

Resting stage abundance in the biogenic fraction of surface sediments from the deep Mediterranean Sea*

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SUMMARY: The presence of resting stages in neritic areas is well known, while their occurrence in the deep sea realm has seldom been considered. Recent investigations showed strict interactions between neritic and deep sea domains, due to up- and down-welling phenomena driven by submarine canyons. To estimate the presence of resting stages in deep bottom sediments, seven sediment cores, collected along a trans-Mediterranean transect by means a multi-corer during the TRANSMED survey (1999), were studied. Most biogenic sediment was composed of Foraminifera tests (tens of thousand tests cm⁻³), *Calciodinellum albatrosianum* and *Leonella granifera* (Dinophyta) cysts (up to thousands cysts cm⁻³). Eleven dinocyst morphotypes were recorded mainly as empty shells (seven calcareous-walled: *C. albatrosianum*, *Calciperidinium asymmetricum*, *Leonella granifera*, *Scrippsiella trochoidea*, *S. precaria* type 1, *S. precaria* type 2, *S. regalis*; four organic-walled: *Impagidinium aculeatum*, unid. dinocyst 1, unid. dinocyst 2 and unid. dinocyst 3), while no metazoan resting eggs were observed. The presence of viable resting stages in deep bottom surface sediments was much lower than in neritic areas, suggesting that oceanic species do not produce cysts for a "benthic resting" strategy. Further taxonomic and biogeographic studies are needed to better understand the ecological dynamics of oceanic plankton in the Mediterranean Sea.

Key words: resting stages, deep sea, Mediterranean, biogenic sediments, cyst morphology.

RESUMEN: ABUNDANCIA DE ESTADIOS QUIESCENTES EN LA FRACCIÓN BIOGÉNICA DE SEDIMENTOS SUPERFICIALES DEL MAR MEDITERRÁNEO PROFUNDO. – La presencia de estadios quiescentes en áreas neríticas es bien conocida, pero su presencia en fondos profundos raramente se considera. Investigaciones recientes han demostrado interacciones estrictas entre los ambientes nerítico y profundo, debido a fenómenos de afloramiento y hundimiento mediados por los cañones submarinos. Para estimar la presencia de estadios quiescentes en sedimentos profundos se estudiaron siete testigos de sedimento, obtenidos durante el proyecto TRANSMED a lo largo de un transecto transmediterráneo, utilizando un tomatestigos múltiple. La mayor parte de sedimento biogénico estaba compuesto por caparazones de foraminíferos (decenas de miles de caparazones cm⁻³), cistes de *Calciodinellum albatrosianum* y *Leonella granifera* (Dinófitos; hasta miles de cistes cm⁻³). Se registraron once morfotipos de dinocistes principalmente como caparazones vacíos (siete con paredes calcáreas: *C. albatrosianum*, *Calciperidinium asymmetricum*, *Leonella granifera*, *Scrippsiella trochoidea*, *S. precaria* tipo 1, *S. precaria* tipo 2, *S. regalis*; cuatro con paredes orgánicas: *Impagidinium aculeatum*, dinociste no identificado 1, dinociste no id. 2 y dinociste no id. 3), mientras que no se observaron huevos de reposo de metazoos. La presencia de estadios quiescentes viables en sedimentos superficiales profundos fue mucho menor que en áreas neríticas, lo que sugiere que las especies oceánicas no producen cistes como estrategia "de quiescencia bentónica". Se precisan más estudios taxonómicos y biogeográficos para comprender mejor la dinámica ecológica del plancton oceánico en el mar Mediterráneo.

Palabras clave: estadios quiescentes, mar profundo, Mediterráneo, sedimentos biogénicos, morfología de cistes.

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INTRODUCTION

Dormancy is a common life cycle trait in marine plankton. Resting stages were recorded in crustaceans (Onbé, 1991; Mauchline, 1998), diatoms (Mc Quoid and Hobson, 1995, 1996), dinoflagellates (Wall and Dale, 1968; Bolch and Hallegraeff, 1990; Sonneman and Hill, 1997; Nehring, 1997) and tintinnids (Reid and John, 1978; Kamiyama, 1996).

Most ecological investigations on plankton organisms producing resting stages focused on neritic areas and dealt with taxonomy (Matsuoka, 1988; Lewis, 1991; Dale *et al.*, 1993; Matsuoka and Cho, 2000), biogeography (Lindley, 1990; Nehring, 1997; Persson *et al.*, 2000), toxic aspects related to harmful algal blooms (Han and Terazaki, 1993; Matsuoka and Fukuyo, 1994; Mackenzie *et al.*, 1996; Ellegaard and Oshima, 1998; Dale *et al.*, 1999), alien species invasions (Hallegraeff and Bolch, 1992; Carlton and Geller, 1993; Hallegraeff, 1998; Hamer *et al.*, 2000), and population dynamics (Uye, 1985; Ishikawa and Taniguchi, 1996) of single taxa. The ecological role of resting stages in plankton-benthos coupling in coastal areas, already suggested by Dale (1983) for dinoflagellates and Uye (1985) for copepods, was recently considered as one of the most important keys to understand the dynamics of the whole plankton community (Boero, 1994; Boero *et al.*, 1996). Marcus and Boero (1998) proposed a synthetic model (the “supply-vertical ecology”) based on this generalised life cycle trait to better explain neritic plankton dynamics.

