

Phytoplankton diversity during the spring bloom in the northwestern Mediterranean Sea

Isabella Percopo^{1,*}, Raffaele Siano^{1,2,a}, Federica Cerino^{1,b}, Diana Sarno² and Adriana Zingone¹

¹ Ecology and Evolution of Plankton, Stazione Zoologica Anton Dohrn, Villa Comunale 80121 Naples, Italy, e-mail: percopo@szn.it

² Taxonomy and Identification of Marine Phytoplankton, Stazione Zoologica Anton Dohrn, Villa Comunale 80121 Naples, Italy

* Corresponding author

Abstract

The section of the Liguro-Provençal basin north of the Balearic Islands is one of the most productive sites in the whole Mediterranean Sea, with intense phytoplankton bloom lasting about 2 months in late winter-early spring. The phytoplankton species composition of the area was investigated using light and electron microscopy to analyze bottle and net samples collected at several stations in spring 2000 and 2003. Serial dilution cultures established from bottle samples were also examined. A total of 168 phytoplankton taxa was identified, consisting of 73 Coscinodiscophyceae, 47 Dinophyceae, 25 Coccolithophyceae and 4 Prymnesiophyceae, 5 Prasinophyceae, 3 Chrysophyceae, 2 Cryptophyceae, 2 Dictyochophyceae, 1 Euglenophyceae, 1 Pelagophyceae, 1 Choanoflagellida, 1 Filosea and 3 *incertae sedis*. We also provided a brief taxonomic description and original micrographs for 25 of the smallest and/or less known species identified in the study area, which may go undetected during routine microscopical analysis of fixed samples. Among these, 10 species were recorded for the first time in the Mediterranean Sea, confirming the need of detailed studies to reveal the biodiversity and biogeography of Mediterranean phytoplankton.

Keywords: check-list; diversity; NW Mediterranean Sea; phytoplankton; serial dilution cultures.

Introduction

The Mediterranean Sea is considered as a miniature ocean (Lacombe et al. 1981, Robinson and Golnaraghi 1995) characterized by a prevalently oligotrophic condition (Azov

1991, Sur et al. 1993, Antoine and Morel 1995, Williams 1998, Duarte et al. 1999). In contrast to other oceans, the Mediterranean Sea has no intense upwelling zones and its deep waters are characterized by very low nutrient concentrations. The extreme oligotrophy of most Mediterranean areas is offset by the presence of a complex hydrography, with deep convection areas, fronts, and gyres where primary production and biomass values are relatively high (Siokou-Frangou et al. 2010). One of these areas is the Liguro-Provençal basin, which is located in the northwestern sector of the Mediterranean basin, south of the French coast and north of the North Balearic front, between the Balearic Islands and Sardinia. In that zone, intense northwesterly winds induce strong vertical movements that promote phytoplankton blooms lasting over 60 days, generally in February and March. These blooms are clearly detected by satellite imagery (D'Ortenzio and Ribera d'Alcalà 2009) and are responsible for approximately 15% of Mediterranean primary production (Marshall and Schott 1979).

In the Liguro-Provençal basin, physical and biogeochemical aspects of offshore waters have been intensively investigated (MEDOC 1970, Gascard 1978, Millot 1987, 1999, Levy et al. 1999, Anderson and Prieur 2000). Information on phytoplankton taxonomic composition is available for nearby coastal areas of the Gulf of Marseille (Gourret 1883, Travers 1971, 1975), Gulf of Lyon (Peragallo and Peragallo 1897–1908, Pavillard 1905, 1916a,b) and the Catalan Sea (Margalef 1969, 1974, Delgado 1990, Descy and Willems 1991), as well as for open waters of the Gulf of Lyon (Velasquez and Cruzado 1995) and the North Balearic front (Estrada 1982, 1991, Delgado et al. 1992, Margalef 1995, Estrada et al. 1999). More extensive phytoplankton assessments of these areas focusing mainly on diatoms and dinoflagellates were published by Velasquez and Cruzado (1995) and Gómez (2003), respectively. Some information on nanoflagellates of the northwestern Mediterranean Sea was reported by Delgado and Fortuño (1991), including scanning electron micrographs of many dinoflagellates, diatoms, and coccolithophores. The latter group was investigated in depth by Cros and Fortuño (2002), who provided a comprehensive iconography of numerous species based on scanning electron microscopy, highlighting the high diversity of this group in the Mediterranean Sea. However, the areas so far investigated only marginally overlap with the Liguro-Provençal basin, where phytoplankton species composition is still poorly known.

In this paper, we present an overview of the phytoplankton species composition in the offshore area of the Liguro-Provençal basin during the late winter-early spring of two different years. Our specific aims were to characterize the diversity of the phytoplankton in this area during the bloom

^a Present address: IFREMER, Centre de Brest, DYNECO/Pelagos, BP 70, 29280 Plouzané, France.

^b Present address: Department of Biological Oceanography, Istituto Nazionale di Oceanografia e Geofisica Sperimentale (OGS), via Picard 54, 34151 S. Croce (TS), Italy.

period and to contribute to the knowledge of the biogeography of the recorded species. In addition, we provide some morphological information on several small and/or poorly known species, which may go undetected because they have a small size, are difficult to identify with traditional methods, and have limited available iconography. The present study was motivated by the need for a better characterization of the marine phytoplankton species composition in one of the most productive areas of the Mediterranean Sea.

Materials and methods

Study area and sampling

The study area ($4^{\circ}29.98$ – $6^{\circ}15.02$ E and $40^{\circ}44.98$ – $42^{\circ}30.00$ N) is located in the central part of the Ligurian Sea, and is delimited by the Sardinian coast and Balearic Islands. It is a highly dynamic area, where complex physical forcing brings nutrients from deep water into the euphotic zone, thus contributing to enhanced phytoplankton new production. During winter, a deep-mixed layer of dense water is formed; it is rich in nutrients (Coste et al. 1972). The breakup of this patch during mixing events, followed by a rapid restratification of the surface waters causes the onset of the bloom (Jacques et al. 1973). These mixing and stratification phases cause this bloom to last about 2 months.

Samples were collected within the project NORBAL (NORTH BALEARIC) during three oceanographic cruises in April–May 2000 (NORBAL 1), March 2003 (NORBAL 4),

and April 2003 (NORBAL 5), with 29 stations visited (Figure 1 and Table 1). At each station, temperature and salinity were sampled using a SBE 911 plus CTD probe (Seabird, Bellevue, WA, USA). A total of 69 water samples (250 ml) were collected with 20 l Niskin bottles at surface (0–5 m) and at different depths (Table 1). Samples were fixed with formaldehyde (0.8% final concentration) neutralized with CaCO_3 . Some additional net samples were collected by horizontal tows with a 20- μm mesh-size plankton net during NORBAL 1 and 4.

Serial dilution cultures

Twenty samples collected during NORBAL 4 and 5 were used to establish serial dilution cultures (SDCs). Following the method of Andersen and Thronsen (2003), five replicates of five 1:10 dilution steps (from 1 ml to 0.1 μl) per sample were incubated in K-medium (Keller et al. 1987) without addition of silicate and kept at 21°C at an irradiance of 70–80 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ and a 12:12 light:dark regime. Culture tubes containing growing algae were examined in light microscopy after 3–6 weeks incubation.

Microscopical examination

All samples were examined in light microscopy (LM) using bright field (BF), phase contrast (PC) and differential interference contrast (DIC) optics with Zeiss Axiophot and Axiovert 200 light microscopes (Carl Zeiss, Oberkochen, Germany) equipped with a Zeiss Axiocam digital camera.

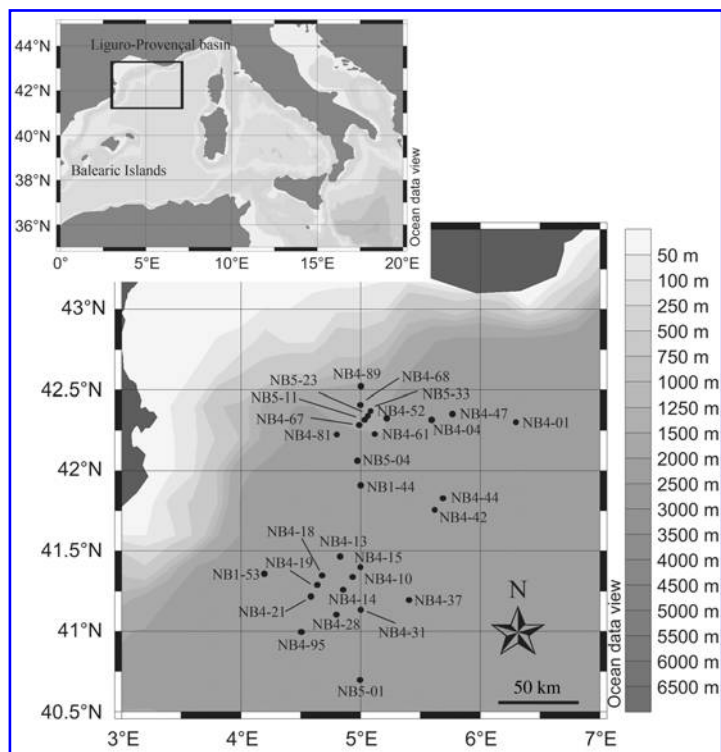


Figure 1 Location of the sampling stations in the Liguro-Provençal basin in the northwestern Mediterranean Sea visited during spring 2000 and 2003.

Table 1 Sampling locations from the Liguro-Provençal basin in the northwestern Mediterranean Sea during three NORBAL (NB) cruises in 2000 and 2003.

Cruise	Station	Depth (m)	Latitude North	Longitude East	Date	Temperature (°C)	Salinity
NB1	44	0	41°50.06	05°00.09	8 April 2000	13.1	38.4
		30				13.1	38.4
	53	5	41°19.98	04°29.98	13 April 2000	13.5	38.3
		15				13.5	38.3
NB4	01	0	42°14.98	06°15.02	6 March 2003	12.8	38.2
		04				0	42°15.00
	10	5	41°22.48	04°59.99	8 March 2003	13.0	38.3
		50				13.0	38.4
		70				13.0	38.4
		13				5	41°24.48
		20				13.0	38.3
		50				13.0	38.3
	14	0	41°14.46	04°57.39	9 March 2003	nd	nd
		15				5	41°21.24
		20				12.9	38.3
		100				12.8	38.3
	18	0	41°17.99	04°51.02	10 March 2003	13.0	38.2
		20				12.8	38.2
		70				12.9	38.3
		19				5	41°15.04
		20				12.8	38.2
		70				12.8	38.3
	21	5	41°11.70	04°43.63	11 March 2003	13.2	38.2
		20				12.8	38.2
		50				12.8	38.2
		100				12.9	38.3
	28	5	41°04.32	04°51.70	12 March 2003	13.2	38.2
		20				13.0	38.2
		50				12.9	38.3
		31				0	41°07.43
		10				13.4	38.2
		30				13.2	38.2
	37	5	41°16.53	05°13.20	13 March 2003	13.3	38.1
		20				13.2	38.1
		50				13.0	38.3
		42				5	41°45.03
		20				13.2	38.1
		70				12.9	38.3
	44	0	41°47.44	05°42.04	17 March 2003	13.4	38.1
		47				0	42°14.98
	52	5	42°14.87	05°14.95	18 March 2003	13.0	38.4
		15				13.0	38.4
		25				13.0	38.4
		61				5	42°13.54
		15				13.0	38.4
		50				13.0	38.4
	67	5	42°16.51	05°00.23	20 March 2003	13.1	38.4
		15				13.1	38.4
		70				13.1	38.5
		68				0	42°22.03
	81	5	42°11.61	04°47.32	21 March 2003	13.2	38.5
		25				13.1	38.5
	89	0	42°30.00	05°00.00	23 March 2003	nd	nd
		95				0	41°00.00
NB5	01	0	40°44.98	05°00.00	18 April 2003	nd	nd
		04				0	42°16.66
		30				13.3	38.3
		11				0	42°17.12
		20				13.6	38.2

(Table 1 continued)

Cruise	Station	Depth (m)	Latitude North	Longitude East	Date	Temperature (°C)	Salinity
	23	0	42°17.53	05°05.30	23 April 2003	15.0	38.2
		25				13.9	38.2
		50				13.3	38.3
	33	0	42°17.29	05°05.89	24 April 2003	15.4	38.1
		30				13.4	38.2
		50				13.3	38.2

nd, no data.

Thirty-seven formaldehyde-preserved and dilution culture samples were observed using transmission (TEM) and scanning (SEM) electron microscopy. For the examination of diatoms in TEM, samples were treated with nitric and sulphuric acids (1:1:4, sample:HNO₃:H₂SO₄), boiled for some seconds in order to remove the organic matter and washed with distilled water. Acid-cleaned material was mounted on Formvar-coated grids. For phytoflagellate identification, one drop of the sample was placed on a 200-mesh copper grid and fixed with 2% osmium tetroxide vapors. The grid was rinsed in distilled water for a few minutes, air-dried, then stained with uranyl acetate (0.5%) for 1 min, rinsed in distilled water and air-dried. All grids were observed with a Philips 400 TEM (Philips Electron Optics BV, Eindhoven, Netherlands). For SEM observations, formaldehyde-preserved samples were placed on 3 µm-pore size nucleopore filters, washed in distilled water, dehydrated in an ethanol series (25%, 50%, 75%, 95% and 100%) and critical point-dried. Dried filters were mounted on stubs, sputter-coated with gold-palladium and observed using a Philips 505 SEM (Philips Electron Optics BV). For phytoflagellate identification, a variable amount, depending on cell concentration, from dilution cultures was fixed with osmium tetroxide (1% final concentration) and processed as above. Some acid-cleaned material was also directly mounted on stub and processed as above for SEM examination.

Suprageneric classification of phytoplankton follows Round et al. (1990) for diatoms, Fensome et al. (1993) for dinoflagellates, Thronsen (1997) for phytoflagellates, and Young et al. (2003) and Silva et al. (2007) for coccolithophores. The main texts used for the identification included Hasle and Syvertsen (1997), Cros and Fortuño (2002) and other specific literature mentioned in the species descriptions provided in the results.

Results

A total of 168 phytoplankton taxa was collected from the Liguro-Provençal basin of the Mediterranean Sea, comprising 73 Coscinodiscophyceae (34 genera), 47 Dinophyceae (22 genera), 25 Coccolithophyceae (18 genera), 4 Prymnesiophyceae (4 genera), 5 Prasinophyceae (5 genera), 3 Chrysophyceae (3 genera), 2 Cryptophyceae (2 genera), 2 Dictyochophyceae (1 genus), 1 Euglenophyceae, 1 Pelagophyceae, 1 Choanoflagellidea, 1 Filosea, and 3 *incertae sedis* (Table 2). The last three groups, along with a number of

dinoflagellates, are unequivocally heterotrophic. However, we included them as they are generally identified in phytoplankton studies.

The following section includes brief taxonomic descriptions for 25 phytoplankton species recorded from the Liguro-Provençal basin (Table 3), along with SEM and/or TEM micrographs and, in some cases, with LM, as well as biogeographic information. The species were selected either because they have never been recorded before in the Mediterranean Sea or were undetected during routine LM observations of field material because they were small and fragile. Description and diagnostic characters for these species are mainly taken from the literature, but in some cases are updated with new observations. The morphometric data are from our own observations.

Coscinodiscophyceae

Arcocellulus cornucervis Hasle, von Stosch et Syvertsen 1983 (Figures 2, 3)

References Hasle et al. 1983, p. 59, figs. 11, 301–333, 408–414; Hasle and Syvertsen 1997, p. 179, pl. 36; Bérard-Therriault et al. 1999, p. 33, pl. 18f–g.

Morphometric data Apical axis: 3.5–8.7 µm; pervalvar axis: 1.5 µm; transapical axis: 0.45 µm; pervalvar to apical axis ratio: 0.17–0.43.

Taxonomic description Cells are slightly curved in girdle view and heterovalvate, with a process valve and a pili valve. The pili valve has two ocelluli from which the pili emerge. The pili do not cross each other and may be missing in small cells (Figure 2). Both valves are lanceolate and ornamented with distinct, very small costae which are only present in the central part of the valve (Figure 3, arrow). The arrangement of the pili, valve ornamentation and curvature, and the pervalvar to apical axis ratio are the main characters used for species identification.

Notes In natural material, the pili are not always visible and the cells can be misidentified as bacteria due to their diminutive size and irregular outline.

Distribution This is the first record of *Arcocellulus cornucervis* in the Mediterranean Sea. The species is usually found in cold-temperate waters, including Helgoland and

Table 2 List of phytoplankton species recorded in the Liguro-Provençal basin, northwestern Mediterranean Sea in spring of 2000 and 2003.

