	0	0	0	0	1	0	0	2	2	2
Protoperidinium avellana (Meunier) Balech	2	0	0	0	0	0	16	0	0	0	0	0
Protoperidinium claudicans (Paulsen) Balech	2	0	0	12	7	13	0	0	0	0	13	0
Protoperidinium compressum (Nie) Balech	0	0	8	0	0	13	0	0	0	15	0	0
Protoperidinium conicum (Gran) Balech	0	0	49	0	7	50	0	30	50	0	26	45
Protoperidinium denticulatum (Gran *et* Braarud) Balech	53	61	356	186	312	288	448	226	327	269	375	134
Protoperidinium latissimum (Kofoid) Balech	0	0	0	0	1	0	0	0	0	2	1	1
Protoperidinium leonis (Pavillard) Balech	0	0	16	0	14	38	0	0	0	15	0	0
Protoperidinium minutum (Kofoid) Loeblich III	2	6	49	17	14	13	48	0	0	60	26	0
Protoperidinium oblongum (Aurivillius) Parke *et* Dodge	5	0	0	0	0	0	0	15	25	0	39	0
Protoperidinium pentagonum (Gran) Balech	0	0	0	0	0	0	0	0	0	0	1	1
Protoperidinium subinerme (Paulsen) Loeblich III	9	6	24	12	22	38	64	45	0	45	91	0
Zygabikodinium lenticulatum (Mangin) Loeblich *et* Loeblich III	0	0	0	6	7	38	48	0	50	60	0	15
Totals	175	719	2761	1386	2957	9620	8385	8175	7900	7079	9933	6712

Gonyaulax scrippsae, and spherical *Alexandrium* spp. were also part of this group. Most cysts (75–97 %) were empty. The few living cysts included spherical *Alexandrium* spp., *Scrippsiella trochoidea*, *Lingulodinium polyedrum*, *Gonyaulax* spp., and round reddish-brown *Protoperidinium*-like cysts.