Recent micro-palaeontological studies focused on dinoflagellate resting stages on the surface sediments of deep waters for taxonomic as well as palaeo-climatic investigations (Zonneveld, 1995; Zonneveld and Brummer, 2000; Vink *et al.*, 2000a; b; Meier, 2002). Nevertheless, due both to sampling difficulties and scant attention to the role of resting stages in the meiobenthic domain (Pati *et al.*, 1999), the presence of cysts in deep sea bottoms has been seldom considered. Dale and Dale (1992) showed a high contribution of empty calcareous oceanic cysts (mostly *Thoracosphaera*=*Calciadinellum albatrosiana*) to the biogenic portion in Atlantic and Pacific Ocean sediments. More recently, Della Tommasa *et al.* (2000) recorded a high concentration of resting stages (both Protoctista and Metazoa) in the Foix Canyon (NW Mediterranean, Spain), showing a storage effect by submarine canyons on coastal resting stage dynamics, driven by downwelling phenomena. The interactions between oceanographic

TABLE 1. – Surface sediment samples from the Mediterranean

Station	Depth (m)	Sampling date	Position
S1	-3870	8/6/99	35°46.292' N; 28°43.147' E
S2	-3055	15/6/99	33°23.176' N; 28°19.042' E
S3	-2950	16/6/99	34°52.909' N; 22°31.968' E
S4	-4000	20/6/99	35°37.181' N; 17°23.370' E
S5	-1290	23/6/99	36°36.664' N; 12°14.744' E
S6	-2850	26/6/99	38°24.046' N; 06°53.721' E
S7	-2755	1/7/99	40°33.990' N; 04°57.137' E

and life cycle patterns is a neglected field in marine ecology; the aim of present work is to evaluate the presence of plankton-originated resting stages on the surface of deep Mediterranean sediments to ascertain their possible role in plankton-benthos coupling in off-shore areas.

MATERIAL AND METHODS

Seven sediment cores, collected at seven stations (S1-S7) in summer 1999 along a horizontal transect from the Eastern to the Western Mediterranean (Fig. 1) by means of a multicorer (mod Maxicorer, i.d. 9.0 cm, depth penetration >20 cm) during the TRANSMED survey, were analysed (Table 1). As described in recent literature (Zonneveld, 1997; Vink *et al.*, 2000a,b; Meier *et al.*, 2002), the uppermost centimeter of the cores was collected to study the most recent material. Each sample was washed with filtered seawater (0.45 µm), ultrasonified for 3 min with a Branson Sonifier and sieved at three mesh sizes (250 µm, 63 µm, and 20 µm) with filtered seawater. Each sieve-fraction was diluted in 30 ml of filtered seawater. The whole fraction >250 µm, and 10% aliquots of the others (250-63 µm, and 63-20 µm) were observed for each sample. Optimal aliquot size was calculated by a preliminary statistical analysis optimising subsampling according to Bros and Cowell (1987). The identification and the isolation of biogenic components from sediment were carried out with an inverted microscope at 50X and 200X connected to a digital video-camera. Resting stage (or “cyst”, according to Belmonte *et al.*, 1995) abundance was compared with that of other biogenic particles grouped according to two categories: Foraminifera tests, and “others” (comprising Mollusca shells, Radiolaria and Tintinnina loricas). Since this study focused on the near-surface layer (0-1 cm), no drying practices were carried out (Dale, 2001; Matsuoka, 2001), therefore the number of observed items was related to one cm³ of wet sediment.

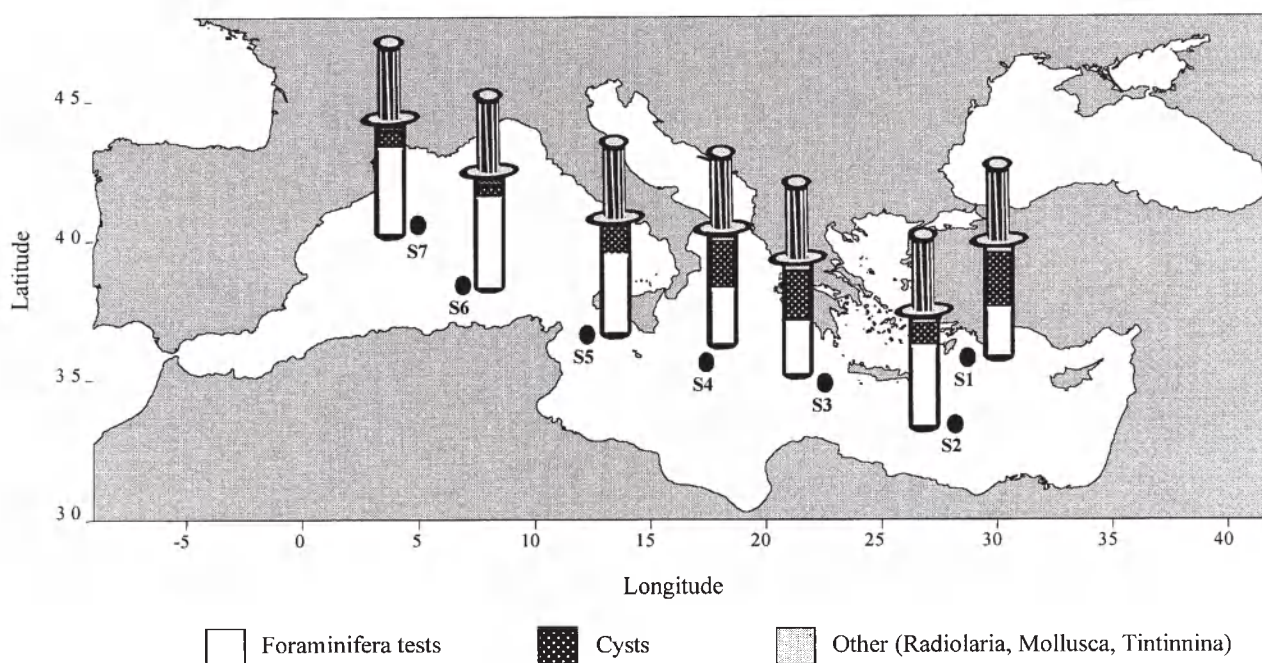


FIG. 1. – Location of sampling stations in the Mediterranean Sea and percentage composition of the observed surface sediments.

RESULTS

Biogenic sediment composition

As shown in Figure 1 the relative abundance of Foraminifera tests varied from 43% (S1) to 85.6% (S6), representing the majority of recorded biogenic particles. *Globigerina bulloides* and *Globorotalia scitula*, found as both empty and full tests, were the most represented species (Table 2). The abundance of foraminiferan empty tests varied from 2,524 tests cm^{-3} (S4) to 27,039 tests cm^{-3} (S2), whereas full ones varied from 786 tests cm^{-3} (S3) to 8,578 tests cm^{-3} (S2).