Class: Coscinodiscophyceae Round <i>et</i> Crawford	
Subclass: Thalassiosirophyceidae Round <i>et</i> Crawford	
Order: Thalassiosirales Glezer <i>et</i> Makarova	
Family: Thalassiosiraceae Lebour	
Genus <i>Thalassiosira</i> Cleve	
<i>Thalassiosira</i> cf. <i>allenii</i> Takano	ER
<i>T. eccentrica</i> (Ehrenberg) Cleve	ER
<i>T. mediterranea</i> (Schröder) Hasle	VR
<i>T. profunda</i> (Hendey) Hasle	ER ^a
<i>T. rotula</i> Meunier	R
<i>T. tenera</i> Proschkina-Lavrenko	ER
<i>Thalassiosira</i> sp. 1	ER
Genus <i>Minidiscus</i> Hasle	
<i>Minidiscus comicus</i> Takano	A ^b
<i>M. trioculatus</i> (Taylor) Hasle	ER
Family: Skeletonemataceae Lebour emend. Round <i>et</i> Crawford	
Genus <i>Skeletonema</i> Greville	
<i>Skeletonema</i> cf. <i>dohrnii</i> Sarno <i>et</i> Kooistra	VR
Genus <i>Detonula</i> Schütt ex De Toni	
<i>Detonula pumila</i> (Castracane) Gran	F
Family: Stephanodiscaceae Glezer <i>et</i> Makarova	
Genus <i>Cyclotella</i> (Kützing) Brébisson	
<i>Cyclotella choctawhatcheeana</i> Prasad	ER ^b
Subclass: Coscinodiscophycidae Round <i>et</i> Crawford	
Order: Coscinodiscales Round <i>et</i> Crawford	
Family: Coscinodiscaceae Kützing emend. Round <i>et</i> Crawford	
Genus <i>Coscinodiscus</i> Ehrenberg emend. Hasle <i>et</i> Sims	
<i>Coscinodiscus</i> spp.	VR
Family: Hemidiscaceae Hendey emend. Simonsen	
Genus <i>Hemidiscus</i> Wallich	
<i>Hemidiscus cuneiformis</i> Wallich	ER
Order: Asterolamprales Round <i>et</i> Crawford	
Family: Asterolampraceae H.L. Smith	
Genus <i>Asteromphalus</i> Ehrenberg	
<i>Asteromphalus</i> cf. <i>parvulus</i> Karsten	ER
Subclass: Biddulphiophycidae Round <i>et</i> Crawford	
Order: Hemiaulales Round <i>et</i> Crawford	
Family: Hemiaulaceae Heiberg	
Genus <i>Cerataulina</i> H. Peragallo ex Schütt	
<i>Cerataulina pelagica</i> (Cleve) Hendey	F
Genus <i>Eucampia</i> Ehrenberg	
<i>Eucampia cornuta</i> (Cleve) Grunow	VR
<i>E. zodiacus</i> Ehrenberg	F
Genus <i>Hemiaulus</i> Ehrenberg	
<i>Hemiaulus hauckii</i> Grunow	VR
Subclass: Lithodesmiophycidae Round <i>et</i> Crawford	
Order: Lithodesmiales Round <i>et</i> Crawford	
Family: Lithodesmiaceae Round	
Genus <i>Ditylum</i> J.W. Bailey ex L.W. Bailey	
<i>Ditylum brightwellii</i> (T. West) Grunow	F
Subclass: Corethrophyceidae Round <i>et</i> Crawford	
Order: Corethrales Round <i>et</i> Crawford	
Family: Corethraceae Lebour	
Genus <i>Corethron</i> Castracane	
<i>Corethron hystrix</i> Hensen	R

(Table 2 continued)

Subclass: Cymatosirophyceidae Round <i>et</i> Crawford	
Order: Cymatosirales Round <i>et</i> Crawford	
Family: Cymatosiraceae Hasle, von Stosch <i>et</i> Syvertsen	
Genus <i>Arcocellulus</i> Hasle, von Stosch <i>et</i> Syvertsen	
<i>Arcocellulus cornucervis</i> Hasle, von Stosch <i>et</i> Syvertsen	A ^a
<i>A. mammifer</i> Hasle, von Stosch <i>et</i> Syvertsen	A ^a
Genus <i>Papiliocellulus</i> Hasle, von Stosch <i>et</i> Syvertsen	
<i>Papiliocellulus simplex</i> Gardner <i>et</i> Crawford	ER ^a
Subclass: Rhizosoleniophycidae Round <i>et</i> Crawford	
Order: Rhizosoleniales Silva	
Family: Rhizosoleniaceae De Toni	
Genus <i>Rhizosolenia</i> Ehrenberg emend. Brightwell	
<i>Rhizosolenia imbricata</i> Brightwell	R
Genus <i>Proboscia</i> Sundström	
<i>Proboscia alata</i> (Brightwell) Sundström	VR
Genus <i>Guinardia</i> H. Peragallo	
<i>Guinardia flaccida</i> (Castracane) H. Peragallo	VR
<i>G. striata</i> (Stolterfoth) Hasle	F
Genus <i>Dactyliosolen</i> Castracane	
<i>Dactyliosolen fragilissimus</i> (Bergon) Hasle	F
<i>D. phuketensis</i> (Sundström) Hasle	F
Genus <i>Neocalyptrella</i> (Norman) Hernández-Becerril <i>et</i> Meave del Castillo	
<i>Neocalyptrella robusta</i> (Norman) Hernández-Becerril <i>et</i> Meave del Castillo	VR
Subclass: Chaetocerotophycidae Round <i>et</i> Crawford	
Order: Chaetocerotales Round <i>et</i> Crawford	
Family: Chaetocerotaceae Ralfs	
Genus <i>Bacteriastrum</i> Shadbolt	
<i>Bacteriastrum comosum</i> Pavillard	VR
<i>B. furcatum</i> Shadbolt	A
Genus <i>Chaetoceros</i> Ehrenberg	
<i>Chaetoceros affinis</i> Lauder	F
<i>C. brevis</i> Schütt	VR
<i>C. cf. convolutus</i> Castracane	F
<i>C. constrictus</i> Gran	F
<i>C. contortus</i> Schütt	A
<i>C. costatus</i> Pavillard	R
<i>C. curvisetus</i> Cleve	A
<i>C. danicus</i> Cleve	VR
<i>C. decipiens</i> Cleve	F
<i>C. diadema</i> (Ehrenberg) Gran	F
<i>C. diversus</i> Cleve	F
<i>C. lauderi</i> Ralfs	R
<i>C. lorenzianus</i> Grunow	F
<i>C. messanensis</i> Castracane	VR
<i>C. peruvianus</i> Brightwell	VR
<i>C. protuberans</i> Lauder	F
<i>C. pseudocurvisetus</i> Mangin	R
<i>C. tenuissimus</i> Meunier	VR
<i>C. teres</i> Cleve	F
<i>Chaetoceros</i> spp.	A
Order: Leptocylindrales Round <i>et</i> Crawford	
Family: Leptocylindraceae Lebour	
Genus <i>Leptocylindrus</i> Cleve	
<i>Leptocylindrus danicus</i> Cleve	A
<i>L. mediterraneus</i> (H. Peragallo) Hasle	F

(Table 2 continued)

Class: Fragilariophyceae Round	
Subclass: Fragilariophycidae Round	
Order: Fragilariales Silva emend. Round	
Family: Fragilariaceae Greville	
Genus <i>Asterionellopsis</i> Round	
<i>Asterionellopsis glacialis</i> (Castracane) Round	A
Order: Thalassionematales Round	
Family: Thalassionemataceae Round	
Genus <i>Thalassionema</i> Grunow	
<i>Thalassionema</i> spp.	F
Genus <i>Lioloma</i> Hasle	
<i>Lioloma</i> sp. 1	VR
Class: Bacillariophyceae Haeckel emend. Mann	
Subclass: Bacillariophycidae Mann	
Order: Achnanthales Silva	
Family: Cocconeidaceae Kützing	
Genus <i>Cocconeis</i> Ehrenberg	
<i>Cocconeis fasciolata</i> (Ehrenberg) Brown	ER ^a
Order: Naviculales Bessey emend. Mann	
Suborder: Naviculineae Hendey	
Family: Naviculaceae Kützing	
Genus <i>Navicula</i> Bory emend. Cox	
<i>Navicula</i> sp. 1	ER
<i>Navicula</i> sp. 2	ER
Genus <i>Haslea</i> Simonsen	
<i>Haslea wawrickae</i> (Hustedt) Simonsen	VR
Family: Pleurosigmaeae Mereschkowsky	
Genus <i>Pleurosigma</i> W. Smith	
<i>Pleurosigma</i> spp.	VR
Family: Plagiotropidaceae Mann	
Genus <i>Plagiotropis</i> Pfitzer	
<i>Plagiotropis lepidoptera</i> (Gregory) Kuntze	VR
Order: Bacillariales Hendey emend. Mann	
Family Bacillariaceae Ehrenberg	
Genus <i>Pseudo-nitzschia</i> H. Peragallo	
<i>Pseudo-nitzschia calliantha</i> Lundholm, Moestrup et Hasle	F
<i>P. delicatissima</i> group	F
<i>P. fraudulentata</i> (Cleve) Hasle	A
<i>P. galaxiae</i> Lundholm et Moestrup	F
<i>P. multistriata</i> (Takano) Takano	VR
Genus <i>Nitzschia</i> Hassall	
<i>Nitzschia longissima</i> (Brébisson) Ralfs	VR
<i>Nitzschia</i> spp.	VR
Genus <i>Cylindrotheca</i> Rabenhorst	
<i>Cylindrotheca closterium</i> (Ehrenberg) Reimann et Lewin	F
Genus <i>Psammodictyon</i> Mann	
<i>Psammodictyon panduriforme</i> (Gregory) Mann	ER
Class: Dinophyceae Pascher	
Subclass: Gymnodiniphycidae Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Order: Gymnodiniales Apstein	
Suborder: Gymnodiniineae Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Family: Gymnodiniaceae (Bergh) Lankester	
Genus <i>Gymnodinium</i> Stein	
<i>Gymnodinium</i> spp.	VR
Genus <i>Amphidinium</i> Claparède et Lachmann	
<i>Amphidinium</i> sp. 1	ER
Genus <i>Cochlodinium</i> Schütt	
<i>Cochlodinium</i> sp. 1	VR

(Table 2 continued)

Genus <i>Gyrodinium</i> Kofoid et Swezy	
<i>Gyrodinium fusiforme</i> Kofoid et Swezy	VR
<i>G. cf. pingue</i> (Schütt) Kofoid et Swezy	VR
<i>Gyrodinium</i> spp.	VR
Genus <i>Torodinium</i> Kofoid et Swezy	
<i>Torodinium robustum</i> Kofoid et Swezy	VR
Family: Warnowiaceae Lindemann	
Genus <i>Warnovia</i> Lindemann	
<i>Warnovia</i> sp. 1	ER
Order: Ptychodiscales Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Family: Amphitholaceae Poche	
Genus <i>Achradina</i> Lohmann	
<i>Achradina pulchra</i> Lohmann	VR
Subclass: Peridiniphycidae Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Order: Gonyaulacales Taylor	
Suborder Cladopyxiineae Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Family: Cladopyxiaceae Stein	
Genus <i>Amphidoma</i> Stein	
<i>Amphidoma caudata</i> Halldal	R
Genus <i>Micracanthodinium</i> Deflandre	
<i>Micracanthodinium</i> spp.	VR
Suborder: Gonyaulacineae Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Family: Gonyaulacaceae Lindemann	
Subfamily: Gonyaulacoideae Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Genus <i>Gonyaulax</i> Diesing	
<i>Gonyaulax polygramma</i> Stein	ER
Suborder: Ceratiineae Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Family: Ceratiaceae Willey et Hickson	
Genus <i>Neoceratium</i> Gómez, Moreira et López-García	
<i>Neoceratium candelabrum</i> (Ehrenberg) Gómez, Moreira et López-García	ER
<i>N. euarquatium</i> (Jørgensen) Gómez, Moreira et López-García	VR
<i>N. furca</i> (Ehrenberg) Gómez, Moreira et López-García	VR
<i>N. fusus</i> (Ehrenberg) Gómez, Moreira et López-García	VR
<i>N. horridum</i> (Gran) Gómez, Moreira et López-García	VR
<i>N. pentagonum</i> (Gourret) Gómez et López-García	VR
<i>N. symmetricum</i> (Pavillard) Gómez, Moreira et López-García	ER
<i>N. teres</i> (Kofoid) Gómez, Moreira et López-García	VR
<i>N. tripos</i> (O.F. Müller) Gómez, Moreira et López-García	VR
Suborder: Goniodomineae Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Family: Goniodomaceae Lindemann	
Subfamily: Goniodomioideae Fensome, Taylor, Norris, Sarjeant, Wharton et Williams	
Genus <i>Goniodoma</i> Stein	
<i>Goniodoma polyedricum</i> (Pouchet) Jørgensen	VR
Order: Peridiniales Haeckel	

(Table 2 continued)

Suborder: Heterocapsineae Fensome, Taylor, Norris, Sarjeant, Wharton <i>et</i> Williams	
Family: Heterocapsaceae Fensome, Taylor, Norris, Sarjeant, Wharton <i>et</i> Williams	
Genus <i>Heterocapsa</i> Stein	
<i>Heterocapsa minima</i> Pomroy	VR ^a
Suborder: Peridiniineae Fensome, Taylor, Norris, Sarjeant, Wharton <i>et</i> Williams	
Family: Peridiniaceae Ehrenberg	
Subfamily: Calciodinelloideae Fensome, Taylor, Norris, Sarjeant, Wharton <i>et</i> Williams	
Genus <i>Scrippsiella</i> Balech ex Loeblich III	
<i>Scrippsiella</i> sp. 1	ER
Family: Congruentidiaceae Schiller	
Subfamily: Congruentidioideae Fensome, Taylor, Norris, Sarjeant, Wharton <i>et</i> Williams	
Genus <i>Protoperidinium</i> : <i>P.</i> cf. <i>brachypus sensu</i> Abé	
<i>Protoperidinium americanum</i> (Gran <i>et</i> Braarud) Balech	ER
<i>P. bipes</i> (Paulsen) Balech	F
<i>P.</i> cf. <i>brachypus sensu</i> Abé	ER
<i>P. depressum</i> (Bailey) Balech	VR
<i>P. oceanicum</i> (Vanhöffen) Balech	ER
<i>P. steinii</i> (Jørgensen) Balech	ER
Subfamily: Diplopsalidoideae Abé	
Genus <i>Diplopsalis</i> Bergh	
<i>Diplopsalis</i> spp.	VR
Genus <i>Preperidinium</i> Mangin	
<i>Preperidinium meunieri</i> (Pavillard) Elbrächter	ER
Order: Uncertain	
Family: Oxytoxaceae Lindemann	
Genus <i>Oxytoxum</i> Stein	
<i>Oxytoxum</i> cf. <i>caudatum</i> Schiller	VR
<i>O. longiceps</i> Schiller	ER
<i>O. scolopax</i> Stein	VR
<i>O. variabile</i> Schiller	R
Subclass: Dinophysiphycidae Mohn ex Fensome, Taylor, Norris, Sarjeant, Wharton <i>et</i> Williams	
Order: Dinophysiales Kofoid	
Family: Dinophysiaceae Stein	
Genus <i>Dinophysis</i> Ehrenberg	
<i>Dinophysis caudata</i> Saville-Kent	ER
<i>D.</i> cf. <i>punctata</i> Jørgensen	ER
<i>D. tripos</i> Gouret	ER
Subclass: Prorocentrophycidae Fensome, Taylor, Norris, Sarjeant, Wharton <i>et</i> Williams	
Order: Prorocentrales Lemmermann	
Family: Prorocentraeeae Stein	
Genus <i>Mesoporos</i> Lillick	
<i>Mesoporos perforatus</i> (Gran) Lillick	R
Genus <i>Prorocentrum</i> Ehrenberg	
<i>Prorocentrum balticum</i> (Lohmann) Loeblich III	ER
<i>P. compressum</i> (Bailey) Abé ex Dodge	VR
<i>P. dentatum</i> Stein	ER
<i>P. donghaiense</i> Lu	VR ^a
<i>P. micans</i> Ehrenberg	VR
<i>P. triestinum</i> Schiller	ER
Subclass: Incertae Sedis	
Order: Thoracosphaerales Tangen	
Family: Thoracosphaeraceae Schiller	

(Table 2 continued)