Organic Peridiniales (Figs 2–6), and Gymnodiniales (Figs 9–11, 17–18) were the least representative morphotypes in the cyst assemblages. Peridiniales were represented by heterotrophic species of the genus *Protoperidinium*, such as *P. conicum*, *P. oblongum*, *P. compressum*, *P. claudicans*, *P. subinerme*,
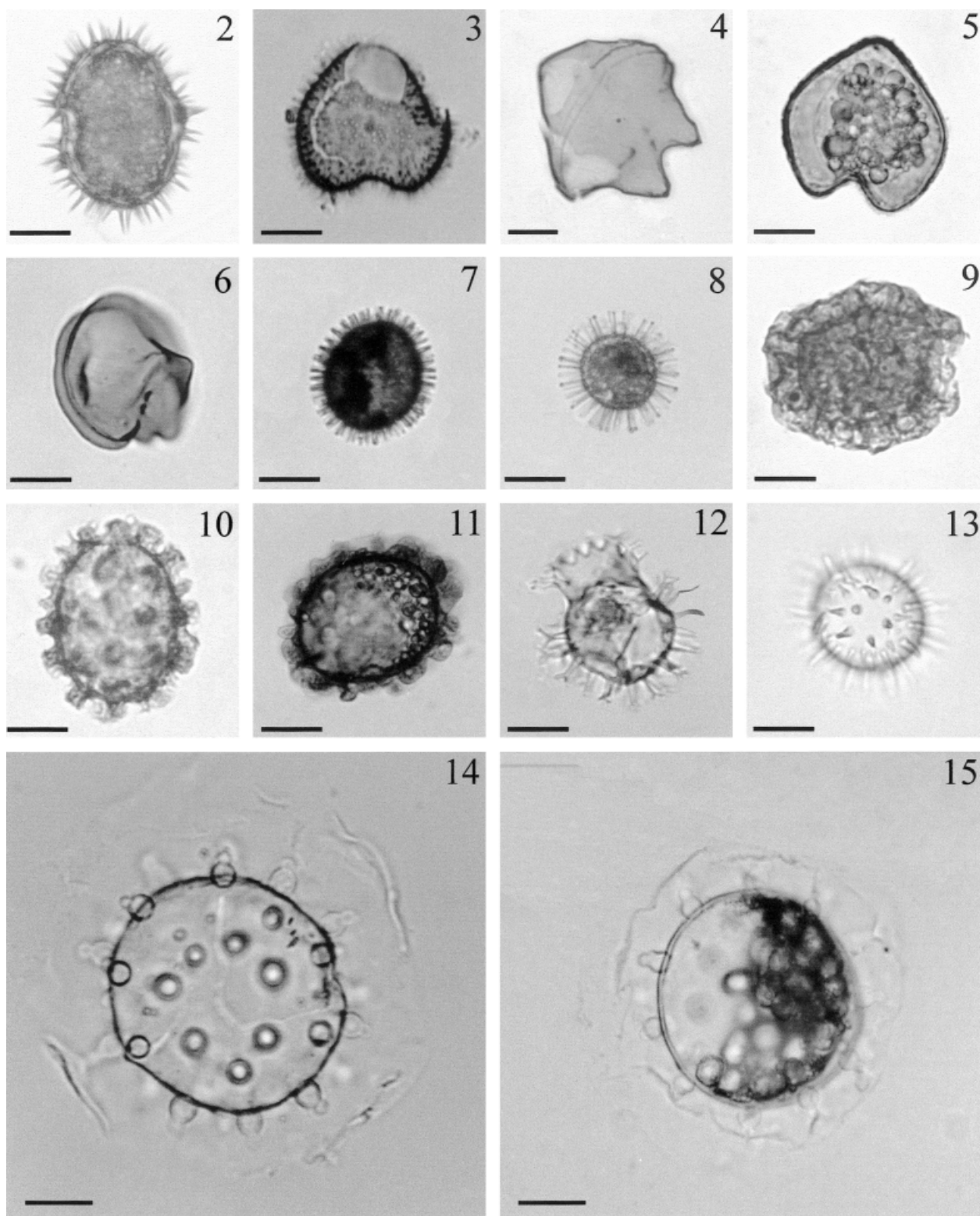
Figs 2–15. Light micrographs of some Peridiniales (2–8), Gymnodiniales (9–11) and Gonyaulacales (12–15) cysts found in recent sediments of Bahía Concepción, Gulf of California. Scale bars = 20 μm. (2) *Protoperidinium conicum*, (3) *Protoperidnium claudicans*, (4) *Protoperidinum leonis,* (5) *Protoperidinum oblongum*, (6) *Protoperidinium subinerme*, (7) *Scrippsiella trochoidea*, (8) *Scrippsiella precaria,* (9) *Polykrikos schwartzii*, (10) *Polykrikos kofoidii*, (11) *Cochlodinium* sp., (12) *Gonyaulax spinifera*, (13) *Lingulodinium polyedrum*, (14) empty cyst of *Pyrophacus steinii*, (15) living cyst of *P. steinii*.