Also resting stages (cysts) were recorded as both full and empty. Their relative abundance was included between 10.8 % in S6 and 54.3 % in S1, mainly due to empty shells (most were *Calciodinellum albatrosianum* and *Leonella granifera*), that varied from 1,326 shells cm^{-3} (S6) to 16,600 shells cm^{-3} (S1). Full cysts ranged from 5 (S1) to 138 cysts cm^{-3} (S7). In S2 and S3 stations, viable (=full) cysts were not recorded. Finally, also the remaining categories (Mollusca, Radiolaria, and Tintinnina) were mostly recorded as empty shells. However, they represented a minority of biogenic particles, with a lower relative abundance than the previously considered categories (from 0.5 % in S5 to 3.5 % in S6) at all sampling stations.

Resting stages (Fig. 2).

Eleven dinoflagellate cyst morphotypes were found, while no metazoan resting eggs were recorded. Seven were calcareous cysts (*Calciodinellum albatrosianum*, *Calciperidinium asymmetricum*, *Leonella granifera*, *Scrippsiella trochoidea*, *S. precaria* type 1, *S. precaria* type 2, *S. regalis*) and four were organic-walled (*Impagidinium aculeatum*, unid. dinocyst 1, unid. dinocyst 2 and unid. dinocyst 3).

Scrippsiella trochoidea (Fig. 2a)

Size, without spines, 35 μm x 30 μm . Ovoidal, calcareous-walled, with pointed, pyramidal spines. Recorded (only as empty shell) from all stations, ranging from 1 cyst cm^{-3} in S3 to 60 cysts cm^{-3} in S2. This morphotype appeared more similar to the coastal *Scrippsiella* species (see *S. trochoidea* in: Sonnemann and Hill, 1997; Montresor *et al.*, 1998; Lewis, 1991; Rubino *et al.*, 2000; or *Scrippsiella* sp. 2 in Belmonte *et al.*, 1995) than to the oceanic *S. cf. trochoidea* recorded by Dale and Dale (1992).

Scrippsiella precaria (type 1, Fig. 2b; type 2, Fig. 2c)

Diameter, without spines, 25 μm (Fig. 2b) and 27 μm (Fig. 2c). Two morphotypes of cysts were attrib-

TABLE 2. – Abundance of biogenic fraction components (n° items cm⁻³ of wet sediment) in the surface sediments from the Mediterranean. E, empty; F, full; T, total.

	E	SI	F	T	E	S2	F	T	E	S3	F	T	E	S4	F	T	E	S5	F	T	E	S6	F	T	E	S7	F	T
Bolivinitidae	0	0	0	0	24	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Fissurina</i> sp.	7,055	580	7,635	12,873	498	13,371	268	4	272	2,077	1,815	3,892	2,602	1,087	3,689	7,612	285	7,897	21,888	1,482	23,370	6	0	0	0	0	0	0
<i>Globigerina bulloides</i>	180	305	485	898	1,395	2,293	932	235	1,167	105	247	352	17	38	55	496	629	1,125	743	1,122	1,865	0	0	0	0	0	0	0
<i>Globigerinoides sacculifer</i>	3,225	1,925	5,150	13,227	6,555	19,782	5,115	547	5,662	322	3,127	3,449	639	817	1,456	570	847	1,417	209	246	455	0	0	0	0	0	0	0
<i>Globorotalia scitula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Globorotalia truncatulinoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ophthalimidium</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Orbulina univversa</i>	6	4	10	17	130	147	132	0	132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Rotaliidae	0	0	0	0	0	0	0	0	0	0	0	0	8	7	15	41	7	48	0	18	18	0	0	0	0	0	0	
<i>Spirulina</i> sp.	0	0	0	0	0	0	1	1	15	0	0	15	0	0	0	11	4	15	12	0	12	0	0	0	0	0	0	
TOTAL Foraminifera	10,466	2,814	13,280	27,039	8,578	35,617	6,448	786	7,234	2,524	5,207	7,731	3,286	1,949	5,235	8,758	1,772	10,530	22,929	2,868	25,797	0	0	0	0	0	0	0
<i>Crescis acicula</i>	89	31	120	164	80	244	107	0	107	56	1	57	17	1	18	35	0	35	305	0	305	0	0	0	0	0	0	0
<i>Euclio pyramidata</i>	63	10	73	151	76	227	88	0	88	28	1	29	0	0	0	34	0	34	101	0	101	0	0	0	0	0	0	0
Unid. Thecosomata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Unid. veliger	126	74	200	534	226	760	90	3	93	75	25	100	0	1	1	260	0	260	463	0	463	0	0	0	0	0	0	0
TOTAL Mollusca	278	115	393	849	382	1,231	285	3	288	159	27	186	17	2	19	359	0	359	941	0	941	0	0	0	0	0	0	0
<i>Anphipyle</i> sp.	0	0	0	0	0	0	11	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cornutella</i> sp.	70	5	75	0	0	0	1	0	1	0	0	0	0	0	0	52	0	52	0	0	0	0	0	0	0	0	0	
Cubosphaeridae	0	0	0	6	0	6	24	0	24	22	0	22	7	0	7	4	0	4	0	0	0	0	0	0	0	0	0	
<i>Echinospaera</i> sp.	0	0	0	0	0	0	0	0	0	15	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Eusacium</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	19	0	0	0	0	0	0	0	0	0	
Laracariidae	0	0	0	0	0	0	0	0	0	7	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Manozonium</i> sp.	115	0	115	57	0	57	11	0	11	30	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pteroscium</i> sp.	0	0	0	0	0	0	0	0	0	7	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Anthocyrtis</i> sp.	100	0	100	66	0	66	44	0	44	60	22	82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Tetrapyle</i> sp.	0	0	0	0	0	0	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
TOTAL Radiolaria	285	5	290	129	0	129	96	0	96	141	22	163	7	0	7	75	0	75	0	0	0	0	0	0	0	0	0	0
<i>Dadaviella ganymedes</i>	0	0	0	0	0	0	0	0	0	0	0	0	7	0	7	0	0	0	0	0	0	0	0	0	0	0	0	
TOTAL Tintinnina	0	0	0	0	0	0	0	0	0	0	0	0	7	0	7	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Calciodinellum albatrosianum</i>	8,695	0	8,695	6,432	0	6,432	310	0	310	4,755	7	4,762	1,560	15	1,575	1,117	4	1,121	4,362	138	4,500	0	0	0	0	0	0	0
<i>Calciperidinium asymmetricum</i>	5	0	5	18	0	18	1	0	1	7	0	7	0	0	0	7	0	7	84	0	84	0	0	0	0	0	0	0
<i>Impagidinium aculeatum</i>	0	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Leonella granifera</i>	7,675	0	7,675	2,265	0	2,265	6,862	0	6,862	2,595	0	2,595	210	15	225	41	4	45	120	0	120	0	0	0	0	0	0	0
<i>Scrippsiella precaria</i> type1	90	0	90	66	0	66	5	0	5	30	0	30	7	0	7	19	0	19	24	0	24	0	0	0	0	0	0	0
<i>Scrippsiella precaria</i> type2	0	0	0	66	0	66	0	0	0	0	0	0	0	0	0	0	0	0	6	0	6	0	0	0	0	0	0	
<i>Scrippsiella regalis</i>	120	0	120	252	0	252	5	0	5	105	0	105	37	0	37	131	0	131	60	0	60	0	0	0	0	0	0	
<i>Scrippsiella trochoidea</i>	5	0	5	60	0	60	1	0	1	37	0	37	7	0	7	7	0	7	12	0	12	0	0	0	0	0	0	
unid. dinocyst 1	10	0	10	12	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
unid. dinocyst 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	7	0	0	0	0	0	0	0	0	0	
unid. dinocyst 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	7	0	0	0	0	0	0	0	0	0	
TOTAL Cysts	16,600	5	16,605	9,171	0	9,171	7,184	0	7,184	7,529	7	7,536	1,821	51	1,872	1,326	8	1,334	4,668	138	4,806	0	0	0	0	0	0	0
TOTAL	27,629	2,939	30,568	37,188	8,960	46,148	14,013	789	14,802	10,353	5,263	15,616	5,138	2,002	7,140	10,518	1,780	12,298	28,538	3,006	31,544	0	0	0	0	0	0	0