Genus <i>Thoracosphaera</i> Kamptner	
<i>Thoracosphaera heimii</i> (Lohmann) Kamptner	VR
Class: Cryptophyceae Fritsch	
Order: Cryptomonadales Engler	
Family: Cryptomonadaceae Ehrenberg	
Genus <i>Plagioselmis</i> Butcher ex Hill	
<i>Plagioselmis prolonga</i> Butcher ex Novarino, Lucas <i>et</i> Morrall	ER
Genus <i>Teleaulax</i> Hill	
<i>Teleaulax acuta</i> (Butcher) Hill	ER
Class: Crysoophyceae Christensen	
Order: Ochromonadales Pascher	
Family: Chrysococcaceae Lemmermann	
Genus <i>Ollicola</i> Vørs	
<i>Ollicola vangoorii</i> (Conrad) Vørs	F
Family: Dinobryaceae Ehrenberg	
Genus <i>Dinobryon</i> Ehrenberg	
<i>Dinobryon faculiferum</i> (Willén) Willén	VR
Order: Chrysosphaerales Bourrelly	
Family: Aurosphaeraceae Schiller	
Genus <i>Meringosphaera</i> Lohmann	
<i>Meringosphaera mediterranea</i> Lohmann	VR
Class: Dictyochophyceae Silva	
Order: Dictyochales Haeckel	
Family: Dictyochaceae Lemmermann	
Genus <i>Dictyocha</i> Ehrenberg	
<i>Dictyocha fibula</i> Ehrenberg	R
<i>D. speculum</i> Ehrenberg	VR
Class: Coccolithophyceae Rothmaler	
Order: Isochrysidales Pascher	
Family: Noelaerhabdaceae Jerkovic emend. Young <i>et</i> Bown	
Genus <i>Emiliania</i> Hay <i>et</i> Mohler	
<i>Emiliania huxleyi</i> (Lohmann) Hay <i>et</i> Mohler	A
Genus <i>Gephyrocapsa</i> Kamptner	
<i>Gephyrocapsa muelleriae</i> Bréhéret	ER
Order: Coccolithales Schwarz emend. Edvardsen <i>et</i> Eikrem	
Family: Calcidiscaceae Young <i>et</i> Bown	
Genus <i>Calcidiscus</i> Kamptner	
<i>Calcidiscus leptoporus</i> (Murray <i>et</i> Blackman) Loeblich <i>et</i> Tappan	R
Genus <i>Umbilicosphaera</i> Lohmann	
<i>Umbilicosphaera foliosa</i> (Kamptner ex Kleijne) Geisen	ER
<i>U. sibogae</i> (Weber-van Bosse) Gaarder	R
Order: Zygodiscales Young <i>et</i> Bown	
Family: Helicosphaeraceae Black emend. Jafar <i>et</i> Martini	
Genus <i>Helicosphaera</i> Kamptner	
<i>Helicosphaera carterii</i> (Wallich) Kamptner	VR
Family: Pontosphaeraceae Lemmermann	
Genus <i>Pontosphaera</i> Lohmann	
<i>Pontosphaera discopora</i> Schiller	VR
<i>P. syracusana</i> Lohmann	VR
Genus <i>Scyphosphaera</i> Lohmann	
<i>Scyphosphaera apsteinii</i> Lohmann	ER
Family: Calyptosphaeraceae Boudreaux <i>et</i> Hay	
Genus <i>Anthosphaera</i> Kamptner emend. Kleijne	
<i>Anthosphaera</i> sp. type B <i>sensu</i> Cros and Fortuño	ER

(Table 2 continued)

Genus <i>Sphaerocalyptra</i> Deflandre	
<i>Sphaerocalyptra quadridentata</i> (Schiller) Deflandre	VR
Genus <i>Poritectolithus</i> Kleijne	
<i>Poritectolithus poritectus</i> (Heimdal) Kleijne	ER
Order: Syracosphaerales Hay emend. Young, Geisen, Cros, Kleijne, Sprengel, Probert et Østergaard	
Family: Syracosphaeraceae (Lohmann) Lemmermann	
Genus <i>Ophiaster</i> Gran emend. Manton et Oates	
<i>Ophiaster</i> spp.	F
Genus <i>Syracosphaera</i> Lohmann	
<i>Syracosphaera corolla</i> Lecal	ER
<i>S. didyma</i> Kleijne et Cros	ER
<i>S. marginaporata</i> Knappertsbusch	ER
<i>S. molischii</i> Schiller type 2	ER
<i>S. prolongata</i> Gran ex Lohmann type 2 sensu Heimdal et Gaarder	ER
<i>S. pulchra</i> Lohmann	F
Family: Calciosoleniaceae Kamptner	
Genus <i>Calciosolenia</i> Gran emend. Young, Geisen, Cros, Kleijne, Sprengel, Probert et Østergaard	
<i>Calciosolenia murrayi</i> Gran	VR
Family: Rhabdosphaeraceae Haeckel	
Genus <i>Rhabdosphaera</i> Haeckel	
<i>Rhabdosphaera clavigera</i> Murray et Blackman	R
Genus <i>Discosphaera</i> Haeckel	
<i>Discosphaera tubifera</i> (Murray et Blackman) Ostenfeld	VR
Genus <i>Acanthoica</i> Lohmann emend. Schiller et Kleijne	
<i>Acanthoica quattropsina</i> Lohmann	VR
Genus <i>Algirosphaera</i> Schlauder emend. Norris	
<i>Algirosphaera robusta</i> (Lohmann) Norris	R
Family: Papposphaeraceae Jordan et Young	
Genus <i>Papposphaera</i> Tangen	
<i>Papposphaera lepida</i> Tangen	F
Class: Prymnesiophyceae Hibberd	
Order: Prymnesiales Papenfuss emend. Edvardsen et Eikrem	
Family: Prymnesiaceae Conrad ex Schmidt	
Genus <i>Chrysochromulina</i> Lackey	
<i>Chrysochromulina kappa</i> Parke et Manton	ER ^a
Genus <i>Hyalolithus</i> Yoshida, Noël, Nakayama, Naganuma et Inouye	
<i>Hyalolithus neolepis</i> Yoshida, Noël, Nakayama, Naganuma et Inouye	ER
Genus <i>Imantonia</i> Reynolds	
<i>Imantonia rotunda</i> Reynolds	ER ^a
Order: Phaeocystales Medlin	
Family: Phaeocystaceae Lagerheim	
Genus <i>Phaeocystis</i> Lagerheim	
<i>Phaeocystis</i> sp. 3 sensu Medlin et Zingone	F
Class: Euglenophyceae Schenichen	
Order: Euglenales Engler	
Family: Eutreptiaceae Hollande	
Genus <i>Eutreptiella</i> de Cuhna	
<i>Eutreptiella</i> spp.	ER
Class: Prasinophyceae Moestrup et Throndsen	
Order: Mamiellales Moestrup	
Family: Mamiellaceae Moestrup	
Genus <i>Mantoniella</i> Desikachary	
<i>Mantoniella squamata</i> (Manton et Parke)	ER

(Table 2 continued)

Desikachary	
Order: Chlorodendrales Fritsch	
Family: Chlorodendraceae Oltmanns	
Genus <i>Pseudoscourfieldia</i> Manton	
<i>Pseudoscourfieldia marina</i> (Throndsen) Manton	ER
Genus <i>Tetraselmis</i> Stein	
<i>Tetraselmis</i> spp.	ER
Genus <i>Pyramimonas</i> Schmarida	
<i>Pyramimonas</i> spp.	F
Genus <i>Micromonas</i> Manton et Parke	
<i>Micromonas pusilla</i> (Butcher) Manton et Parke	ER
Class: Pelagophyceae Andersen et Saunders	
Order: Pelagomonadales Andersen et Saunders	
Genus <i>Pelagomonas</i> Andersen et Saunders	
<i>Pelagomonas calceolata</i> Andersen et Saunders	ER ^a
Class: Choanoflagellidea Kent	
Order: Acanthoecida Norris	
Genus <i>Parvicorbicula</i> (Meunier) Deflandre	
<i>Parvicorbicula socialis</i> (Meunier) Deflandre	A
Class: Filosea Leidy	
Order: Euglyphina Copeland	
Family: Paulinellidae de Saedeleer	
Genus <i>Paulinella</i> Page	
<i>Paulinella ovalis</i> (Wulff) Johnson, Hargraves et Sieburth	ER
INCERTAE SEDIS	
Genus <i>Commation</i> Thomsen et Larsen	
<i>Commation cryoporinum</i> Thomsen et Larsen	ER
Genus <i>Leucocryptos</i> Butcher	
<i>Leucocryptos marina</i> (Braarud) Butcher	R
Genus <i>Rhizomonas</i> Kent	
<i>Rhizomonas setigera</i> (Pavillard) Patterson, Nygaard, Steinberg et Turley	F

A, abundant ($>10^5$ cells l^{-1}); F, frequent (10^4 – 10^5 cells l^{-1}); R, rare ($<10^4$ cells l^{-1}); VR, very rare ($<5 \times 10^3$ cells l^{-1}); ER, extremely rare, only observed in electron microscopy or serial dilution culture; ^aindicates first occurrence in Mediterranean Sea; ^bindicates first occurrence in northwestern Mediterranean Sea.

Bremerhaven waters in the German sector of the North Sea (Hasle et al. 1983) and other temperate waters of the northern hemisphere (Bratbak et al. 1990, Hasle and Syvertsen 1997). It has also been reported from the Gulf of St. Lawrence, Eastern Canada (Bérard-Therriault et al. 1999), and from the South Island in New Zealand (Hasle and Syvertsen 1997).

***Arcocellulus mammifer* Hasle, von Stosch et Syvertsen 1983 (Figures 4–7)**

Reference Hasle et al. 1983, p. 55, figs. 10, 272–300, 415–421.

Morphometric data Apical axis: 2.9–5.8 μm ; perivalvar axis: 1.6–4.0 μm ; transapical axis: 1.0–1.3 μm ; perivalvar to apical axis ratio: 0.3–0.7.

Taxonomic description Cells are markedly curved in girdle view with pili crossing each other (Figures 4 and 5).

Table 3 List of 25 illustrated phytoplankton species sampled during the NORBAL (NB) cruises in the northwestern Mediterranean Sea.

Species	Cruise	Station	NS	SDC	NET	LM	EM
Coscinodiscophyceae							
<i>Arcocellulus cornucervis</i>	NB1	44, 53	×			×	×
<i>A. mammifer</i>	NB4	04, 10, 13, 15, 18, 19, 21, 28, 31, 37, 42, 52, 61, 67	×	×		×	×
	NB5	04	×				×
<i>Minidiscus comicus</i>	NB4	04, 10, 28, 47	×	×		×	×
	NB5	01, 33	×	×		×	×
<i>M. trioculatus</i>	NB1	47	×				×
	NB4	28, 37		×		×	×
<i>Papiliocellulus simplex</i>	NB4	28, 37		×		×	×
<i>Thalassiosira profunda</i>	NB4	10, 28		×		×	×
<i>T. tenera</i>	NB4	44, 52		×	×		×
Dinophyceae							
<i>Heterocapsa minima</i>	NB4	13, 31	×				×
<i>Prorocentrum donghaiense</i>	NB4	13	×				×
<i>Protoperdinium americanum</i>	NB4	52			×		×
<i>P. cf. brachypus</i>	NB4	52			×		×
Coccolithophyceae							
<i>Anthosphaera</i> sp. type B	NB1	44	×				×
<i>Gephyrocapsa muellerae</i>	NB1	44	×				×
	NB4	31	×				×
<i>Poritectolithus poritectus</i>	NB4	52			×		×
<i>Syracosphaera corolla</i>	NB1	44	×				×
<i>S. didyma</i>	NB4	13	×				×
<i>S. marginaporata</i>	NB1	44	×				×
<i>S. molischii</i> type 2	NB1	44	×				×
<i>S. prolongata</i>	NB4	13, 52	×		×		×
<i>Umbilicosphaera foliosa</i>	NB4	52			×		×
Prymnesiophyceae							
<i>Chrysochromulina kappa</i>	NB4	01, 14, 28		×		×	×
	NB5	01		×		×	×
<i>Hyalolithus neolepis</i>	NB4	13, 31, 44, 68, 89, 95	×			×	×
<i>Phaeocystis</i> sp. 3	NB4	01		×		×	×
Cryptophyceae							
<i>Plagioselmis prolonga</i>	NB4	44	×			×	×
<i>Teleaulax acuta</i>	NB4	44	×			×	×

NS, natural sample; SDC, serial dilution culture; NET, net sample; LM, light microscopy; EM, electron microscopy.

In EM, small spines (spinules) are visible in the terminal part of the pili (Figure 7). Valves are oblong to circular. They have a velum which has irregularly shaped perforations of different size (ricoida velum) (Figure 6). This velum is a constant character helping the identification of the species, particularly when it loses the typical shape and pili. This species usually occurs as solitary cells or in pairs. In old cultures, cells appear nearly rectangular, without pili and may form long chains of more than 10 cells, joined to each other by the valvar face. The species can be distinguished from the congeneric *Arcocellulus cornucervis* by the presence of the velum, by the more pronounced valve curvature, pili that cross each other and the larger perivalvar axis.

Distribution This is the first record of *Arcocellulus mammifer* in the Mediterranean Sea. The species has been recorded in plankton and benthos samples from cold-temperate waters of Helgoland and Bremerhaven in the German sector

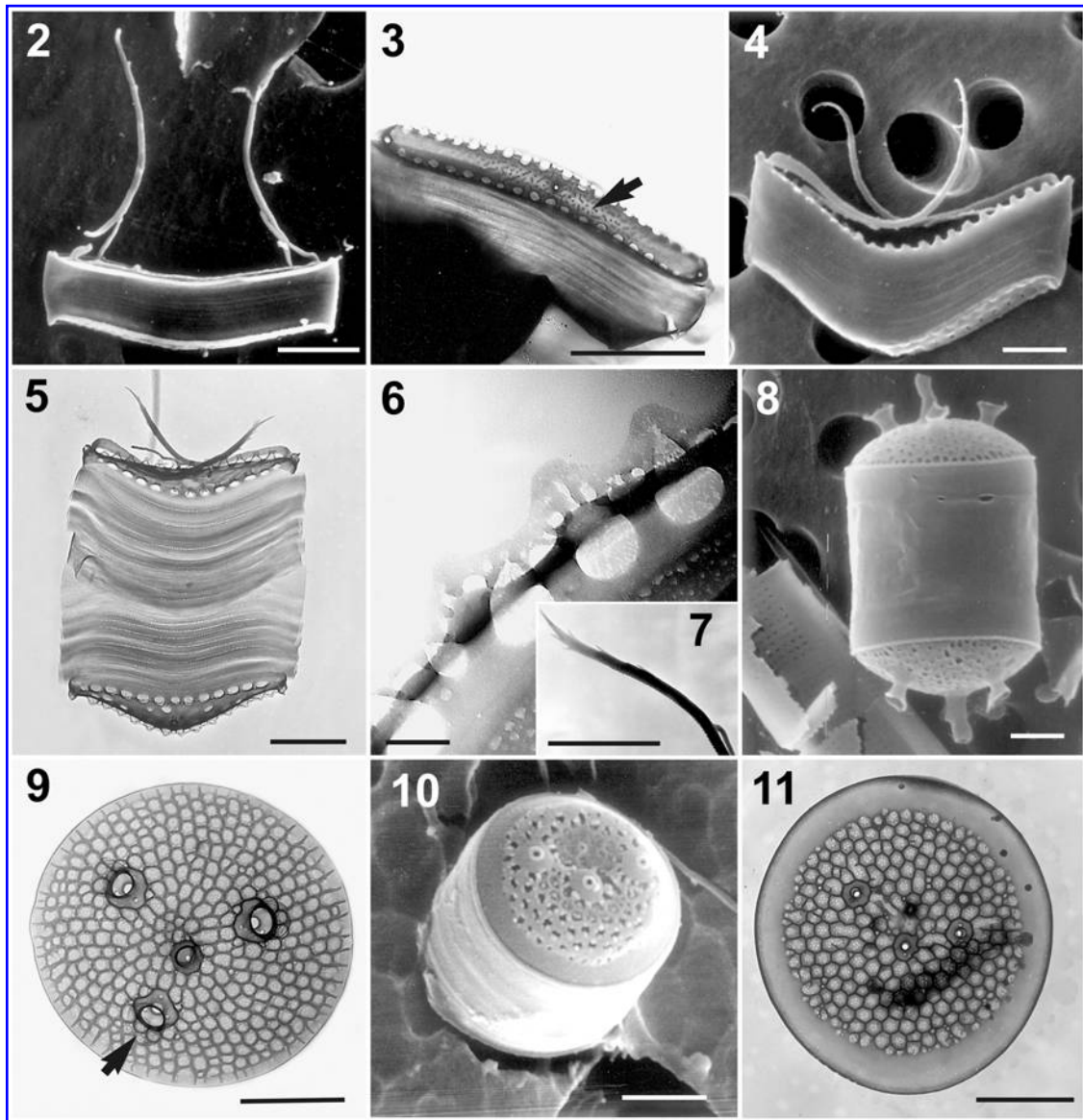
of the North Sea, and in subtropical coastal waters of the Gulf of Mexico (Hasle et al. 1983).