Gymnodiniales in order of abundance, by *Polykrikos kofoidii*, *Polykrikos schwartzii*, *Pheopolykrikos hart-* *manii*, and *Cochlodinium* sp., and cysts of the toxic dinoflagellate *Gymnodinium catenatum* (Figs 16–18),
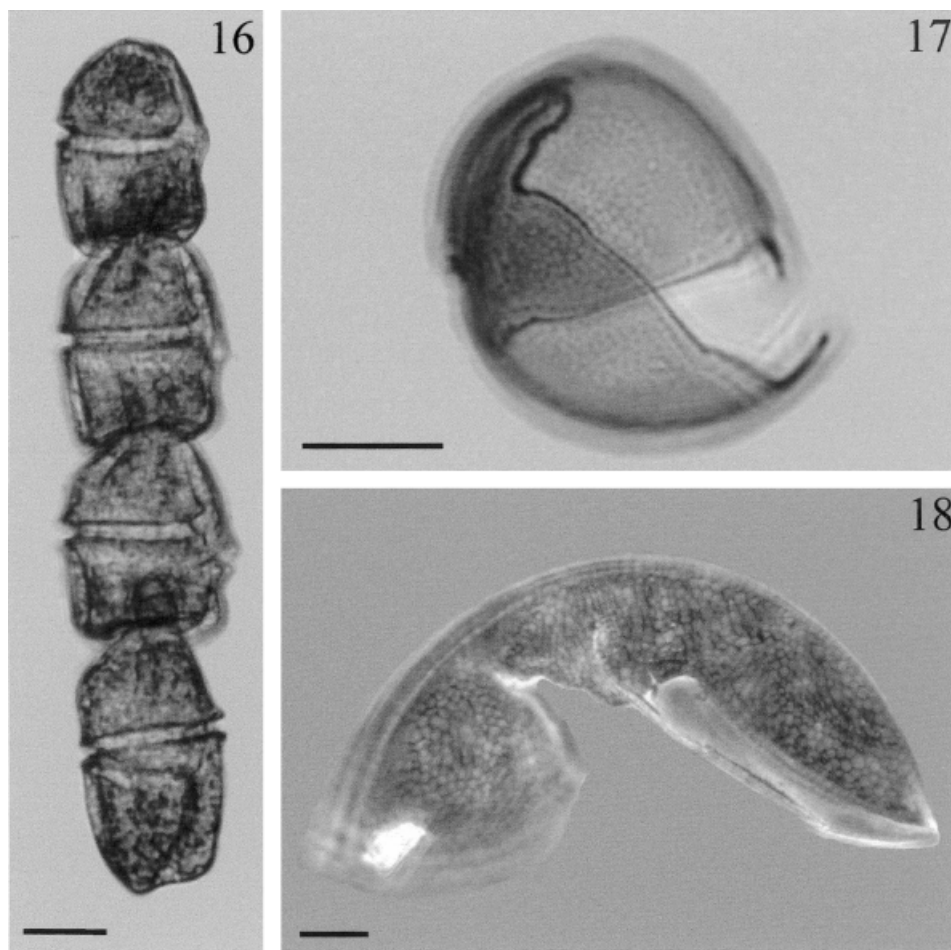
Figs 16–18. Light micrographs of motile stage and cyst of *Gymnodinium catenatum*. Scale bars = 20 μm. (16) Four-cell stage, (17–18) ruptured cyst showing wall reticulations (phase optics).

which were found in very small quantities at all sampling stations (1–4 % total abundance).

Cyst germination

From cyst germination assays, we were able to define cyst-theca relationships and to confirm identification only at the species level for *Alexandrium margalefii* Balech (Figs 19–23), *Scrippsiella trochoidea* (Figs 24–26), and *Lingulodinium polyedrum* (Figs 27–28). A cyst of *Diplopsalis* sp. was successfully germinated (Figs 29–30), but we could not obtain enough motile cells for identification at the species level. In most cases, it was possible to identify species of the genus *Protoperidinium* only by cyst morphology and archeopyle.

Cysts of *Alexandrium margalefii* were spherical and mucilaginous, with clear granular contents and yellow accumulation body (Fig. 19). Four cyst germinations were successfully conducted in GSe medium (Fig. 20), after 4 or 5 days of incubation, and a culture of motile form was easily established and maintained for 6 months (Fig. 21). Cultured cells were spheroidal, 29–37 μm long and 31–40 μm wide.

Gray-black cysts of *Scrippsiella trochoidea* were spherical to ovoid, covered with numerous calcareous spines of variable length, and had a red accumulation body (Figs 7, 24). Some of these cysts were successfully germinated in GSe medium (Fig. 25), and a clonal culture was established (Fig. 26). Vegetative cells grown in the culture were 19.5 to 30 μm long and 17 to 23 μm wide. Occasionally, this culture produced calcareous cysts with characteristics identical to those originally isolated from sediments.

Lingulodinium polyedrum cysts were spherical and surrounded by elongated processes (Fig. 27), having large accumulation granules. Empty cysts were completely transparent (Fig. 13) and usually found collapsed in the sediments. A clonal culture was also established for this species. Cultured cells were 43–50 μm long and 37–47 μm wide.