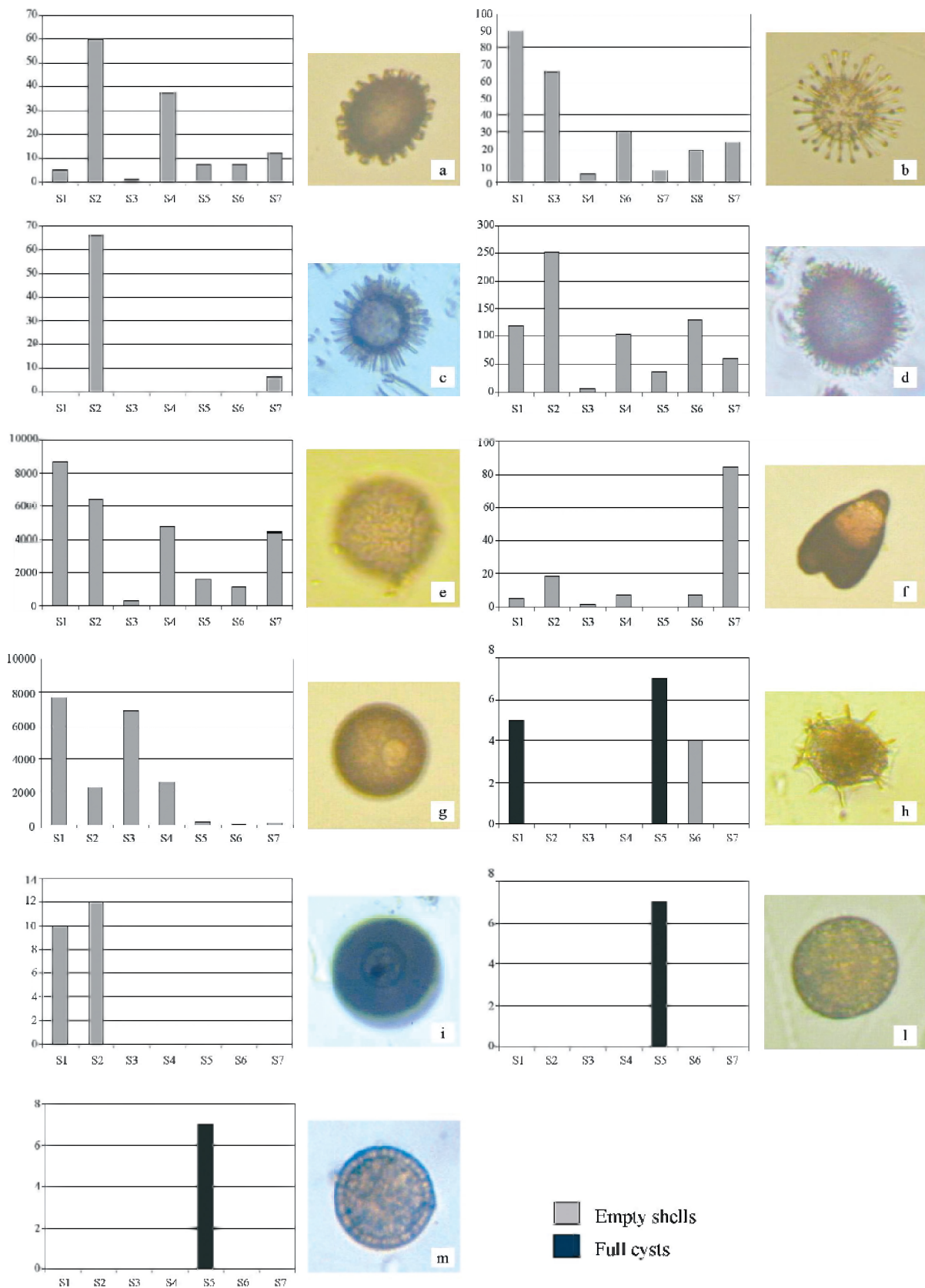


FIG. 2. – Abundance of cysts (n° items cm⁻³ of wet sediment) in surface sediments from the Mediterranean stations S1-S7. a, *Scrippsiella trochoidea*; b, *Scrippsiella precaria* type 1; c, *S. precaria* type 2; d, *Scrippsiella regalis*; e, *Calciadinellum albatrosianum*; f, *Calciperidinium asymmetricum*; g, *Leonella granifera*; h, *Impagidinium aculeatum*; i, unid. dinocyst 1; j, unid. dinocyst 2; k, unid. dinocyst 3. See text for details.

uted to *S. precaria* as type 1 (with capitate spines) and type 2 (with pointed spines) respectively, this species being polymorphic (Montresor and Zingone, 1988). Type 1 was present at all stations (only as empty shells), ranging from 5 (S3) to 90 cysts cm⁻³ (S1). Type 2 was recorded (only as empty shells) at S2 (66 cysts cm⁻³) and S7 stations (6 cysts cm⁻³).