***Minidiscus comicus* Takano 1981 (Figures 8, 9)**

References Takano 1981, p. 32, figs. 1a, 2–13; Bérard-Therriault et al. 1999, p. 20, pl. 2d; Aké-Castillo et al. 2001, p. 105, figs. 4, 5.

Morphometric data Cell diameter: 2.7–4.3 μm .

Taxonomic description Cells are usually solitary, sometimes in pairs. In culture, cells are often cylindrical in girdle view due to the marked development of cingular bands, and have convex valves (Figure 8), whereas in natural samples they often have a lenticular shape. The circular valve is



Figures 2–11 Centric diatoms of the Liguro-Provençal basin in the northwestern Mediterranean Sea.

(2) *Arcocellulus cornucervis* cell in girdle view, natural sample, SEM. (3) *A. cornucervis* valve in oblique view with wrinkled costae (arrow) and the single process ornamenting the valve, natural sample, TEM. (4) *Arcocellulus mammifer* cell in girdle view, cultured material, SEM. (5) *A. mammifer* cell in girdle view, culture material, TEM. (6) *A. mammifer* areolae showing velum, culture material, TEM. (7) *A. mammifer* terminal part of pilus, culture material, TEM. (8) *Minidiscus comicus* cell in girdle view, culture material, SEM. (9) *M. comicus* cell in valve view showing fuloportulae with three satellite pores (arrow), culture material, TEM. (10) *M. trioculatus* cell in oblique view, natural sample, SEM. (11) *M. trioculatus* cell in valve view showing a distinct hyaline margin, culture material, TEM. Scale bars=2 μm (Figures 2, 3, 5, 7); 1 μm (Figures 4, 8–11); 0.2 μm (Figure 6).

slightly convex, with no distinct mantle. Three to four fuloportulae with three satellite pores on each process base are located halfway between the valve center and the margin (Figure 9, arrow). One rimoportula with a long external tube is present at the center of the valve (Figure 9).

Notes A long, straight filament, possibly made of chitin, emerges from one of the processes and runs obliquely with respect to the valve face. This is at times clearly visible also in LM, allowing for the species identification (data not shown).

Distribution The species was described from Japanese waters (Takano 1981) and it was later recorded from the French Atlantic coasts (Chrétiennot-Dinet and Guillocheau 1987), English Channel (Aké-Castillo et al. 2001), Caspian Sea (Genkal and Makarova 1985), Atlantic North American and Argentine waters (Lange 1985), Gulf of St. Lawrence, Eastern Canada (Bérard-Therriault et al. 1999), Gulf of Mexico (Aké-Castillo et al. 2001) and Xiamen, Fujian, China (Gao et al. 1992). In the Mediterranean, it is present in the Adriatic (Hasle and Syvertsen 1997) and Tyrrhenian seas (Ribera d'Alcalá et al. 2004).

***Minidiscus trioculatus* (Taylor) Hasle 1973 (Figures 10, 11)**

Basionym *Coscinodiscus trioculatus* Taylor 1967, p. 437, pl. 5, fig. 43.

References Hasle 1973, p. 29, figs. 101–108; Bérard-Therriault et al. 1999, p. 20, pl. 2c; Aké-Castillo et al. 2001, p. 105, figs. 1–3.

Morphometric data Cell diameter: 2.2–3.9 μm .

Taxonomic description Cells are small in diameter, with relatively flat valves. Each valve has hexagonal areolae and two or three fuloportulae distant from the prominent hyaline margin. Each fuloportula has two satellite pores on its basal part. One small rimoportula is located near the center of the valve and is sometimes associated with one areola different in size and shape from the others (Figures 10, 11). The species can be distinguished from *Minidiscus comicus* in EM.

Distribution The species is cosmopolitan (Hasle 1973, Bérard-Therriault et al. 1999, Aké-Castillo et al. 2001). In the Mediterranean Sea, it has been recorded from the Tyrrhenian (Giuffrè et al. 1991) and Adriatic seas (Hasle and Syvertsen 1997), and along the Catalan coasts (Estrada 1979, Delgado and Fortuño 1991).

***Papiliocellulus simplex* Gardner et Crawford 1992 (Figures 12–16)**

Reference Gardner and Crawford 1992, p. 247, figs. 1–8.

Morphometric data Apical axis: 3–11 μm ; pervalvar axis: 7 μm ; transapical axis: 1.5–2.6 μm .

Taxonomic description Cells are very small and solitary, with one chloroplast (Figure 14). Cells are elliptical in valve view, rectangular in girdle view and heterovalvate. Both valves have a central annulus, whereas only one valve has a central tubular process (Figures 12, 13, 15). An ocellulus with four porelli is present at each apex of both valves (Figure 16). A zigzag interstria runs along the apical axis, departing from the ocelluli and crossing the annulus. The ridge of the valve is not as well-developed as in the congeneric species *Papiliocellulus elegans* Hasle, von Stosch et Syvertsen (Hasle et al. 1983).

Distribution This is the first record of *Papiliocellulus simplex* in the Mediterranean Sea. The species has been found previously only in the type locality, i.e., from South Wales and Charmouth, Dorset, England (Gardner and Crawford 1992).

***Thalassiosira profunda* (Hendey) Hasle 1973 (Figures 17–19)**

Basionym *Cylindropyxis profunda* Hendey 1964, p. 93, pl. 23, fig. 9.

References Hasle 1972, p. 66, fig. 9; Hasle 1973, p. 31, figs. 98–101; Hallegraeff 1984, p. 499, fig. 13; Aké-Castillo et al. 1999, p. 45, pl. 18, figs. 134–135.

Morphometric data Cell diameter: 1.25–2.70 μm .

Taxonomic description Cells are extremely small, usually solitary, rarely forming chains of three to four cells connected by a thread. Each valve generally has four marginal fuloportulae, each with four satellite pores, and one to two central fuloportulae with two to three satellite pores (Figure 17). The central fuloportulae are associated with a central areola (Figures 17, 18). One short rimoportula is present between two marginal fuloportulae (Figures 17, 18, arrows). The poroid areolae are often very weakly silicified. They are rectangular in the central part of the valve, becoming elongated toward the margin. The cingulum is comprised of a valvocopula, scattered with minute pores, and several smooth cingular bands (Figure 19).

Distribution This is the first record of *Thalassiosira profunda* in the Mediterranean Sea. The species has been described from the Bay of Biscay, off the French and Spanish Atlantic coasts (Hendey 1964) and subsequently recorded in the Gulf of Tehuantepec in Mexico (Aké-Castillo et al. 1999), the sub-arctic North Pacific Ocean (Taylor and Waters 1982), and Australian waters (Hasle 1973, Hallegraeff 1984).

***Thalassiosira tenera* Proschkina-Lavrenko 1961 (Figures 20–22)**

References Proschkina-Lavrenko 1961, p. 33, pl. 1, figs. 1–4, pl. 2, figs. 5–7; Hasle and Fryxell 1977, p. 28, figs. 54–65; Harris et al. 1995, p. 121, figs. 6, 24; Bérard-Therriault et al. 1999, p. 28, pl. 12a–b; Hoppenrath et al. 2009, p. 60, fig. 25g–l.

Morphometric data Cell diameter: 11.2–16.3 μm ; 13–16 areolae in 10 μm ; 4–6 fuloportulae in 10 μm .

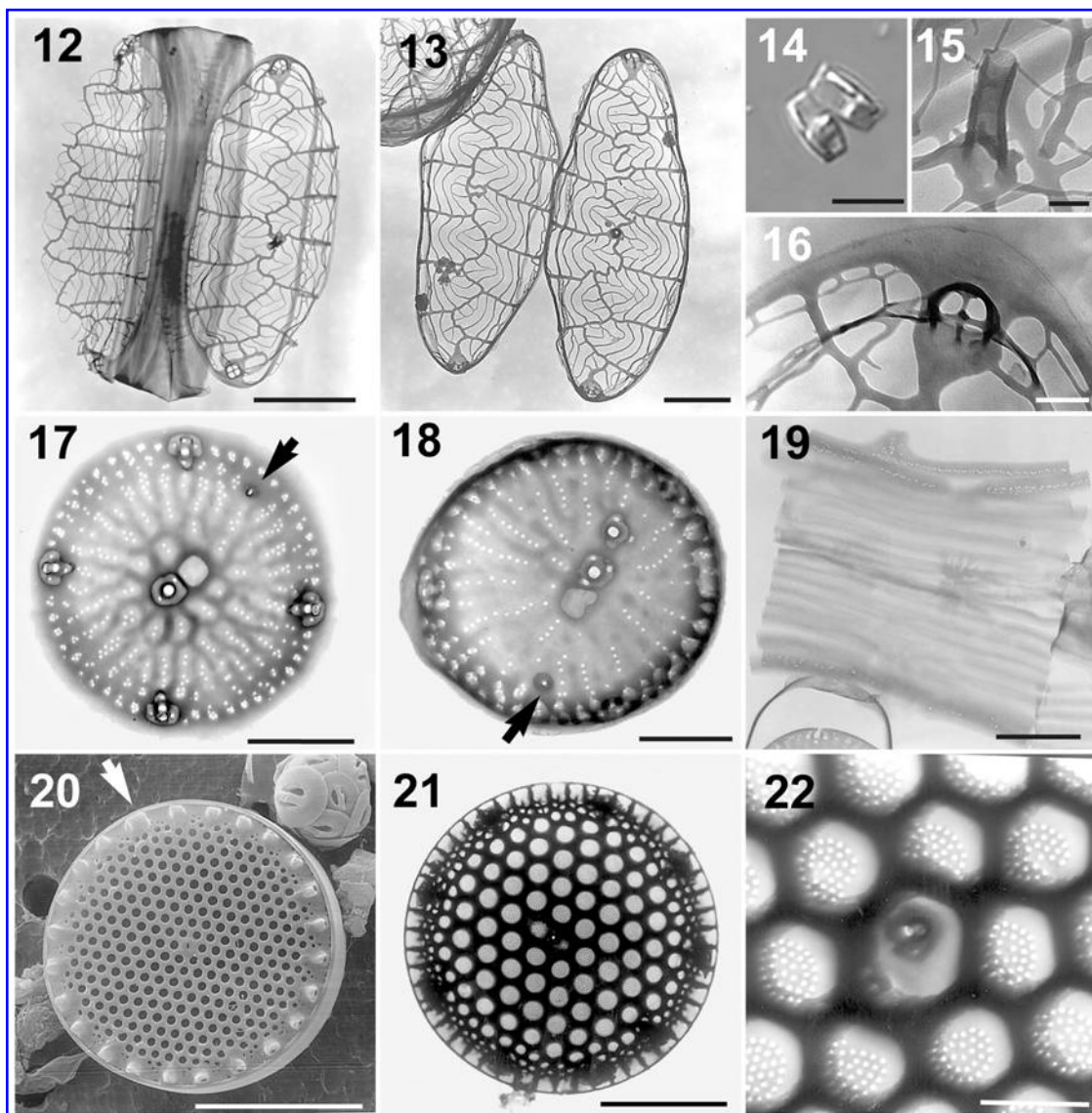
Taxonomic description Cells have a small, flat valve surface, with distinct hexagonal areolae with a circular foramen. A fuloportula is present in the valve center (Figures 20–22). Central and marginal fuloportulae are sometimes covered by a siliceous cap. A rimoportula is located between two marginal fuloportulae (Figure 20, arrow).

Distribution The species is cosmopolitan (Hasle and Fryxell 1977). In the Mediterranean Sea, it has been recorded from the Greek (Hasle and Fryxell 1977) and Turkish coasts (Koray 2001).

Dinophyceae***Heterocapsa minima* Pomroy 1989 (Figures 23, 24)**

Reference Pomroy 1989, p. 132, figs. 1–5.

Morphometric data Length: 7.9–10.6 μm ; width: 5.0–8.3 μm .

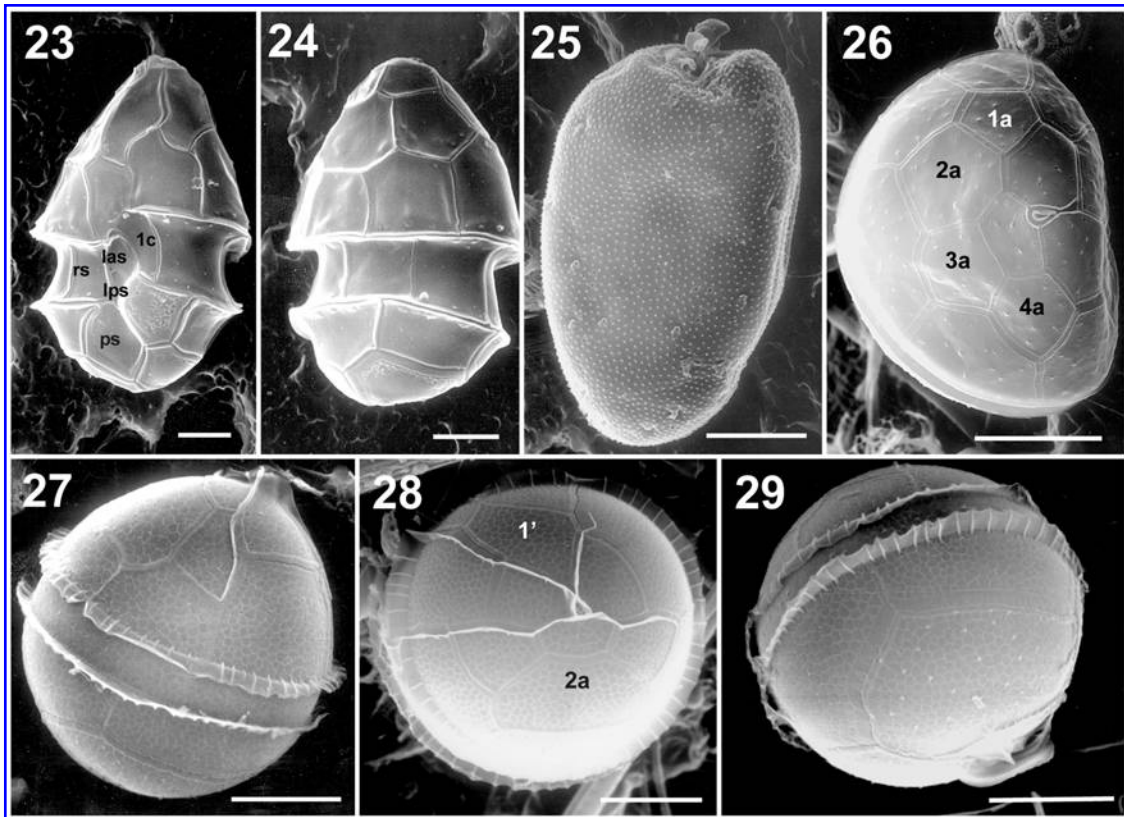


Figures 12–22 Centric diatoms of the Liguro-Provençal basin in the northwestern Mediterranean Sea.

(12) *Papiliocellulus simplex* valves and cingular bands, cultured material, TEM. (13) *P. simplex*, two valves, cultured material, TEM. (14) *P. simplex* two cells in girdle view, cultured material, LM. (15) *P. simplex* detail of the process valve, cultured material, TEM. (16) *P. simplex* valve apex with an ocellulus, cultured material, TEM. (17) *Thalassiosira profunda* valve with one central fuloportula. The arrow points at the rimoportula, cultured material, TEM. (18) *T. profunda* valve with two central fuloportulae. The arrow points at the rimoportula, cultured material, TEM. (19) *T. profunda* cingulum. Note the valvocopula with small pores and the smooth cingular bands, cultured material, TEM. (20) *Thalassiosira tenera* cell in valve view. The arrow points at the rimoportula, natural sample, SEM. (21) *T. tenera* cell in valve view, natural sample, TEM. (22) *T. tenera* central fuloportula, natural sample, TEM. Scale bars=10 μm (Figure 20); 5 μm (Figures 14, 21); 1 μm (Figures 12, 13, 17–19, 22); 0.1 μm (Figures 15, 16).