Spatial distribution and abundance of cyst assemblages

Cyst abundance had a strong correlation with sediment characteristics and location (Fig. 31A). In
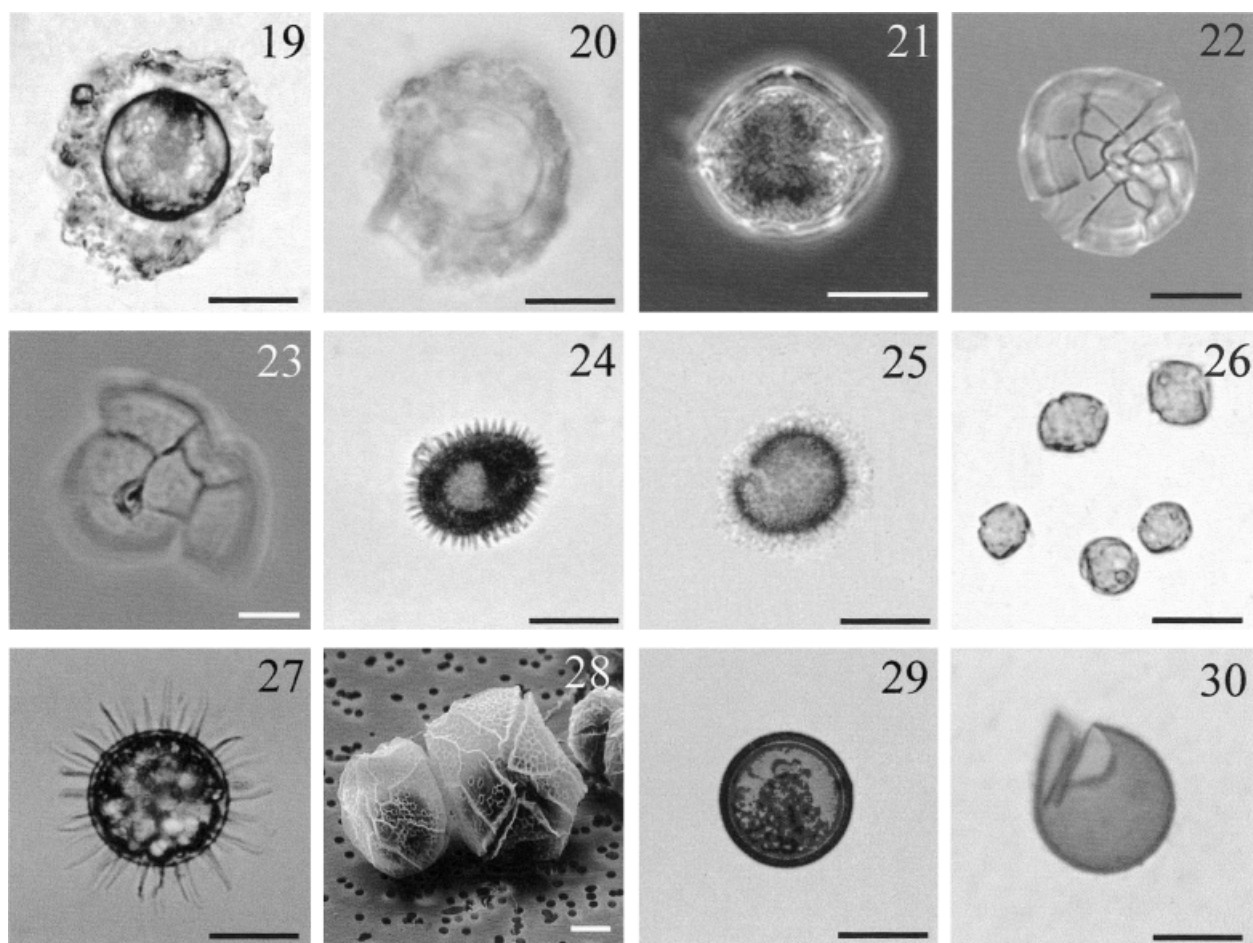
Figs 19–30. Cyst-theca relationships obtained from germination experiments. Scale bars = 20 μm unless specified. (19) *Alexandrium margalefii* living cyst, (20) *A. margalefii* empty cyst, (21) *A. margalefii* motile cell (phase optics), (22) details of *A. margalefii* plates (phase optics), (23) *A. margalefii* apical pore (phase optics), (24) *Scrippsiella trochoidea* living cyst, (25) *S. trochoidea* empty cyst, (26) *S. trochoidea* motile cells, (27) *Lingulodinium polyedrum* living cysts, (28) SEM photograph of the motile phase of *L. polyedrum*, scale bar = 10 μm, (29) *Diplopsalis* sp. living cyst, (30) *Diplopsalis* sp. empty cyst.