Scrippsiella regalis (Fig. 2d)

Diameter, without spines, 44 µm. Spherical, with short pointed spines. Cyst morphology similar to that of *S. trochoidea* living in neritic areas (Janofske, 2000). Already recorded in the western equatorial Atlantic Ocean (Vink *et al.*, 2000a), this species was present in all samples (only as empty shells), ranging from 5 (S5) to 252 cysts cm⁻³ (S2).

Calciadinellum albatrosianum (Fig. 2e)

Diameter, 25 µm. Spherical, calcareous-walled, surface scaled, archeopyle shape as described by Janofske and Karwath (2000). *C. albatrosianum* cysts have been recorded in equatorial Atlantic Ocean by Janofske and Karwath (2000); they have been also recorded as *Thoracosphaera albatrosiana* by Dale and Dale (1992) in Atlantic and Pacific deep areas and by Della Tommasa *et al.* (2000) in the Foix Canyon in NW Mediterranean. Vink *et al.* (2000a) recorded it (as *Sphaerodinella? albatrosiana* cysts) in the western equatorial Atlantic Ocean. In this study, *C. albatrosianum* was the most abundant recorded dinocyst. Empty cysts were present in all samples, varying from 310 (S3) to 8,695 cysts cm⁻³ (S1). Full cysts were recorded only in the central and western Mediterranean sediments (from S4 to S7 samples), ranging from 4 (S6) to 138 cysts cm⁻³ (S7).

Calciperidinium asymmetricum (Fig. 2f)

Size, 62 µm x 48 µm. Heart-shaped, bilobate antapex, calcareous-walled, trapezoidal archeopyle. Already recorded by Wall *et al.* (1973, pp. 25-26, Pl. 1 Fig. 22) and Nehring (1997, type B, Fig. 35, p. 320), this species has been described by Versteeg (1993) from the Upper Pleistocene fossil assemblages in the southern continental margin of Crete. In this study, *C. asymmetricum* was observed (only as empty shells) in all samples except in S6. Its abundance varied from 1 (S3) to 84 cysts cm⁻³ (S7).

Leonella granifera (Fig. 2g)

Diameter, 22 µm. Spherical, calcareous-walled, smooth surface, circular archeopyle as described by Janofske and Karwath (2000). *L. granifera* cysts have been recorded in plankton samples from the equatorial Atlantic Ocean (Kerntopf, 1997; Janofske and Karwath, 2000); they have been also recorded as *Thoracosphaera granifera* by Dale and Dale (1992) in sediment trap contents from the Atlantic and Pacific Oceans; Vink *et al.* (2000a) recorded them (as *Orthopithonella? granifera*) from the western equatorial Atlantic Ocean. In this study, *L. granifera* was the second most abundant dinocyst. Empty cysts were present in all samples, varying from 41 (S6) to 7,675 cysts cm⁻³ (S1). Full cysts were recorded only in S4 and S7 samples (respectively 15 and 4 cysts cm⁻³).

Impagidinium aculeatum (Fig. 2h)

Size without crest, 30 µm x 22 µm. Oval, organic-walled, crested surface. *Impagidinium*, typically described as a pelagic genus (Wall *et al.*, 1977; Harland, 1983; Marret, 1994), was recently found also in shelfward areas in western Atlantic sediments (Vink *et al.*, 2000b). In this study, *Impagidinium aculeatum* was recorded as both full cysts (5 cysts cm⁻³ in S1, and 7 cysts cm⁻³ in S5) and empty shells (4 cysts cm⁻³ in S6).

Unidentified dinocyst 1 (Fig. 2i)

Diameter, 52 µm. Spherical, smooth surface, organic-walled, round archeopyle. Paleontological studies include similar "round brown" cysts in the genus *Brigantedinium* (Vink *et al.*, 2000b) but there are no records for cysts with a round archeopyle like that reported here. In this study the unid. dinocyst 1 has been recorded only from eastern Mediterranean sediments as empty shells (10 cysts cm⁻³ in S1, and 12 cysts cm⁻³ at S2).

Unidentified dinocyst 2 (Fig. 2l)

Diameter, 45 µm. Spherical, smooth surface, with a thin organic wall, brownish in colour. This morphotype has been recorded only at S5 as a full cyst (7 cysts cm⁻³).

Unidentified dinocyst 3 (Fig. 2m)

Diameter, 28 µm. Spherical, smooth surface,

with a thick organic wall, brownish in colour. This morphotype has been recorded only at S5 as a full cyst (7 cysts cm⁻³).

DISCUSSION

Resting stages highly contributed (in terms of abundance) to the biogenic fraction of surface sediments from deep Mediterranean Sea that was dominated by Foraminifera tests. Resting stages were recorded only as dinocysts; neither metazoan nor ciliates cysts were observed. Eleven dinocyst morphotypes were found and most of them were empty. Therefore, the cyst contribution to Mediterranean deep areas, in terms of both diversity and viable cysts, was lower than to Mediterranean coastal areas (Montresor *et al.*, 1998; Rubino *et al.*, 2000). Nevertheless, recent investigations are increasing the number of recorded species in those deep areas: a taxonomic survey on calcareous dinoflagellates from Mediterranean sediments revealed 14 species including one new genus and four new species (Meier *et al.*, 2002).

The low number of viable cysts recorded in this study confirmed previous observations carried out on surface sediments from the equatorial Atlantic Ocean (Vink *et al.*, 2000a,b), Arabian Sea (Zonneveld, 1997), and on sediment trap contents from both Central Pacific and Central Atlantic Oceans (Dale & Dale, 1992). Janofske and Karwath (2000) found viable cysts of the oceanic species *Calciodinellum albatrosianum* and *Leonella granifera* in plankton samples collected in the uppermost water layers. So that, as suggested by Dale and Dale (1992), the oceanic cysts should guarantee the species to have a buoyancy regulation mechanism to remain strategically placed in the water column.