Taxonomic description Cells are small, with a conical epitheca and rounded, slightly asymmetrical hypotheca (Figures 23, 24) as wide as the epitheca. The cingulum is displaced less than one times its width. The sulcus has five plates. A small left posterior sulcal plate (lps) and a conspicuous left anterior sulcal plate (las) are evident in the central part of the sulcal area (Figure 23). The posterior sulcal plate is rather large and pentagonal. The theca is covered with organic, triangular body scales (not observed in our specimens), which are a remnant of the endosymbiotic prasinophyte from which the chloroplasts of this species derive (Hansen 1995).

Notes The species was identified by shape and size of the cell and the shape of most thecal plates, which perfectly match the holotype of *Heterocapsa minima* showed by Pomroy (1989). However, in that paper the first cingular plate 1c was interpreted as las, whereas only one relatively large platelet, identified as lps, was described in the central part of the sulcus. Our specimen (Figure 23) clearly has two plates, namely, the actual las and a small lps, in the same position as the lps of Pomroy (1989), who probably missed the suture between these two small plates. This interpretation of the sulcus has already been suggested in a study describ-



Figures 23–29 Dinophyceae of the Liguro-Provençal basin in the northwestern Mediterranean Sea.

(23) *Heterocapsa minima* cell in ventral view. Note the five sulcal plates (las, left anterior sulcal; lps, left posterior sulcal; rs, right sulcal; ps, posterior sulcal) and the first cingular plate (1c), net sample, SEM. (24) *H. minima* cell in dorsal view, net sample, SEM. (25) *Prorocentrum donghaiense* right valve, net sample, SEM. (26) *Protoperidinium americanum* cell in apical view. Note the four intercalary plates (1a, 2a, 3a, 4a). (27) *Protoperidinium* cf. *brachypus* cell in right-lateral view, net sample, SEM. (28) *P.* cf. *brachypus* cell in apical view, net sample, SEM. (29) *P.* cf. *brachypus* cell in right-posterior view, the sulcal wing probably covering the left antapical spine, net sample, SEM. Scale bars=10 μm (Figures 26–29); 5 μm (Figure 25); 1 μm (Figures 23, 24).

ing another small species in this genus, *H. rotundata* Hansen (Hansen 1995). Had this suture been observed, the sulcal plate arrangement of *H. minima* would match that of our specimen. Compared to *H. minima*, *H. rotundata* has the same sulcal plate arrangement but the sulcal posterior plate is smaller, the hypotheca is shorter and narrower, and the theca is considerably thinner and smoother. In addition, the body scales of the two species may be slightly different (Hansen 1995).

Distribution This is the first record of *Heterocapsa minima* in the Mediterranean Sea. The species is also commonly found in the Gulf of Naples in the Tyrrhenian Sea (D. Sarno and A. Zingone, unpublished data). The species was described from the Celtic Sea (Pomroy 1989) and later reported from the North Sea (Hansen and Larsen 1992, Kuylenstierna and Karlson 2000, Hoppenrath 2004).

***Prorocentrum donghaiense* Lu 2001 (Figure 25)**

Reference Lu and Goebel 2001, p. 338, fig. 2.

Morphometric data Length: 16.5 μm ; width: 9.5 μm .

Taxonomic description Cells are asymmetrical, with a rounded posterior end and a slightly indented anterior margin. The periflagellar area on the right valve is V-shaped. Knob-like spines cover the whole cell surface. Several circular thecal pores are scattered on the cell surface, sometimes arranged in rows of three or four (Figure 25). Less numerous trichocyst pores are distributed mainly close to the margins of the hypothecal plates.

Notes Our specimen perfectly matches the original description of *Prorocentrum donghaiense* (Lu and Goebel 2001). Similar specimens isolated from the Gulf of Naples were genetically identical to *P. donghaiense* (R. Siano, unpublished data). Moreover, this species resembles *P. maximum* (Gourret) Schiller, originally described from the Gulf of Marseille as *Postprorocentrum maximum* Gourret. In the original diagnosis showing an incomplete line drawing, there is no indication of cell size. Schiller (1933) transferred the species to *Prorocentrum maximum* Schiller, mistakenly omitting the name of Gourret from the authority, and he provided two new line drawings of specimens from the Adriatic Sea. One drawing shows pores of different size scattered on the whole theca, which are also mentioned in the diagnosis (Schiller

1933). This first occurrence of *P. donghaiense* in the Mediterranean Sea, not far from the type locality of *P. maximum*, raises some doubts whether the two species are distinct. Indeed, *P. donghaiense* is very similar to *P. maximum* in the shape of the theca and dimensions. Different from the original illustration of *P. maximum* (Schiller 1933), *P. donghaiense* has large trichocyst pores mainly distributed close to the valve margins, whereas small pores are scattered on the whole surface but are barely visible in LM. Indeed no SEM micrographs of *P. maximum* have ever been provided; such images may have revealed the pore patterns on the cell surface. Unfortunately, in describing *P. donghaiense*, Lu and Goebel (2001) did not discuss the close resemblance with *P. maximum*, likely because the latter species had been synonymized with *P. mexicanum* Tafall (Dodge 1975, Faust et al. 1999). This synonymy was subsequently invalidated by Gómez (2005). Given the poor quality of illustrations in the old literature and the taxonomic and nomenclatural uncertainty regarding *P. maximum*, we believe that all similar specimens in the Mediterranean Sea will be identified hereafter as *P. donghaiense*, leaving the enigma of the relationships between *P. maximum* and *P. donghaiense* unresolved.

Distribution The species was recorded in East (Qi and Yang 2003, Lu et al. 2005) and South China seas and in Hong Kong (Hodgkiss and Yang 2001). It was reported by Horiguchi (1990) as *Prorocentrum dentatum* Stein from Korean and Japanese coastal waters. This is the first report of this species in the Mediterranean Sea; it is also relatively common in the Gulf of Naples (D. Sarno and A. Zingone, unpublished data).

***Protoperidinium americanum* (Gran et Braarud) Balech 1974 (Figure 26)**

Basionym *Peridinium americanum* Gran and Braarud 1935, p. 377, fig. 54.

References Lewis and Dodge 1987, p. 119, figs. 1–7; Bérard-Therriault et al. 1999, p. 177, pl. 97a–c, f.

Morphometric data Cell width: 35 μm .

Taxonomic description The species is characterized by the presence of four intercalary plates on the epitheca, which is quite unusual since congeneric species only have two or three intercalary plates. The apical pore is attached to the first apical plate by a canal plate. Trichocysts are scattered on the thecal plates (Figure 26). Only an anterior view of one specimen was observed in SEM.

Distribution *Protoperidinium americanum* has been reported from the west coasts of Ireland (Gran and Braarud 1935), Britain (Parke and Dixon 1976) and Scotland (Lewis and Dodge 1987), from northwestern Spain (Gaarder 1954), the Gulf of St. Lawrence, Eastern Canada (Bérard-Therriault et al. 1999), Gulf of Maine and South Atlantic waters (Borge 1987). This is the first occurrence of this species in the

Mediterranean Sea, which has been previously reported only as resting cysts in the Gulf of Naples (Montresor et al. 1998).

***Protoperidinium cf. brachypus* Abé 1981 (Figures 27–29)**

Reference Abé 1981, p. 224, fig. 20, not *Protoperidinium brachypus* Schiller 1937.

Morphometric data Length: 36 μm ; width: 30 μm .

Taxonomic description Cells are ovoid in ventral view and almost circular in cross section, with an equatorial girdle. Both epithecal and hypothecal margins are rounded (Figure 27). The cingulum has a well-developed wing with radial ribs. A small apical horn (Figure 27) and two antapical spines are present (Figure 29). The 1' (first apical) plate has six sides (para) and the 2a (second intercalary) is a large hexagonal plate (hexa) (Figure 28). Four longitudinal sutures with narrow lists are visible, of which the right anterior does not reach the cingulum (Figure 28). The ornamentation of the theca is a fine reticulation.

Notes Our specimens match the plate pattern and shape of single plates originally described for *Protoperidinium brachypus* by Abé (1981). The narrow longitudinal lists on the epitheca are also very similar to those illustrated by Abé (1981). However, *P. brachypus* is larger (55–63 μm long and 46–55 μm wide) and its overall body shape is described and drawn as bi-conical, rather than spherical. Our specimens also show some similarities with *P. capurroi* Balech, a species with rounded cells described from the southwestern Atlantic (Balech 1971), and *P. capurroi* var. *pellucidum* (Balech) Balech, which matches our specimens in cell size. Later, Balech (1994) suggested that *P. brachypus* and *P. capurroi* could possibly belong to the same species, but without making any formal statement on this matter. Therefore, this taxonomic uncertainty and the lack of original illustrations other than line drawings prevent us from correctly assigning our specimens to either of the two above species, i.e., *P. brachypus* or *P. capurroi*. A ventral view of our specimens is missing, but would not have solved the identification problem.

Distribution There is no information on the distribution of *Protoperidinium brachypus* and *P. capurroi* (Gómez 2005), outside their type locality occurrence in Shimoda, Japan (Abé 1981) and southwestern Atlantic (Balech 1971), respectively.

Coccolithophyceae

***Anthosphaera* sp. type B sensu Cros and Fortuño 2002 (Figure 30)**

Reference Cros and Fortuño 2002, p. 60, fig. 88b.

Morphometric data Coccosphere diameter: 2.9 μm ; body coccolith diameter: 0.6 μm ; circum-flagellar coccolith height: ca. 1.3 μm .

Taxonomic description Monothecate dimorphic coccosphere. The cell body is oval. The body coccoliths have a thin rim constituted of a ring, one-crystal wide, and a central dome formed by few crystals. The circum-flagellar coccoliths have flat leaf-like process (fragarioliths) with straight sides (Figure 30).

Notes *Anthosphaera* sp. type B can be distinguished from *A. fragaria* Kamptner by the body and circum-flagellar coccolith morphology and size. Both types of coccoliths of *A. fragaria* are bigger, and body coccoliths have a more prominent dome-shaped central part and a proximal rim comprising three rows of crystals. Our *Anthosphaera* sp. type B specimens are smaller than those reported by Cros and Fortuño (2002).

Distribution This species has only been reported from the northwestern Mediterranean Sea (Cros and Fortuño 2002).

***Gephyrocapsa muelleriae* Bréhéret 1978 (Figure 31)**

References Bréhéret 1978, p. 448, pl. 2, figs. 3–4; Samtleben 1980, p. 106, pl. 14, figs. 6–8, pl. 15, figs. 1–4; Kleijne 1993, p. 230, pl. 2, fig. 4; Cros and Fortuño 2002, p. 46, fig. 61a; Young et al. 2003, p. 10, pl. 2, figs. 6–9; Malinverno et al. 2008, p. 44, fig. 16.

Morphometric data Coccosphere diameter: 4.7–8.2 μm ; body coccoliths (placoliths) length: 3.5–3.7 μm .

Taxonomic description Monothecate monomorphic coccosphere. The cell body is spherical. The body coccoliths (placoliths) have a narrow central area and a bar forming an angle of 45° to the long axis of the coccolith (Figure 31). The larger placoliths and the larger angle of the bar distinguish *Gephyrocapsa muelleriae* from the congeneric species *G. ericsonii* McIntyre et Bé.

Distribution This species has a cosmopolitan distribution. In the Mediterranean Sea, it has been recorded in both eastern (Kimor and Wood 1975, Malinverno et al. 2008) and western basins (Cros and Fortuño 2002).

***Poritectolithus poritectus* (Heimdal) Kleijne 1991 (Figures 32, 33)**

Basionym *Helladosphaera poritectum* Heimdal in Heimdal et Gaarder 1980, p. 7, pl. 2, fig. 15a–b.

References Cros and Fortuño 2002, p. 66, fig. 102a–b; Young et al. 2003, p. 102, figs. 1–3.

Morphometric data Coccosphere diameter: 8.5 μm ; body coccolith length: 1.8 μm ; body coccolith width: 1.3 μm ; body coccolith height: 0.4 μm ; circum-flagellar coccolith length: 1.9 μm .

Taxonomic description Monothecate dimorphic coccosphere. The cell body is irregular in shape. The dome-

shaped body coccoliths are formed by large crystallites with an evident rim. The circum-flagellar coccoliths (helladoliths) have a flared wall and a large protrusion (Figures 32, 33).

Distribution The species has been reported from the northwestern (Cros and Fortuño 2002) and eastern basins of the Mediterranean Sea as *Poritectolithus* cf. *poritectus*. It has also been recorded in the Caribbean Sea (Winter et al. 2002) and Indian Ocean (Takahashi 1981).

***Syracosphaera corolla* Lecal 1965 (Figures 34, 35)**

Synonyms *Gaarderia corolla* (Lecal) Kleijne 1993, p. 252, pl. 1, figs. 1–4; *Syracolithus corolla* Lecal 1965, p. 252, pl. 1, fig. 2; *Umbellosphaera corolla* (Lecal) Gaarder in Heimdal and Gaarder 1981, p. 62, 64, pl. 11, figs. 52–57.

References Cros and Fortuño 2002, p. 29, fig. 29; Young et al. 2003, p. 44, figs. 13–15; Malinverno et al. 2008, p. 105, fig. 76.

Morphometric data Body coccoliths: 2.2 μm ; exothecal coccolith length: 4.4 μm .

Taxonomic description Dithecate monomorphic coccosphere. Cell body is oval. Body coccoliths have a beaded mid-wall flange and a chiral distal flange (Figure 34). Exothecal coccoliths have a petaloid-shaped distal flange showing chirality, with an evident anticlockwise direction (Figure 35).

Distribution This species has been recorded in both western (Cros and Fortuño 2002) and eastern basins (Malinverno et al. 2008) of the Mediterranean Sea. It has also been reported from both Atlantic and Pacific oceans (Heimdal 1993).

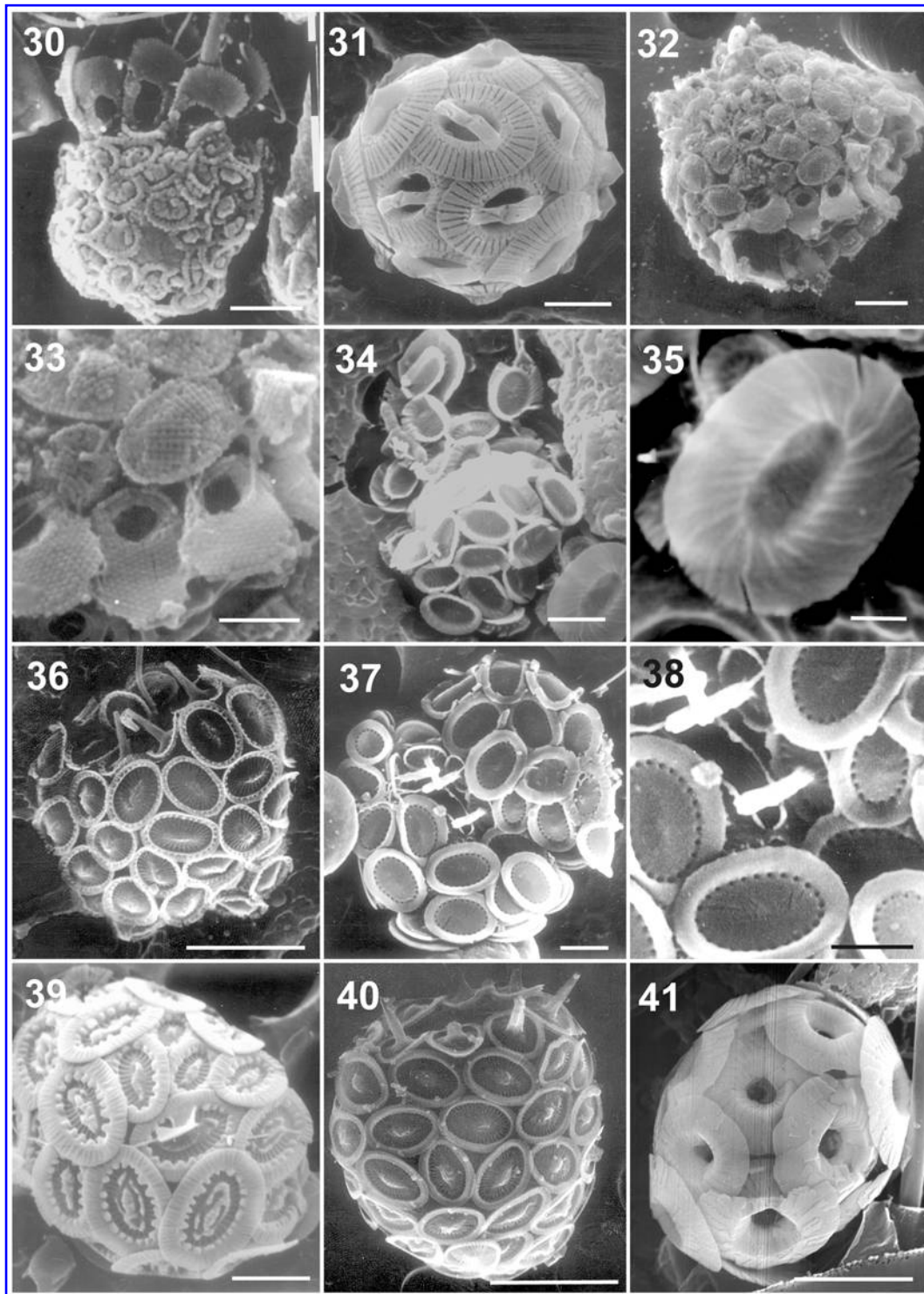
***Syracosphaera didyma* Kleijne et Cros 2009 (Figure 36)**

Synonyms *Syracosphaera exigua* auct. non Okada et McIntyre 1977, p. 21, pl. 8, figs. 10–11; *Syracosphaera* sp. type D *sensu* Kleijne 1993, p. 242, pl. 6, figs. 7–8.