places with green mud, from 6×10^3 to 9.9×10^3 cysts g^{-1} wet weight were found. Where sediments were composed of volcanoclastic and calcareous sands, cysts numbered below 4×10^3 cysts g^{-1}. Cluster analysis clearly showed this difference, and the dendogram grouped the central basin (stations 7–9) and inner (10–12) area with a high percentage similarity. These areas, mainly composed of green mud, were the most protected areas (Fig. 32), and had the highest cyst abundance (mainly Gonyaulacales and calcareous Peridiniales) (Table I).

Discussion

In this subtropical bay in the Gulf of California, as in saline, highly saline, or stratified subtropical environments of the Atlantic Ocean (Wall *et al.* 1977, Sonneman and Hill 1997, Blanco 1989a–c. Godhe *et al.* 2000), we found cyst assemblages to be primarily composed of calcareous Peridiniales and Gonyaula-

cales cysts, dominant among them being *Scrippsiella trochoidea* and *Lingulodinium polyedrum*.

Lingulodinium polyedrum has been found in many parts of the world (Tomas 1996), including the Pacific coast of California and Mexico (Sweeney 1975, Wall 1986). The motile and resting stages occur in estuaries, coastal bays, and inner neritic and neritic regions of temperate and subtropical waters (Margalef 1956, Sweeney 1975). Moreover, extensive study of cyst distribution in modern marine sediments, such as in the eastern United States, South Africa, Argentina, and Peru have shown that this species is distributed from cool temperate to tropical waters (Wall *et al.* 1977). Previous reports from the Gulf of California (south and Pacific regions) also indicate that cyst assemblages were dominated by Gonyaulacales, including *L. polyedrum* (Wall 1986, Martínez-Hernández and Hernández-Campos 1991). However, in deep basins such as at Guaymas, cyst assemblages were composed mainly of *Gonyaulax spinifera*, *Protoperidinium conicoides* (Paulsen) Balech and *Protoperidinium pen-*
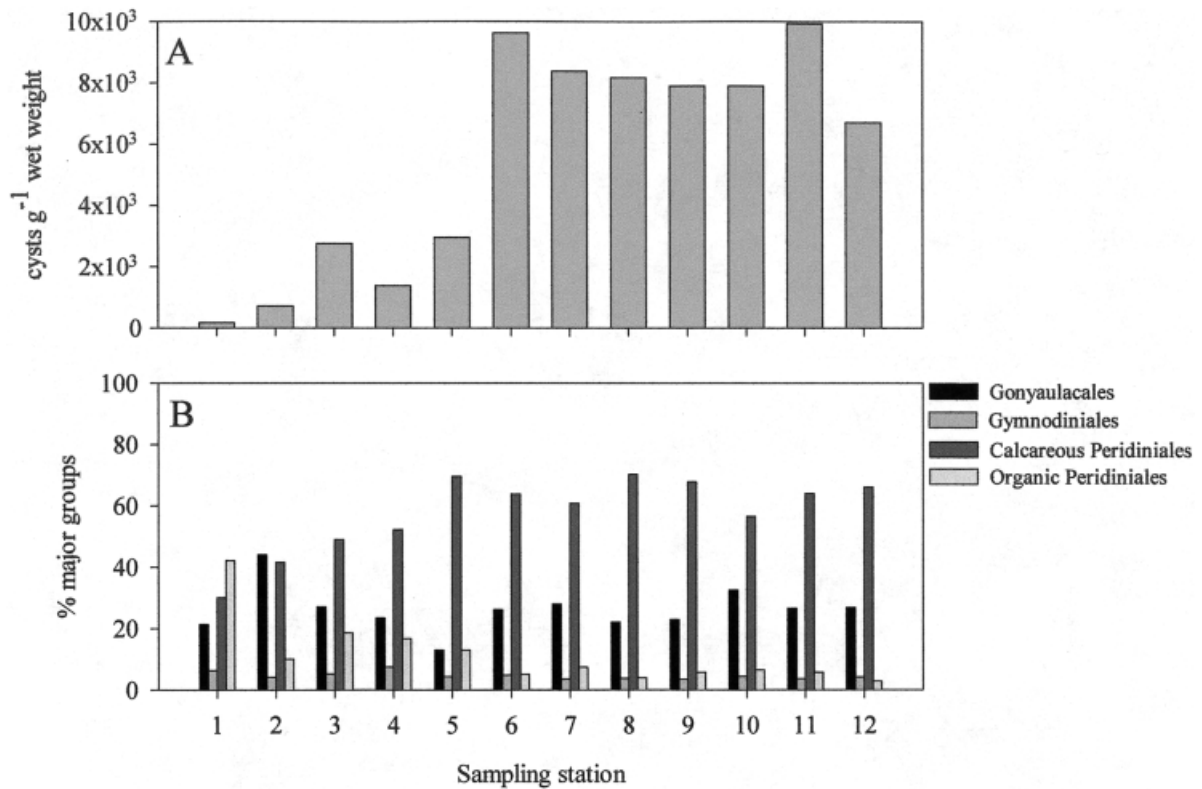
Fig. 31. Total abundance and percentage composition of the major groups of dinoflagellate cysts g^{-1} wet weight.
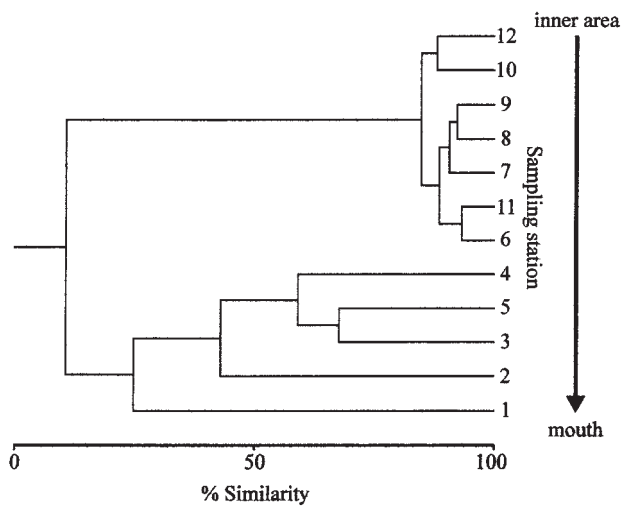