Because of high distances from the bottom to the water surface, it should be difficult for a motile stage emerging from a cyst to reestablish contact with the plankton of upper layers; therefore, Dale and Dale (1992) hypothesized that the ecological role of cysts produced by oceanic species should not be considered in the framework of a "benthic resting" strategy. These suggestions seem to be confirmed by culture experiments carried out on oceanic species by Janofske and Karwath (2000) who showed that the obtained cysts were not hypnozygotes or resting cysts, being unconnected to a sexual phase. The estimated cyst sinking time (Anderson *et al.*, 1985) should allow an oceanic specimen to encyst, fall to

an optimal nutritionally richer water layer, and then excyst completing its life cycle in a few tens of meters. This would explain the high abundance of empty shells in the deep sea sediments as a by-product of dinoflagellates living in the upper waters.

In general, our data validated this hypothesis; nevertheless, full cysts of dinoflagellates classically considered as oceanic (*I. aculeatum*, *C. albatrosianum*, *L. granifera*) beside full cysts of unknown species (unid. dinocyst 2, unid. dinocyst 3) were found. As noted by Dale (1996) the cyst distribution in the deep sea bottom is broader than the distribution of the respective motile stages in the water column. Therefore, cyst assemblages found in the deep sea should derive from long distance transport rather than production from overlying surface waters (Dale, 1996; Dale and Dale, 1992). In such way, the ecological role of oceanic cysts as dispersal stages (Dale and Dale, 1992) would be fulfilled, and the few non-hatched cysts that fall to the bottom should be considered as a small investment of each species, akin to a bet-hedging strategy (Philippi and Seger, 1989), to be moved away by deep mixing currents. Moreover, a key role in cyst dispersal should be played by bottom geomorphology and water mass circulation at different scales. In fact, the evidence of high cyst diversity at some deep sites (e.g. submarine canyons, Della Tommasa *et al.*, 2000) was attributed to particular geomorphological situations that improve the transport speed of cysts from (neritic) production areas to the storage (deep) ones.

In this study, four cyst morphotypes belonged to species typically considered as oceanic (*C. albatrosianum*, *L. granifera*, *I. aculeatum*, *Scrippsiella regalis*); three ones to species typically considered as coastal (*Scrippsiella precaria* type 1, *S. precaria* type 2, *Scrippsiella trochoidea*); and the remaining four ones (*Calciperidinium asymmetricum*, unid. dinocyst 1, unid. dinocyst 2, unid. dinocyst 3) with an unknown distribution. Most knowledge on oceanic cysts is based on morphological observation. Nevertheless, morphological differences between cysts do not reflect taxonomic differences. Polymorphic cysts belonging to the same species are very common (Lewis, 1991; Montresor and Zingone, 1988; Matsuoka and Cho, 2000). On the other hand, some convergences on cyst morphology have been recorded in dinoflagellate species (Matsuoka, 1988; Lewis, 1990; Harland, 1992; Janofske, 2000). The *S. trochoidea* cyst, here reported from surface sediments of deep Mediterranean Sea (Fig. 2a), is more similar to the coastal *S. trochoidea* than to the "oceanic" *S.*

cf. *trochoidea* recorded by Dale and Dale (1992) from Pacific and Atlantic Oceans. Recently Janofske and Karwath (2000) clarified the taxonomy of *C. albatrosianum* and *L. granifera* until then considered as “calcispheres” (Dale and Dale, 1992; Janofske, 1996; Kerntopf, 1997).

Life cycle investigations could clarify the role of cysts for oceanic species, or for under-thermocline habitats, where slow processes and apparent constant conditions are punctuated by episodic events (Smith, 1994). Recently, Penna and Magnani (1999) assayed rDNA targeted probes to identify *Alexandrium* species which cause harmful algal blooms (HAB; Han and Terazaki, 1993; Hallegraeff *et al.*, 1998); Bolch (2001) amplified rDNA sequences of some dinoflagellate species from single cysts; Okazaki *et al.* (2001) produced a monoclonal antibody to assess *S. trochoidea* cyst abundance in muddy bottom sediments. Therefore, an integrated approach using emerging techniques such as molecular ones together with detailed oceanographical data on water mass movements at different scales can strongly contribute to monitoring and investigating taxonomy, dispersal potential, and population dynamics of existing dinoflagellates in the Mediterranean Sea.