References Young et al. 2003, p. 44, figs. 9, 12; Cros and Fortuño 2002, p. 41, fig. 53a–d; Malinverno et al. 2008, p. 104, fig. 75; Kleijne and Cros 2009, p. 430, pl. 3, figs. 1–6.

Morphometric data Coccosphere long axis: 9.3 μm ; body coccoliths length: 3.1 μm ; circum-flagellar coccoliths spine length: 2.0 μm .

Taxonomic description Dithecate dimorphic coccosphere. The cell body is spherical. The body coccoliths have beaded mid-wall flange and a distal flange with nodules on its inner part. The circum-flagellar coccoliths have beaded mid-wall flange and a robust spine (Figure 36). No exothecal coccoliths were observed.



Figures 30–41 Coccolithophyceae of the Liguro-Provençal basin in the northwestern Mediterranean Sea.

(30) *Anthosphaera* sp. type B complete coccosphere with fragarioliths, natural sample, SEM. (31) *Gephyrocapsa muellerae* complete coccosphere, natural sample, SEM. (32) *Poritectolitus poritectus* complete coccosphere, net sample, SEM. (33) *P. poritectus* detail of circum-flagellar coccoliths, net sample, SEM. (34) *Syracosphaera corolla* coccosphere showing endothecal and exothecal coccoliths, natural sample, SEM. (35) *S. corolla* detail of an exothecal coccolith, natural sample, SEM. (36) *Syracosphaera didyma* coccosphere showing endothecal and circum-flagellar coccoliths, natural sample, SEM. (37) *Syracosphaera marginaporata* collapsed coccosphere, natural sample, SEM. (38) *S. marginaporata* detail of the circum-flagellar area, natural sample, SEM. (39) *Syracosphaera molischii* coccosphere showing endothecal coccoliths, natural sample, SEM. (40) *Syracosphaera prolongata* coccosphere showing endothecal and circum-flagellar coccoliths, natural sample, SEM. (41) *Umbilicosphaera foliosa* complete coccosphere, net sample, SEM. Scale bars=5 μm (Figures 36, 40, 41); 2 μm (Figures 31, 32, 34, 39); 1 μm (Figures 30, 33, 37, 38); 0.5 μm (Figure 35).

Notes The association of *Syracosphaera didyma* with *Homozygosphaera arethusae* (Kamptner) Kleijne is still uncertain, as Cros et al. (2000) only reported two ambiguous combination coccospheres.

Distribution The species has been recorded in the north-western (Cros and Fortuño 2002) and eastern Mediterranean Sea (Malinverno et al. 2008).

***Syracosphaera marginaporata* Knappertsbusch 1993 (Figures 37, 38)**

Synonyms *Syracosphaera* sp. A *sensu* Samtleben and Schröder 1990, pl. 1, fig. 3; *Syracosphaera* type H *sensu* Kleijne 1993, p. 5, fig. 6.

References Knappertsbusch 1993, p. 72, pl. 2, figs. 1–4; Cros and Fortuño 2002, p. 30, fig. 30a–d; Young et al. 2003, p. 46, figs. 13–15; Malinverno et al. 2008, p. 98, fig. 68.

Morphometric data Coccosphere diameter: 4.3–6.9 μm ; body coccolith length: 1.8 μm ; body coccolith width: 1.4 μm ; circum-flagellar coccolith length: 1.1 μm ; circum-flagellar coccolith width: 0.68 μm .

Taxonomic description Dithecate dimorphic coccosphere. The cell body is spherical. The body coccoliths are flat with a smooth distal flange (Figure 37). The circum-flagellar coccoliths are smaller than the body ones and bear a spine (Figure 38). The central area is smooth with a ring of pores on the margin. No exothecal coccoliths were observed.

Distribution The species has been reported from both the western (Cros and Fortuño 2002) and eastern basins (Malinverno et al. 2008) of the Mediterranean Sea. It has also been recorded in the Norwegian–Greenland Sea (Samtleben et al. 1995) and in the North Atlantic Ocean (Knappertsbusch 1993).

***Syracosphaera molischii* Schiller 1925 (Figure 39)**

Synonyms *Caneosphaera molischii* (Schiller) Gaarder in Gaarder and Heimdal 1977, p. 66, pl. 7, figs. 40–46, pl. 8, figs. 47–49; *Syracosphaera corrugis* Okada et McIntyre 1977, p. 24, pl. 8, figs. 4–5; *Syracosphaera elatensis* Winter in Winter et al. 1979, p. 207, pl. 3, figs. 11–13.

References Schiller 1925, p. 21, fig. K; Cros and Fortuño 2002, p. 30, fig. 31a–d; Young et al. 2003, p. 46, figs. 4, 7.

Morphometric data Coccosphere major axis: 7.7 μm ; coccosphere minor axis: 6.0 μm ; body coccolith length: 2.9 μm ; body coccolith width: 2.1 μm .

Taxonomic description Dithecate dimorphic coccosphere. Cell body is ovoid. The body coccoliths have a broad

distal flange. The outer part of distal flange has low radial ridges and the inner part has teeth-like projections. A slightly developed ridge is located centrally, parallel to the long axis of the plate (Figure 39). The circum-flagellar coccoliths (caneoliths) are smaller than the body ones and bear a conspicuous central spine. No exothecal coccoliths were observed. Our specimen corresponds to *S. molischii* type 2 (see Young et al. 2003, Malinverno et al. 2008).

Notes Cros et al. (2000) illustrated a single collapsed coccosphere from the northwestern Mediterranean Sea, showing dimorphic endothecal coccoliths of *Syracosphaera molischii* in combination with both ordinary and circum-flagellar coccoliths of *Anthosphaera fragaria*.

Distribution This species has been recorded in the north-western Mediterranean Sea (Cros and Fortuño 2002). It has also been reported in the Norwegian Sea, Atlantic, Indian and Pacific oceans and in Australian waters (Heimdal 1993).

***Syracosphaera prolongata* Gran ex Lohmann type 2 *sensu* Heimdal and Gaarder 1981 (Figure 40)**

References Heimdal and Gaarder 1981, p. 62, pl. 10, figs. 48–50; Young et al. 2003, p. 42, figs. 12, 15.

Morphometric data Coccosphere long axis: 10 μm ; body coccolith width: 2.4–2.8 μm .

Taxonomic description Dithecate dimorphic coccosphere. The cell body is ovoid to elongate. The body coccoliths have three smooth flanges and the central area has laths converging in the center and forming a twisted mound (Figure 40). The circum-flagellar coccoliths have a central spine. No exothecal coccoliths were observed.

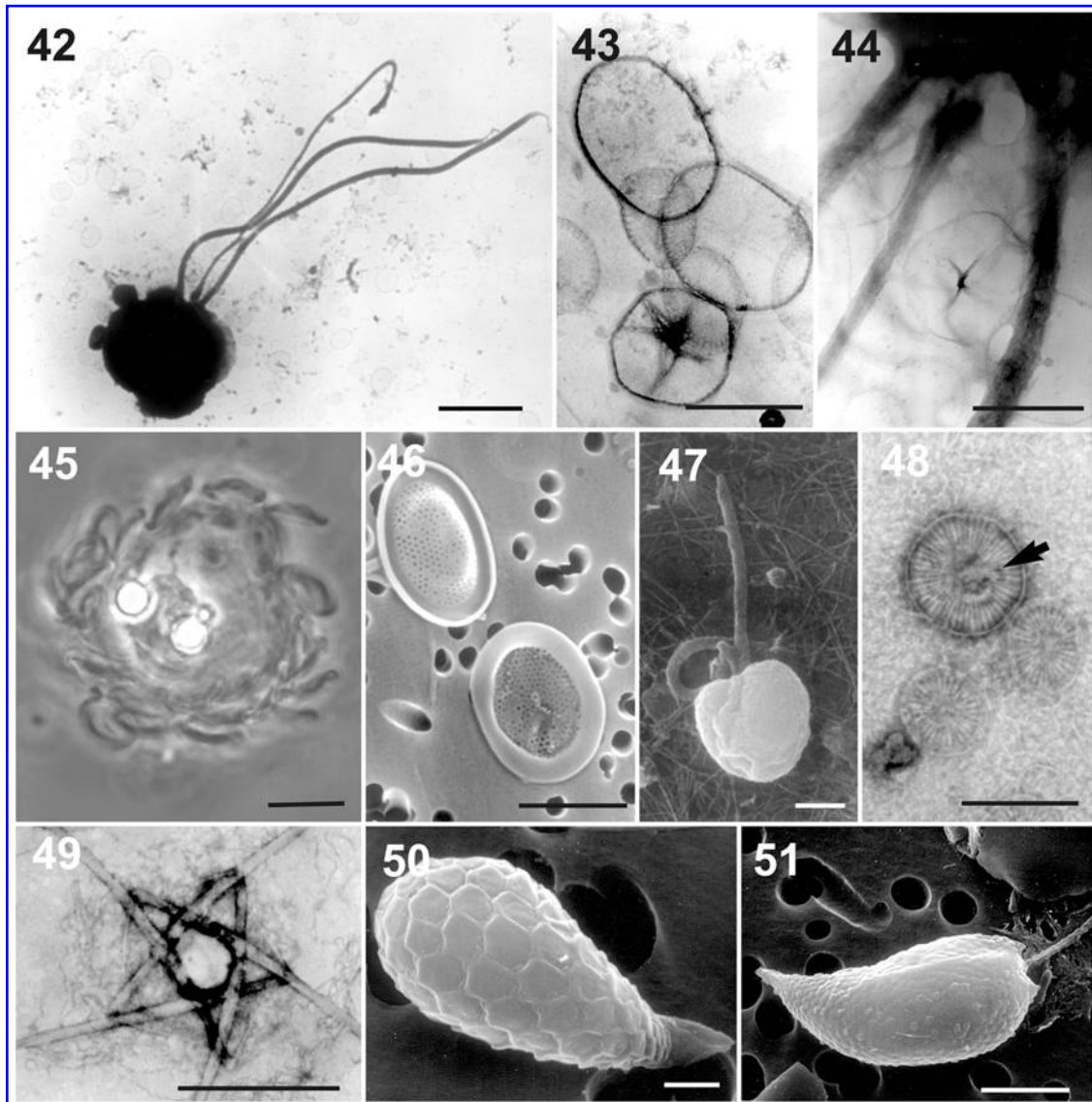
Distribution The species is present in the northwestern Mediterranean Sea (Cros and Fortuño 2002), along Egyptian (Kimor and Wood 1975) and Tunisian coasts (Saugestad and Heimdal 2002) and the Gulf of Naples (D. Sarno and A. Zingone, unpublished data). The species has also been reported from the Atlantic Ocean (Heimdal 1993).

***Umbilicosphaera foliosa* (Kamptner ex Kleijne) Geisen 2003 (Figure 41)**

Basionym *Cycloplacolithus foliosus* Kamptner 1963, p. 167, pl. 7, fig. 38.

Synonyms *Cyclococcolithus mirabilis* (Lohmann) Kamptner 1954, p. 24, figs. 21–23; *Umbilicosphaera mirabilis* Lohmann 1902, p. 139, pl. 17, figs. 1–2; *Umbilicosphaera sibogae* var. *foliosa* (Kamptner) Okada et McIntyre 1977, p. 13, pl. 4, fig. 1.

References Cros and Fortuño 2002, p. 49, fig. 64a–b; Young et al. 2003, p. 20, figs. 10–12; Malinverno et al. 2008, p. 35, fig. 7.



Figures 42–51 Prymnesiophyceae and Cryptophyceae of the Liguro-Provençal basin in the northwestern Mediterranean Sea. (42) *Chrysochromulina kappa* cell with two flagella and a haptonema, cultured material, TEM. (43) *C. kappa* three types of scales, cultured material, TEM. (44) *C. kappa* spine scale at the haptonema base, cultured material, TEM. (45) *Hyalolithus neolepis* cell with typical hat-shaped siliceous scales, net sample, LM. (46) *H. neolepis* proximal and distal view of two scales, net sample, SEM. (47) *Phaeocystis* sp. cell with two flagella and the short haptonema, natural sample, SEM. (48) *Phaeocystis* sp. different scales. Note the subcircular structure in the larger scale (arrow), cultured material, TEM. (49) *Phaeocystis* sp. three detail of the five-filament structure, cultured material, TEM. (50) *Plagioselmis prolonga* cell in dorsal view, natural sample, SEM. (51) *Teleaulax acuta* cell with the typical pointed posterior end, natural sample, SEM. Scale bars=10 μm (Figure 45); 5 μm (Figures 46, 51); 1 μm (Figures 42, 47, 50); 0.5 μm (Figures 43, 44, 49); 0.2 μm (Figure 48).

Morphometric data Coccosphere diameter: 12 μm ; body coccolith diameter: 5.5 μm .

Taxonomic description Monothecate monomorphic coccosphere. The cell body is spherical. The body coccoliths (placoliths) have small opening and distal shield larger than the proximal shield (Figure 41). One or more hook-like spines are often visible in the central area.

Distribution The species has been recorded from the eastern (Malinverno et al. 2008) and western basins (Cros

and Fortuño 2002) of the Mediterranean Sea, including the Gulf of Salerno (A. Zingone, unpublished data). It has been recorded in Atlantic, Pacific and Australian waters (Heimdal 1993).

Prymnesiophyceae

Chrysochromulina kappa Parke et Manton 1955 (Figures 42–44)

Reference Parke et al. 1955, p. 583, pl. 1–4.

Morphometric data Cell diameter: 3.2–4.0 μm ; haptonema length: 9.7 μm ; flagellum length: 10.0–12.6 μm ; large plate scales: 0.6–0.7 \times 0.4–0.5 μm ; small plate scales: 0.2–0.3 \times 0.3–0.4 μm ; spine scales: 0.5–0.6 μm .

Taxonomic description Cells are spherical to subspherical in shape, with two chloroplasts. When fully extended, the haptonema has approximately the same length as the flagella (Figure 42). Cells are covered with three types of scales of different size and ornamentation: large plate scales with a raised rim, small plate scales and very few spine scales located near the haptonemal base (Figures 43, 44). Both types of plate scales have a crossing pattern of microfibrils.

Distribution The species has been reported from British (Parke et al. 1955) and Norwegian waters as *Chrysochromulina* cf. *kappa* in Thronsen (1969). This is the first occurrence of this species in the Mediterranean Sea, except for a previous report from Greece (Nikolaidis and Moustaka-Gouni 1990) that lacks confirmation in EM (see below).

Notes In LM, *Chrysochromulina kappa* can be confused with the related species *C. minor* Parke et Manton, *C. brachycylindra* Hällfors et Thomsen, *C. leadbeaterii* Estep, Davis, Hargraves et Sieburth, sharing similar cell diameter and length of the flagella and haptonema. The species identification can only be confirmed in EM by the examination of the scale shape and size.

***Hyalolithus neolepis* Yoshida, Noël, Nakayama, Naganuma et Inouye 2006 (Figures 45, 46)**

Reference Yoshida et al. 2006, p. 214, figs. 1–2.

Morphometric data Cell diameter with scales: 30 μm ; scale length: 7.6 μm ; scale width: 5.0 μm .