Fig. 32. Dendogram resulting from cluster analysis based on cyst assemblage similarities.

tagonum (Martínez-Hernández and Hernández-Campos 1991); calcareous and *Alexandrium*-like cysts were absent. The difference might be explained by the restriction of calcareous, *Lingulodinium poly-edrum*, and *Alexandrium*-like cysts to protected areas in the Gulf of California, or that palynological methods used by other investigators destroyed some cysts. The possibility that destruction of cysts occurred is supported by information from Wall (1986) and

Martínez-Hernández and Hernández-Campos (1991) regarding the presence of a thin-walled and delicate variety of *Lingulodinium polyedrum* cysts in the Gulf of California.

The conclusion that cysts of *Scrippsiella trochoidea* were the most numerous in calcareous cyst assemblages has to be considered carefully, because many species of the genus *Scrippsiella* can occur together. Along the Japanese coast, for example, it was confirmed that *S. crystallina* Lewis, *S. hexaprecingula* Horiguchi *et* Chihara, *S. precaria* Montresor *et* Zigone, and *S. rotunda* Lewis occurred along with the previously recorded *S. trochoidea* (Horiguchi and Chihara 1983, Ishikawa and Taniguchi 1993). In Italy, the assemblage of calcareous cyst-forming species is composed of ten different morphotypes, including *S. trochoidea*, *S. lachrymosa* Lewis, and *S. precaria* (Montresor *et al.* 1994). So far, only *S. trochoidea* has been reported in the Gulf of California, so a specific survey to define precisely the taxonomic character of this group needs to be considered.