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REFERENCES

- Anderson, D. M., J.J. Lively, E.M. Reardon and C.A. Price. – 1985. Sinking characteristics of dinoflagellate cysts. *Limnol. Oceanogr.*, 30(5): 1000-1009.
- Belmonte, G., P. Castello, M.R. Piccinni, S. Quarta, F. Rubino, S. Geraci and F. Boero. – 1995. Resting stages in marine sediments off the Italian coast. In: A. Elefteriou, A.D. Ansel and C.J. Smith (eds): *Biology and ecology of shallow coastal waters*, pp. 53-58. Olsen and Olsen, Fredensborg.
- Boero, F. – 1994. Fluctuations and variations in coastal marine environments. *P.S.Z.N.I: Mar. Ecol.*, 15: 3-25.
- Boero, F., G. Belmonte, G. Fanelli, S. Piraino and F. Rubino. – 1996. The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? *Trends Ecol. Evol.*, 11(4): 177-180.
- Bolch, C.J. – 2001. PCR protocols for genetic identification of dinoflagellates directly from single cysts and plankton cells. *Phycologia*, 40(2): 162-167.
- Bolch, C.J. and G.M. Hallegraeff. – 1990. Dinoflagellate cysts in recent marine sediments from Tasmania, Australia. *Bot. Mar.*, 33: 173-192.
- Bros, W.E. and B.C. Cowell. – 1987. A technique for optimizing sample size replication. *J. Exp. Mar. Biol. Ecol.*, 114: 63-71.
- Carlton, J.T. and J.B. Geller. – 1993. Ecological roulette: the global transport of nonindigenous marine organisms. *Science*, 261(5117): 78-82.
- Dale, B. – 1983. Dinoflagellate resting cysts: “benthic plankton”. In: G.A. Fryxell (ed.), *Survival Strategies of the Algae*, pp. 69-136. Cambridge University Press, New York.
- Dale, B. – 1996. Dinoflagellate cyst ecology: modeling and ecological applications. In: J. Janssonius and D.C. McGregor (eds.), *Palynology: principles and applications*, 3: 1249-1275. American Association of Stratigraphic Palynologists Foundation.
- Dale, B. – 2001. Marine dinoflagellate cysts as indicators of eutrophication and industrial pollution: a discussion. *Sci. Tot. Env.*, 264 (3): 235-240.
- Dale, B. and A.L. Dale. – 1992. *Dinoflagellate contribution to the deep sea*. Ocean Biocenosis Series n° 5. Woods Hole Oceanographic Institution, Woods Hole.
- Dale, B., M. Montresor, A. Zingone and K. Zonneveld. – 1993. The cyst-motile stage relationship of the dinoflagellates *Diplopetta symmetrica* and *Diplopsalopsis latipeltata*. *Eur. J. Phycol.*, 28: 129-137.
- Dale, B., T.A. Thorsen and A. Fjellsa. – 1999. Dinoflagellate cysts as indicators of cultural eutrophication in the Oslofjord, Norway. *Estuar. Coast. Shelf Sci.*, 48: 371-382.
- Della Tommasa, L., G. Belmonte, A. Palanques, P. Puig and F. Boero. – 2000. Resting stages in a submarine canyon: a component of shallow-deep sea coupling? *Hydrobiologia*, 440: 249-260.
- 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 comparison with Australian and Spanish strains of *Gymnodinium catenatum*. *Phycologia*, 37(5): 369-378.
- Hallegraeff, G.M. – 1998. Transport of toxic dinoflagellates via ships' ballast water: bioeconomic risk assessment and efficacy of possible ballast water management strategies. *Mar. Ecol. Prog. Ser.*, 168: 297-309.
- Hallegraeff, G.M. and C.J. Bolch. – 1992. Transport of diatom and dinoflagellate resting spores in ships' ballast water: implications for plankton biogeography and aquaculture. *J. Plankton Res.*, 14: 1067-1084.
- Hallegraeff, G.M., J.A. Marshall, J. Valentine and S. Hardiman. – 1998. Short cyst-dormancy period of an Australian isolate of the toxic dinoflagellate *Alexandrium catenella*. *Mar. Freshwater Res.*, 49: 415-420.
- Hamer, J.P., T.A. McCollin and I.A.N. Lucas. – 2000. Dinoflagellate cysts in ballast tank sediments: between tank variability. *Mar. Pollut. Bull.*, 40(9): 731-733.
- Han, M.-S. and M. Terazaki. – 1993. A toxic dinoflagellate bloom of *Alexandrium tamarense* (Lebour) Balech in Tokyo Bay. *J. Plankton Res.*, 12(15): 1425-1428.
- Harland, R. – 1982. A review of recent and quaternary organic-walled dinoflagellate cysts of the genus *Protoperidinium*. *Palaeontology*, 25(2): 369-397.
- Harland, R. – 1983. Dinoflagellates cysts in bottom sediments from the North Atlantic Ocean and adjacent seas. *Palaeontology*, 26(2): 321-387.
- Ishikawa, A. and A. Taniguchi. – 1996. Contribution of benthic cysts to the population dynamics of *Scrippsiella* spp. (Dinophyceae) in Onagawa Bay, northeast Japan. *Mar. Ecol. Prog. Ser.*, 140: 169-178.
- Janofske, D. – 1996. Ultrastructure types in Recent “calcispheres”. *Bull. Inst. Océanogr. Monaco*, 14: 295-303.
- Janofske, D. – 2000. *Scrippsiella trochoidea* and *Scrippsiella regalis*, nov. comb. (Peridinales, Dinophyceae): a comparison. *J. Phycol.*, 36(1): 178-189.
- Janofske, D. and B. Karwath. – 2000. Oceanic calcareous dinoflagellates of the equatorial Atlantic Ocean: cyst-theca relationship, taxonomy and aspects on ecology. *Ber. FB Geowiss. Univ. Bremen*, 152: 94-133.
- Kamiyama, T. – 1996. Determination of the abundance of viable tintinnid cysts in marine sediments in Hiroshima Bay, the Seto Inland Sea of Japan, using a modified MPN method. *J. Plankton Res.*, 18(7): 1253-1259.