Taxonomic description Cells are spherical to subspherical in shape and have two yellowish and rounded chloroplasts (Figure 45). Cells are covered with typical hat-shaped siliceous scales (Figure 46). The central area of these scales is perforated by small pores and cup-shaped, with a concavity at its top produced by the presence of two bulges (Figure 46). The marginal rim of the scale is smooth and bent upwards.

Distribution The siliceous scales of this species are found worldwide, including in the Adriatic Sea (Yoshida et al. 2006). Whole cells have been recorded only in Japanese waters (Yoshida et al. 2006) from which they have been cultured. This is the first occurrence of whole cells in the Mediterranean Sea, where they are also found in the Gulf of Naples (A. Zingone, unpublished data).

***Phaeocystis* sp. 3 sensu Medlin and Zingone 2007 (Figures 47–49)**

Reference Medlin and Zingone 2007, p. 12, fig. 6g.

Morphometric data Cell diameter: 3.5 μm ; larger circular scales: 0.19–0.22 μm ; smaller oval scales: 0.16–0.18 \times 0.14–0.15 μm .

Taxonomic description Cells show the typical heart-like shape with the two flagella and the haptonema emerging from a depression in the cell body (Figure 47). The flagella are subequal in length. Cells are covered by two layers of different body scales: the external layer has larger, circular plates and the internal one has smaller, oval plates (Figure 48). In the larger scales, a subcircular structure is at times visible in the middle of the scale surface (Figure 48, arrow). The five-filament structure ejected by the cells has a five-pointed star in its center, often surrounded by dense material, possibly of mucous nature, with a circular hole in the center of the star-like structure (Figure 49).

Distribution The species (strains MEDNS2 and MEDSN3) was recorded for the first time in the northwestern Mediterranean Sea and initially attributed to *Phaeocystis cordata* Zingone et Chrétiennot-Dinet (Zingone et al. 1999). However, the scales of *P. cordata* are oval (0.25 \times 0.18 μm). In addition, molecular analysis places *Phaeocystis* sp. 3 within the *P. globosa*-complex rather than with *P. cordata* (Medlin and Zingone 2007).

Cryptophyceae

***Plagioselmis prolunga* Butcher ex Novarino, Lucas et Morrall 1994 (Figure 50)**

References Butcher 1967, p. 18, pl. 1, fig. 9, pl. 14, fig. 2; Hill 1992a, p. 165, figs. 1A–P; Novarino et al. 1994, p. 90, figs. 1–18; Novarino 2005, p. 62, fig. 8; Cerino and Zingone 2006, p. 367, figs. 9–13.

Morphometric data Length: 6.0–13.0 μm ; width: 3.0–5.9 μm .

Taxonomic description Cells have a tear-drop shape with a round anterior end and a prominent tail at the posterior end (Figure 50). Cells bear two slightly subequal flagella, the right one shorter than the left one. A furrow runs posteriorly from the vestibulum along the ventral surface and extends for about one-third of the cell length. The inner periplast component has hexagonal plates, which are absent in the vestibular area and on the tail.

Distribution Largely distributed worldwide, *Plagioselmis prolunga* has been recorded in British waters (Butcher 1967), Irish and Baltic seas (Hill 1992a), Skagerrak, North Sea (Kuylenstierna and Karlson 1994), La Rochelle, France (Pastoureaud et al. 2003, Charles et al. 2005, Novarino 2005), and San Francisco Bay (Cloern and Dufford 2005) and Salton Sea in California (Barlow and Kugrens 2002). In the Mediterranean Sea, the species has been recorded along Spanish coasts and the Alboran Sea (Margalef 1969, Novarino 2005), Gulf of Naples (Cerino and Zingone 2006), and Adriatic Sea near the Po River delta lagoon (Andreoli et al. 1986).

***Teleaulax acuta* (Butcher) Hill 1991 (Figure 51)**

Basionym *Cryptomonas acuta* Butcher 1952, pl. 2, figs. 51–53.

References Butcher 1967, pl. 5, fig. 4, pl. 18, fig. 6; Hill 1991, p. 178, figs. 16–24; Hill 1992b, p. 173, fig. 1a–m; Bérard-Therriault et al. 1999, p. 250, pl. 116e; Cerino and Zingone 2006, p. 373, figs. 45–46.

Morphometric data Length: 8.1 μm ; width: 3.8 μm .

Taxonomic description Cells have a strongly rostrate anterior and a pointed posterior end. Flagella are sub-equal in length. Cells have a long, deep furrow extending for about half the cell length (Figure 51). The periplast has an inner sheet, without discrete plates (Figure 51).

Distribution In the Mediterranean Sea, the species has been recorded in the Gulf of Naples (Cerino and Zingone 2006) and in Alboran Sea and Barcelona coastal waters (Novarino 2005). It has been also reported from British coastal waters (Butcher 1952, 1967), Baltic Sea (Hill 1992b), North Sea (Novarino et al. 1997), Gulf of St. Lawrence in eastern Canada (Bérard-Therriault et al. 1999), Salton Sea in California (Barlow and Kugrens 2002), and Victoria in Australia (Hill 1991).

Discussion

The eukaryotic phytoplankton assemblage in the Liguro-Provençal basin of the Mediterranean Sea is relatively speciose in the spring season, with a total number of 168 taxa recorded during the 2-year study. This is certainly a conservative estimate, considering that, originally, this study was not strictly focused on species diversity and hence the identification of some groups of species, e.g., the unarmored dinoflagellates, was not properly addressed. Our species list is dominated by diatoms, which cover almost half of the total diversity recorded in the area. Most of these diatoms (e.g., *Chaetoceros* spp., *Thalassiosira* spp., *Pseudo-nitzschia* spp.) are a common component of the spring phytoplankton bloom occurring in other areas of the Mediterranean Sea (Siokou-Frangou et al. 2010), while others are very rare. Velasquez and Cruzado (1995) revised the diatom flora of the northwestern Mediterranean Sea based on literature since 1883 and their own material. They came up with a list of 753 taxa, including 504 pennates and 249 centrics. In this study, the low number of diatom species recorded with 54 centrics and 19 pennates can be explained by the sampling strategy which was limited both in space and time and did not include coastal, benthic and picoplanktonic species. Nonetheless, 17 taxa from our species list were not reported in the review of Velasquez and Cruzado (1995) (Table 3). However, among these 17 taxa, a few (e.g., *Cyclotella choctawhatcheeana*, *Dactyliosolen phuketensis*, *Pseudo-nitzschia galaxiae*) had not even been described in 1995, obviously preventing them from appearing in previous reports. Identification inaccura-

cies may have also contributed to the lack of records for some species. For example, *Thalassiosira* cf. *allenii* may have been misidentified as *T. nordenskiöldii* Cleve (Marino and Modigh 1981), a species that is typical of cold waters of the Northern Hemisphere (Hasle 1978) and has never been documented in the Mediterranean Sea. In other cases, identification can only be accurately verified through electron microscopy, which has not been frequently used in past studies. Here, we reported the presence of a number of tiny diatoms mainly because they grew well in sufficient numbers in our SDCs and could later be observed in TEM. More specifically, four diatom species, *Arcocellulus cornucervis*, *A. mammifer*, *Papiliocellulus simplex* and *Thalassiosira profunda*, represent new records for the Mediterranean Sea.

We did not record a high number of dinoflagellate species in the Liguro-Provençal basin, although Gómez (2003) recently reported 673 species of dinoflagellates making a rather diversified group in the Mediterranean Sea. However, the diversity of dinoflagellates is better assessed through net sampling, which we used for only a very minor portion of our collections. In addition, dinoflagellates are more abundant and diverse during the summer months. We also observed many athecate unidentified dinoflagellates in the nano-sized fraction of the plankton (<20 μm) in our preserved samples, but not in our SDCs, which would have allowed us to use EM for an accurate identification at the species level. In fact, the diversity of small dinoflagellates can be better addressed with a modified SDC technique, using multiwell plates which allow the observation of less abundant species (Siano et al. 2009). Nonetheless, we provide new information with the first occurrence of *Heterocapsa minima*, *Prorocentrum donghaiense*, vegetative cells of *Protoperidinium americanum* and *P. brachypus* (or *P. capurroi*) in the Mediterranean Sea.

The use of culture experiments (SDCs) during the NORBAL cruises allowed us to address a usually neglected component of the phytoplankton, i.e., the small, naked and soft flagellates. This protocol only reveals the viability of culturable species, which are known to represent a small fraction of all living microscopic eukaryotes in the sea. Some very important fraction of the flagellates could only be detected and identified in cultured material. Among them, EM-identified *Chrysochromulina kappa* and *Imantonia rotunda* are reported for the first time in the Mediterranean Sea. In addition, we identified the pelagophyte *Pelagomonas calceolata* based on its typical cell shape, single flagellum and the peculiar swimming behavior. Pelagophytes have so far been detected in the Mediterranean Sea only through their characteristic pigment signature (Claustre et al. 1994, Barlow et al. 1997, Brunet et al. 2006, 2007) and DNA sequencing (Diez et al. 2001, Massana et al. 2004, McDonald et al. 2007). Coccolithophores were numerous in the Liguro-Provençal basin, but all of them have been already reported from the northwestern Mediterranean Sea (Cros and Fortuño 2002).

One of the main results of this study is the discovery of many small species usually overlooked with routine identification protocols, which nonetheless can be highly relevant

to the pelagic food web. In this survey, 17 species, mainly diatoms and flagellates, belong to the eukaryotic picoplankton (<3 µm), and some of them were very abundant during the bloom period, such as *Minidiscus comicus*, which contributed up to 40% of total cell numbers and 20% of total biomass during the NORBAL 4 cruise in March (Iennaco 2004). Picoeukaryotes are indeed a rather diverse group, with more than 70 species described to date (Vaulot et al. 2008). Their relevance in terms of biomass and primary productivity has been shown in different marine pelagic ecosystems (Li 1994, Marañón et al. 2001, Worden et al. 2004, Buck et al. 2008). Nonetheless, small unicellular eukaryotes have received much less attention than the prokaryotes over the last decades, judging by the absence of a taxonomic overview of marine eukaryotic picoplankton since the work of Thomsen (1986).

The high number of new records in this study clearly indicates that the phytoplankton biodiversity of the Mediterranean Sea is far from being completely known. Thorough taxonomic investigations are warranted in more areas and periods of the year in order to get a more complete appreciation of this diversity. It is a most useful task which can provide a baseline for future comparisons, contributing to the identification of phytoplankton shifts in species composition in relation to climate change or harmful/toxic species invasions. In addition, sound taxonomic information is needed to allow interpretation of the huge amount of molecular data that is rapidly accumulating.

Acknowledgments

We wish to thank the crew of the Urania and the project and cruise organisers Dr. Lia Santoleri (ISAC-CNR), Dr. Maurizio Ribera d'Alcalà and Dr. Daniele Iudicone (Stazione Zoologica Anton Dohrn). A special thank to Ivano Iennaco who contributed to the identification of phytoplankton species, to Gennaro Iamunno and Franco Iamunno for technical assistance with EM and ISAC-CNR for providing physico-chemical data. This work falls within the scope of the European Network of Excellence on Marine Biodiversity and Ecosystem Functioning in European Seas (MARBEF).

References

- Abé, T.H. 1981. Studies on the family Peridiniidae, an unfinished monograph of the armoured Dinoflagellata. *Publ. Seto Mar. Biol. Lab.* 6: 1–409.
- Aké-Castillo, J.A., D.U. Hernández-Becerril and M.E. Meave del Castillo. 1999. Species of the genus *Thalassiosira* (Bacillariophyceae) from the Gulf of Tehuantepec, Mexico. *Bot. Mar.* 42: 487–503.
- Aké-Castillo, J.A., D.U. Hernández-Becerril, M.E. Meave del Castillo and E. Bravo-Sierra. 2001. Species of *Minidiscus* (Bacillariophyceae) in the Mexican Pacific Ocean. *Cryptogam. Algal.* 21: 101–107.
- Andersen, P. and J. Thronsen. 2003. Estimating cell numbers. In: (G.M. Hallegraeff, D.M. Anderson and A.D. Cembella, eds) *Manual on harmful marine microalgae*. UNESCO Publishing, Paris. pp. 99–129.
- Anderson, V. and L. Prieur. 2000. One month study in the open NW Mediterranean Sea (DYNAPROC experiment, May 1995): overview of the hydrobiogeochemical structures and effects of wind events. *Deep-Sea Res.* 47: 397–422.
- Andreoli, C., C. Tolomio, N. Rascio and L. Talarico. 1986. Some observations on a cryptophyceae responsible for a winter red bloom. *G. Bot. Ital.* 120: 70–71.
- Antoine, D. and A. Morel. 1995. Algal pigment distribution and primary production in the eastern Mediterranean as derived from coastal zone color scanner observations. *J. Geophys. Res.* 100: 16193–16209.
- Azov, Y. 1991. Eastern Mediterranean, a marine desert? *Mar. Pollut. Bull.* 23: 225–232.
- Balech, E. 1971. Microplancton de la campana oceanografica Productividad III. *Rev. Mus. Argent. Cienc. Nat. Bernardino Rivadavia, Inst. Nac. Invest. Cienc. Nat. Hidrobiol.* 3: 1–202.
- Balech, E. 1994. Contribucion a la taxinomia y nomenclatura del genero *Protoperidinium* (Dinoflagellata). *Rev. Mus. Argent. Cienc. Nat. Bernardino Rivadavia, Inst. Nac. Invest. Cienc. Nat. Hidrobiol.* 7: 61–80.
- Barlow, R.G., R.F.C. Mantoura, D.G. Cummings and T.W. Fileman. 1997. Pigment chemotaxonomic distributions of phytoplankton during summer in the western Mediterranean. *Deep-Sea Res. II* 44: 833–850.
- Barlow, S.B. and P. Kugrens. 2002. Cryptomonads from the Salton Sea, California. *Hydrobiologia* 473: 129–137.
- Bérard-Therriault, L., M. Poulin and L. Bossé. 1999. *Guide d'identification du phytoplancton marin de l'estuaire et du golfe du Saint-Laurent incluant également certains protozoaires*. *Publ. spéc. can. sci. halieut. aquat.* 128: 1–387.
- Borgese, M.B. 1987. Two armored dinoflagellates from the southwestern Atlantic Ocean: a new species of *Protoperidinium* and a first record and redescription for *Gonyaulax alaskensis*. *J. Phycol.* 34: 332–337.
- Bratbak, G., M. Heldal, S. Norland and T.F. Thingstad. 1990. Viruses as partners in spring bloom microbial trophodynamics. *Appl. Environ. Microbiol.* 56: 1400–1405.
- Bréhéré, J.G. 1978. New existing and Quaternary forms of Gephyrocapsaceae (Coccolithophorides) Family. *C.R. Hebd. Séances Acad. Sci. Paris* 287: 447–449.
- Brunet, C., R. Casotti, V. Vantrepotte, F. Corato and F. Conversano. 2006. Picophytoplankton diversity and photoacclimation in the Strait of Sicily (Mediterranean Sea) in summer. I. Mesoscale variations. *Aquat. Microb. Ecol.* 44: 127–141.
- Brunet, C., R. Casotti, V. Vantrepotte and F. Conversano. 2007. Vertical variability and diel dynamics of picophytoplankton in the Strait of Sicily, Mediterranean Sea, in summer. *Mar. Ecol. Prog. Ser.* 346: 15–26.
- Buck, K.R., F.R. Chavez and A.S. Davis. 2008. *Minidiscus trioculatus*, a small diatom with a large presence in the upwelling systems of central California. *Nova Hedwigia* 133: 1–6.
- Butcher, R.W. 1952. Contribution to our knowledge of the smaller marine algae. *J. Mar. Biol. Ass. UK* 21: 175–191.
- Butcher, R.W. 1967. An introductory account of the smaller algae of the British coastal waters. Part IV: Cryptophyceae. *Fish. Invest.* 4: 1–54.
- Cerino, F. and A. Zingone. 2006. A survey of cryptomonad diversity and seasonality at a coastal Mediterranean site. *Eur. J. Phycol.* 41: 363–378.
- Charles F., F. Lantoine, S. Brugel, M.-J. Chrétiennot-Dinet, I. Quiroga and B. Rivière. 2005. Seasonal survey of the phytoplankton biomass, composition and production in a littoral NW Mediterranean site, with special emphasis on the picoplanktonic contribution. *Estuar. Coast. Shelf Sci.* 65: 199–212.