Despite the dominance of *Lingulodinium polyedrum* and *Scrippsiella* cysts, the occurrence of *Gymnodinium catenatum* and *Alexandrium* cysts are of particular importance because this constitutes the first record of their occurrence in the Gulf of California. The presence of these cysts might be a useful tool for explaining population dynamics of potentially toxic species, such as *Alexandrium minutum* Halim, *A. pseudogonyaulax* (Biecheler) Horiguchi *ex* Kita *et*

Fukuyo, and *A. catenella* (Whedon *et* Kofoid) Balech that have been found in this bay (Lechuga-Devéze and Morquecho 1998, Morquecho and Lechuga-Devéze 2001). These species and *Gymnodinium catenatum*, could be sources of paralytic toxins in mollusks, measured with concentrations exceeding the maximum allowed for human consumption (Sierra-Beltrán *et al.* 1996. Lechuga-Devéze and Morquecho 1998). Since *Alexandrium* cysts represented 4–11 % of the assemblage, it is reasonable to consider this organism as a source of toxicity. *Alexandrium tamarense* (Lebour) Balech cysts have proven to be approximately ten times more toxic than motile cells. Dale (1977) and Riegman (1998) have suggested that sediments in eutrophic areas act to select toxic algal species. It is important to mention that two hydrological scenarios develop in Bahía Concepción. During autumn and winter the water column is homogeneous, whereas in summer, strong stratification below 20 m promotes hypoxic and anoxic conditions, generation of H_2S, and accumulation of organic matter and nutrients (Gilmartin and Revelante 1978, Bustillos-Guzmán *et al.* 2000, Lechuga-Devéze *et al.* 2001).

The characteristic seasonal eutrophication process in Bahía Concepción should be studied using the occurrence of *Lingulodinium polyedrum* cysts in marine sediments as an indicator. Eppley and Harrison (1975) suggested that the motile stage prefers regions of high nutrient concentration. It has been shown that this species is a good indicator of high nutrient supply, since a high concentration of their cysts associated strongly with high eutrophication (Dale *et al.* 1999).

The first record of *Alexandrium margalefii* in Mexico is reported in the survey presented here. This was confirmed by theca dissection (Figs 19, 20) and by DNA sequencing and restriction fragment length polymorphism analyses (Band-Schmidt pers. com.). It is important to point out that there is a lack of information about the distribution of this species, since it was described for a specimen collected from the north of Spain (Balech 1995). Previously, cysts had been found only in Australian sediments (Hallegraeff *et al.* 1991), and motile cells of heterotrophic dinoflagellates, such as *Protoperidinium americanum, P. denticulatum* and *P. latissimum*, have not been reported for the Gulf of California. Furthermore, we had expected to germinate *Alexandrium affine* (Inoue *et* Fukuyo) Balech cysts because blooms of this species were recently recorded (pers. obs.), and cysts were obtained in the laboratory from vegetative cells (Band-Schmidt pers. com.). It is possible that resting cells of this species are an important component of the spherical *Alexandrium* spp. cyst group.

Hydrodynamic motion, together with biological-ecological properties of water types, play major roles in determining cyst distribution in bottom sediment thanatocoenoses (Wall *et al.* 1977). Distribution and abundance patterns of cyst assemblages show that Bahía Concepción is a suitable environment for their accumulation and retention. The central basin of this bay has biogenic characteristics and is mainly composed of green mud (Mendahl *et al.* 1997). Additionally, the currents produced by tides are of low intensity (Obeso-Nieblas *et al.* 1996). Therefore these characteristics suggest that Bahía Concepción, more than the nearby central and upper Gulf of California, acts as a large sediment trap that retains organic matter including dinoflagellate cysts that probably represent a local meroplanktonic community.

In summary, this study gives the first qualitative and quantitative features of cyst assemblages in one of the largest subtropical bays of the Gulf of California, and it identified species, such as *Alexandrium margalefii, Protoperidinium americanum, P. denticulatum,* and *P. latissimum* that previously have not been found there. Furthermore, *Lingulodinium polyedrum*, *Alexandrium*, and *Scrippsiella* cysts might be important dinoflagellates contributing to the productivity of this ecosystem. It is clear that an accurate survey on taxonomy of this group of species is needed. Our research was oriented to defining hydrological conditions that cause dinoflagellate occurrence and seasonal cyst flux, as well as establishing cyst-theca relationships, mainly of morphotypes with complex taxonomy and toxigenic qualities.

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