- Kasahara, S., S. Uye and T. Onbè – 1974. Calanoid copepods eggs in sea bottom-muds. *Mar. Biol.*, 26: 167-171.
- Kerntopf, B. – 1997. Dinoflagellate distribution patterns and preservation in the Equatorial Atlantic and offshore North-West Africa. *Ber. FB Geowiss. Univ. Bremen*, 103: 136 pp.
- Lewis, J. – 1990. The cyst-theca relationship of *Oblea rotunda* (Diplopsalidaceae, Dinophyceae). *Br. phycol. J.*, 25: 339-351.
- Lewis, J. – 1991. Cyst-theca relationship in *Scrippsiella* (Dinophyceae) and related Orthoperidinioid genera. *Bot. Mar.*, 34: 91-106.
- Lewis, J., J.D. Dodge and P. Tett – 1984. Cyst-theca relationship in some *Protoperidinium* species (Peridinales) from Scottish sea lochs. *J. Micropaleontol.*, 3(2): 25-34.
- Lindley, J.A. – 1990. Distribution of overwintering calanoid copepod eggs in sea-bed sediments around southern Britain. *Mar. Biol.*, 104: 209-217.
- Mackenzie, L., D. White, Y. Oshima and J. Kapa. – 1996. The resting cyst and toxicity of *Alexandrium ostenfeldii* (Dinophyceae) in New Zealand. *Phycologia*, 35(2): 148-155.
- Marcus, N.H. – 1995. Seasonal study of planktonic copepods and their benthic resting eggs in northern California coastal waters. *Mar. Biol.*, 123: 459-465.
- Marcus, N.H. and F. Boero. – 1998. Minireview: the importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnol. Oceanogr.*, 43 (5): 763-768.
- Marret, F. – 1994. Distribution of dinoflagellate cysts in recent marine sediments from the east Equatorial Atlantic (Gulf of Guinea). *Rev. Palaeobot. Palynol.*, 84: 1-22.
- Matsuoka, K. – 1988. Cyst-theca relationships in the diplopsalid group (Peridinales, Dinophyceae). *Rev. Palaeobot. Palynol.*, 56: 95-122.
- Matsuoka, K. – 2001. Further evidence for a marine dinoflagellate cyst as an indicator of eutrophication in Yokohama Port, Tokyo Bay, Japan. Comments on a discussion by B. Dale. *Sci. Tot. Env.*, 264: 221-233.
- Matsuoka, K. and H.-J. Cho – 2000. Morphological variation in cysts of the gymnodinialean dinoflagellate *Polykrikos*. *Micropaleontology*, 46(4): 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.
- Mauchline, J. – 1998. The biology of calanoid copepods. *Adv. Mar. Biol.*, 33: 268-272.
- Mc Quoid, M.R. and L.A. Hobson – 1995. Importance of resting stages in diatom seasonal succession. *J. Phycol.*, 31: 44-50.
- Mc Quoid, M.R. and L.A. Hobson – 1996. Diatom resting stages. *J. Phycol.*, 32: 889-902.
- Meier, K.J.S., D. Janofske and H. Willems. – 2002. New calcareous dinoflagellates (Calciadinelloideae) from the Mediterranean Sea. *J. Phycol.*, 38: 602-615.
- Montresor, M. and A. Zingone. – 1988. *Scrippsiella precaria* sp. nov. (Dinophyceae), a marine dinoflagellate from the Gulf of Naples. *Phycologia*, 27(3): 387-394.
- Montresor, M., A. Zingone and D. Sarno. – 1998. Dinoflagellate cyst production at a coastal Mediterranean site. *J. Plankton Res.*, 20 (12): 2291-2312.
- Nehring, S. – 1997. Dinoflagellate resting cysts from recent German coastal sediments. *Bot. Mar.*, 40: 307-324.
- Onbè, T. – 1991. Some aspects of the biology of resting eggs of marine cladocerans. In: Wenner, A. and A. Kuris (eds.), *Crustacean egg production*. A.A. Belkema, pp. 41-55.
- Okazaki, K., T. Iwaoka, N. Murakami, I. Kazuhiko and S. Montani. – 2001. Production of monoclonal antibody against *Scrippsiella trochoidea* cysts and its application to analysis during cyst formation and enzyme-linked immunosorbent assay. *Biosci. Biotechnol. Biochem.*, 65(2): 470-473.
- Pati, A.C., G. Belmonte, V.U. Ceccherelli and F. Boero. – 1999. The inactive temporary component: an unexplored fraction of meiobenthos. *Mar. Biol.*, 134: 419-427.
- Penna, A. and M. Magnani. – 1999. Identification of *Alexandrium* (Dinophyceae) species using PCR and rDNA-targeted probes. *J. Phycol.*, 35: 615-621.
- Persson, A., A. Godhe and B. Karlson. – 2000. Dinoflagellate cysts in recent sediments from the West Coast of Sweden. *Bot. Mar.*, 43: 69-79.
- Philippi, T. and J. Seger. – 1989. Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.*, 4(2): 41-44.
- Reid, P.C. and A.W.G. John. – 1978. Tintinnid cysts. *J. Mar. Biol. Ass. U.K.*, 58: 551-557.
- Rigby, G. and G.M. Hallegraeff – 1996. Ballast water controls to minimise the translocation and establishment of toxic marine phytoplankton - what progress have we made and where we going? In: T. Yasumoto et al. (eds.), *Harmful and Toxic Algal Blooms*, pp. 201-204.
- Rubino, F., G. Belmonte, A.M. Miglietta, S. Geraci and F. Boero. – 2000. Resting stages of plankton in recent North Adriatic sediments. *P.S.Z.N.I: Mar. Ecol.*, 21(3-4): 263-286.
- Smith, C.R. – 1994. Tempo and mode in deep-sea benthic ecology: punctuated equilibrium revisited. *Palaios*, 9: 3-13.
- 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.
- Uye, S.-I. – 1985. Resting egg production as a life history strategy of marine planktonic copepods. *Bull. Mar. Sci.*, 37(2): 440-449.
- Versteegh, G.J.M. – 1993. New Pliocene and Pleistocene calcareous dinoflagellate cysts from southern Italy and Crete. *Rev. Palaeobot. Palynol.*, 78: 353-380.
- Vink, A., K.A.F. Zonneveld and H. Willems. – 2000a. Distributions of calcareous dinoflagellate cysts in surface sediments of the western equatorial Atlantic Ocean, and their potential use in palaeoceanography. *Mar. Micropaleontol.*, 38: 149-180.
- Vink, A., K.A.F. Zonneveld and H. Willems. – 2000b. Organic-walled dinoflagellate cysts in western equatorial Atlantic surface sediments: distributions and their relation to environment. *Rev. Palaeobot. Palynol.*, 112: 247-286.
- Wall, D. and B. Dale. – 1968. Modern dinoflagellate cysts and evolution of the peridinales. *Micropaleontology*, 14(3): 265-304.
- Wall, D., B. Dale and K. Harada. – 1973. Descriptions of new fossil dinoflagellates from the Late Quaternary of the Black Sea. *Micropaleontology*, 19: 18-31.
- Wall, D., B. Dale, G.P. Lohmann and W.K. Smith. – 1977. The environmental and climatic distribution of dinoflagellate cysts in modern marine sediments from regions in the North and South Atlantic Oceans and adjacent seas. *Mar. Micropaleontol.*, 2: 121-200.
- Zonneveld, K.A.F. – 1995. Palaeoclimatic and palaeoecological changes during the last deglaciation in the Eastern Mediterranean - implications for dinoflagellate ecology. *Rev. Palaeobot. Palynol.*, 84: 221-253.
- Zonneveld, K.A.F. and G.J.A. Brummer. – 2000. (Palaeo-)ecological significance, transport and preservation of organic-walled dinoflagellate cysts in the Somali Basin, NW Arabian Sea. *Deep-Sea Res. II*, 47: 2229-2256.