- Chrétiennot-Dinet, M.-J. and N. Guillocheau. 1987. Etude de diatomées d'écosystèmes marins côtiers. Observations nouvelles en microscopie électronique. *Cah. Biol. Mar.* 28: 271–279.
- Claustre, H., P. Kerherve, J.C. Marty, L. Prieur, C. Videau and J.H. Hecq. 1994. Phytoplankton dynamics associated with a geostrophic front: ecological and biogeochemical implications. *J. Mar. Res.* 52: 711–742.
- Cloern, J.E. and R. Dufford. 2005. Phytoplankton community ecology: principles applied in San Francisco Bay. *Mar. Ecol. Prog. Ser.* 285: 11–28.
- Coste, B., J. Gostan and H.J. Minas. 1972. Influence des conditions hivernales sur les productions phyto et zooplanctoniques en Méditerranée Nord-Occidentale. I: Structures hydrologiques et distribution de sels nutritifs. *Mar. Biol.* 18: 320–348.
- Cros, L. and J.-M. Fortuño. 2002. Atlas of northwestern Mediterranean coccolithophores. *Sci. Mar.* 66: 7–182.
- Cros, L., A. Kleijne, A. Zeltner, C. Billard and J.R. Young. 2000. New example of holococcolith-heterococcolith combination coccospheres and their implication for coccolithophorid biology. *Mar. Micropaleontol.* 39: 1–34.
- Delgado, M. 1990. Phytoplankton distribution along the Spanish coast of the Alboran Sea. *Sci. Mar.* 54: 169–178.
- Delgado, M. and J.-M. Fortuño. 1991. Atlas de fitoplancton del Mar Mediterráneo. *Sci. Mar.* 55(Suppl 1): 1–133.
- Delgado, M., M. Latasa and M. Estrada. 1992. Variability in the size-fractionated distribution of the phytoplankton across the Catalan front of the north-west Mediterranean. *J. Plankton Res.* 14: 753–771.
- Descy, J.-P. and C. Willems. 1991. Contribution to the knowledge of the River Moselle phytoplankton. *Cryptogam. Algol.* 12: 87–100.
- Diez, B., C. Pedrós-Alió, T.L. Marsh and R. Massana. 2001. Application of denaturing gradient gel electrophoresis (DGGE) to study the diversity of marine picoeukaryotic assemblages and comparison of DGGE with other molecular techniques. *Appl. Environ. Microbiol.* 67: 2942–2951.
- Dodge, J.D. 1975. The Prorocentrales (Dinophyceae). II. Revision of the taxonomy within the genus *Prorocentrum*. *Bot. J. Linn. Soc.* 71: 103–125.
- D'Ortenzio F. and M. Ribera d'Alcalà. 2009. On the trophic regimes of the Mediterranean Sea: a satellite analysis. *Biogeosciences* 6: 139–148.
- Duarte, C.M., S. Agustí, H. Kennedy and D. Vaqué. 1999. The Mediterranean climate as a template for Mediterranean marine ecosystems: the example of the northeast Spanish littoral. *Prog. Oceanogr.* 44: 245–270.
- Estrada, M. 1979. Observaciones sobre la heterogeneidad del fitoplancton en una zona costera del mar Catalan. *Inv. Pesq.* 43: 637–666.
- Estrada, M. 1982. Phytoplankton of the western Mediterranean at the beginning of autumn. *Int. Rev. Gesamten Hydrobiol. Hydrogr.* 67: 517–532.
- Estrada, M. 1991. Phytoplankton assemblages across a NW Mediterranean front: changes from winter mixing to spring stratification. *Oecol. Aquat.* 10: 157–185.
- Estrada, M., R.A. Varela, J. Salat, A. Cruzado and E. Arias. 1999. Spatio-temporal variability of the winter phytoplankton distribution across the Catalan and North Balearic fronts (NW Mediterranean). *J. Plankton Res.* 21: 1–20.
- Faust, M.A., J. Larsen and Ø. Moestrup. 1999. Potentially toxic phytoplankton. 3. Genus *Prorocentrum* (Dinophyceae). In: (J.A. Lindley, ed) *ICES identification leaflets for plankton*. ICES, Leaflet no. 184, Copenhagen. pp. 1–24.
- Fensome, R.A., F.J.R. Taylor, G. Norris, W.A.S. Sarjeant, D.J. Wharton and G.L. Williams. 1993. *A classification of living and fossil dinoflagellates*. Micropaleontology, Special Publication Number 7. Sheridan Press, Hanover. pp. 351.
- Gaarder, K.R. 1954. Dinoflagellatae from the Michael Sars North Atlantic deep sea expedition 1910. *Rep. Scient. Results Michael Sars N. Atlant. Deep Sea Exped.* 1910, University of Bergen, John Grieg, Bergen 2: 1–62.
- Gaarder, K.R. and B.R. Heimdal. 1977. A revision of the genus *Syracosphaera* Lohmann (Coccolithineae). *Meteor. Forsch. Ergeb. D.* 24: 54–71.
- Gao, Y.-H., Z.-D. Cheng and D.-X. Jin. 1992. *Minidiscus* a new recorded nanodiatom genus from China. *Acta Phytotaxon. Sin.* 30: 273–296.
- Gardner, C. and R.M. Crawford. 1992. A description of the diatom *Papiliocellulus simplex* sp. nov. (Cymatosiraceae, Bacillariophyta) using light and electron microscopy. *Phycologia* 31: 246–252.
- Gascard, J.-C. 1978. Mediterranean deep water formation, baroclinic instability and oceanic eddies. *Oceanol. Acta* 1: 315–330.
- Genkal, S.I. and V.I. Makarova. 1985. Diatomvye vodorosli, novye dlya planktona Kapiiiskogo i Azoskogo morei (Bacillariophyta planctonica nova e maribus Caspio et Maetico). *Nov. Sist. Nizhi. Rastenii* 22: 35–37.
- Giuffré, G., R.M. Palmieri and D. Tomasello. 1991. Seasonal sequences of diatom colonization in a vertical profile in a Mediterranean meromictic brackish lake. *G. Bot. Ital.* 125: 817–830.
- Gómez, F. 2003. Checklist of Mediterranean free-living dinoflagellates. *Bot. Mar.* 46: 215–242.
- Gómez, F. 2005. A list of free-living dinoflagellate species in the world's oceans. *Acta Bot. Croat.* 64: 129–212.
- Gourret, P.A.M. 1883. Sur les Périдиниens du golfe de Marseille. *Ann. Mus. Hist. Nat. Marseille* 8: 1–37.
- Gran, H.H. and T. Braarud. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity). *J. Biol. Board Can.* 1: 279–467.
- Hallegraeff, G.M. 1984. Species of the diatom genus *Thalassiosira* in Australian waters. *Bot. Mar.* 27: 495–513.
- Hansen, G. 1995. Analysis of the thecal plate pattern in the dinoflagellate *Heterocapsa rotundata* (Lohmann) comb. nov. (= *Katodinium rotundatum* (Lohmann) Loeblich). *Phycologia* 34: 166–170.
- Hansen, G. and J. Larsen. 1992. Dinoflagellater i danske farvande. In: (H.A. Thomsen, ed) *Plankton i de indre danske farvande*. Havforskning fra Miljøstyrelsen 11. Scantryk, Copenhagen. pp. 45–155.
- Harris, A.S.D., L.K. Medlin, J. Lewis and K.J. Jones. 1995. *Thalassiosira* species (Bacillariophyceae) from a Scottish sea-loch. *Eur. J. Phycol.* 30: 117–131.
- Hasle, G.R. 1972. *Thalassiosira subtilis* (Bacillariophyceae) and two allied species. *Norw. J. Bot.* 19: 111–137.
- Hasle, G.R. 1973. Thalassiosiraceae, a new diatom family. *Norw. J. Bot.* 20: 67–69.
- Hasle, G.R. 1978. Some *Thalassiosira* species with one central process (Bacillariophyceae). *Norw. J. Bot.* 25: 77–110.
- Hasle, G.R. and G.A. Fryxell. 1977. The genus *Thalassiosira*, some species with a linear areola array. *Nova Hedwigia, Beih.* 54: 15–66.
- Hasle, G.R. and E.E. Syvertsen. 1997. Marine diatoms. In: (C.R. Tomas, ed) *Identifying marine phytoplankton*. Academic Press, San Diego. pp. 5–385.
- Hasle, G.R., H.A. von Stosch and E.E. Syvertsen. 1983. Cymatosiraceae, a new diatom family. *Bacillaria* 6: 9–156.

- Heimdal, B.R. 1993. Modern coccolithophorids. In: (C.R. Tomas, ed) *Identifying marine phytoplankton*. Academic Press, San Diego. pp. 731–858.
- Heimdal, B.R. and K.R. Gaarder. 1980. Coccolithophorids from the northern part of the eastern central Atlantic. I. Holococcolithophorids. *Meteor Forsch. Ergebn.* 32: 1–14.
- Heimdal, B.R. and K.R. Gaarder. 1981. Coccolithophorids from the northern part of the eastern central Atlantic. II. Heterococcolithophorids. *Meteor Forsch. Ergebn.* 33: 37–69.
- Hendey, N.I. 1964. *An introductory account of the smaller algae of British coastal waters. V. Bacillariophyceae (Diatoms)*. Her Majesty's Stationery Office, London. pp. 317.
- Hill, D.R.A. 1991. A revised circumscription of *Cryptomonas* (Cryptophyceae) based on examination of Australian strains. *Phycologia* 30: 170–188.
- Hill, D.R.A. 1992a. *Plagioselmis prolonga* Butcher (Cryptophyceae). *Ann. Bot. Fenn.* 29: 165–166.
- Hill, D.R.A. 1992b. *Teleaulax acuta* (Butcher) Hill (Cryptophyceae). Baltic Sea Phytoplankton identification Sheet No. 12. *Ann. Bot. Fenn.* 29: 173–174.
- Hodgkiss, I.J. and Z.B. Yang. 2001. New and dominant species from Sam Xing Wan, Sai Kung during the 1998 massive fish killing red tide in Hong Kong. In: (G.M. Hallegraeff, S.I. Blackburn, C.J. Bolch and R.J. Lewis, eds) *Harmful algal blooms*. Intergovernmental Oceanographic Commission of UNESCO, Paris. pp. 62–65.
- Hoppenrath, M. 2004. A revised checklist of planktonic diatoms and dinoflagellates from Helgoland (North Sea, German Bight). *Helgol. Mar. Res.* 58: 243–251.
- Hoppenrath, M., M. Elbrächter and G. Drebes. 2009. *Marine phytoplankton: selected microphytoplankton species from the North Sea around Helgoland and Sylt*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. pp. 264.
- Horiguchi, T. 1990. *Prorocentrum dentatum*. In: (Y. Fukuyo, ed) *Red tide organisms in Japan*. Japan Fisheries Resource Conservation Association, Tokyo. pp. 26–27.
- Iennaco, I. 2004. Evoluzione spaziale del fitoplancton in un esperimento lagrangiano nel Mediterraneo Nord-Occidentale. *Tesi di Laurea. Università degli Studi di Napoli Parthenope*. pp. 175.
- Jacques, G., H.J. Minas, M. Minas and P. Nival. 1973. Influence des conditions hivernales sur les productions phyto et zooplantoniques en Méditerranée Nord-Occidentale. II: Biomasse et production phytoplantonique. *Mar. Biol.* 23: 251–265.
- Kamptner, E. 1954. Untersuchungen über den Feinbau der Coccolithen. *Arch. Protistenkd.* 100: 1–90.
- Kamptner, E. 1963. Coccolithinen-skelettreste aus Tiefseeablagerungen des Pazifischen Ozeans. *Ann. Nathist. Mus. Wien* 66: 139–204.
- Keller, M.D., R.C. Selvin, W. Claus and R.R.L. Guillard. 1987. Media for the culture of oceanic ultraphytoplankton. *J. Phycol.* 23: 633–638.
- Kimor, B. and E.J.F. Wood. 1975. A plankton study in the eastern Mediterranean Sea. *Mar. Biol.* 29: 321–333.
- Kleijne, A. 1993. *Morphology, taxonomy and distribution of extant coccolithophorids (Calcareous nannoplankton)*. Ph.D. Thesis. University of Amsterdam, Amsterdam. pp. 321.
- Kleijne, A. and L. Cros. 2009. Ten new extant species of the coccolithophore *Syracosphaera* and a revised classification scheme for the genus. *Micropaleontology* 55: 425–462.
- Knappertsbusch, M. 1993. Geographic-distribution of living and Holocene coccolithophores in the Mediterranean Sea. *Mar. Micropaleontol.* 21: 219–247.
- Koray, T. 2001. Türkiye Denizleri Fitoplankton Türleri Kontrol Listesi (A check-list for phytoplankton of Turkish seas). *J. Fish. Aquat. Sc.* 18: 1–23.
- Kuylensstierna, M. and B. Karlson. 1994. Seasonality and composition of pico- and nanoplanktonic cyanobacteria and protists in the Skagerrak. *Bot. Mar.* 37: 17–33.
- Kuylensstierna, M. and B. Karlson. 2000. Checklist of phytoplankton in Skagerrak–Kattegat. <http://www.marbot.gu.se/SSS/SSShome>. (last access 03/05/2010).
- Lacombe, H., J.-C. Gascard, J. Gonella and J.P. Bethoux. 1981. Response of the Mediterranean to the water and energy fluxes across its surface, on seasonal and interannual scales. *Oceanol. Acta* 4: 247–255.
- Lange, C. 1985. Spatial and seasonal variations of diatom assemblages off the Argentinian coast (Southwestern Atlantic). *Oceanol. Acta* 8: 361–369.
- Lecal, J. 1965. Coccolithophorides littoraux de Banyuls. *Vie Milieu* 16: 251–270.
- Levy, M., L. Memery and G. Madec. 1999. The onset of the spring bloom in the MEDOC area: mesoscale spatial variability. *Deep-Sea Res.* 46: 1137–1160.
- Lewis, J. and J.D. Dodge. 1987. The cyst-theca relationship of *Protoperdinium americanum* (Gran and Braarud) Balech. *J. Micro-paleontol.* 6: 113–121.
- Li, W.K.W. 1994. Primary productivity of prochlorophytes, cyanobacteria, and eucaryotic ultraphytoplankton measurements from flow cytometric sorting. *Limnol. Oceanogr.* 39: 169–175.
- Lohmann, H. 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, zugleich ein Beitrag zur Kenntnis des Mittelmeerauftriebs. *Arch. Protistenkd.* 1: 89–165.
- Lu, D. and J. Goebel. 2001. Five red tide species in genus *Prorocentrum* including the description of *Prorocentrum donghaiense* Lu sp. nov. from the East China Sea. *Chin. J. Oceanol. Limnol.* 19: 337–344.
- Lu, D., J. Goebel, Y. Qi, J. Zou, X. Han, Y. Gao and Y. Li. 2005. Morphological and genetic study of *Prorocentrum donghaiense* Lu from the East China Sea, and comparison with some related *Prorocentrum* species. *Harmful Algae* 4: 493–505.
- Malinverno, E., M.D. Dimiza, M.V. Triantaphyllou, M.D. Dermitzakis and C. Corselli. 2008. *Coccolithophores of the Eastern Mediterranean Sea: a look into the marine microworld*. ION Publications, Peristeri. pp. 183.
- Marañón, E., P.M. Holligon, R. Barciela, N. González, B. Mourino, M.J. Pazò and M. Varela. 2001. Patterns of phytoplankton size structure and productivity in contrasting open-ocean environments. *Mar. Ecol. Prog. Ser.* 216: 43–56.
- Margalef, R. 1969. Composición específica del fitoplancton de la costa catalano-levantina (Mediterráneo occidental) en 1962–1967. *Invest. Pesq.* 33: 345–380.
- Margalef, R. 1974. *Ecologia*. Omega, Barcelona. pp. 951.
- Margalef, R. 1995. Fitoplancton del NW del Mediterraneo (Mar Catalan) en junio del 1993, y factores que condicionan su producción y distribución. *Mem. R. Acad. Ciencias Artes Barcelona* 60: 3–56.
- Marino, D. and M. Modigh. 1981. An annotated check-list of planktonic diatoms from the Gulf of Naples. *Mar. Ecol.* 2: 317–333.
- Marshall, J. and F. Schott. 1979. Open ocean convection: observations, theory, and models. *Rev. Geophys.* 37: 1–64.
- Massana, R., J. Castresana, V. Balagué, L. Guillou, K. Romari, A. Groisillier, K. Valentin and C. Pedrós-Alió. 2004. Phylogenetic and ecological analysis of novel marine stramenopiles. *Appl. Environ. Microbiol.* 70: 3528–3534.
- McDonald, S.M., D. Sarno, D.J. Scanlan and A. Zingone. 2007. Genetic diversity of eucaryotic ultraphytoplankton in the Gulf of Naples during an annual cycle. *Aquat. Microb. Ecol.* 50: 75–89.

- Medlin, L. and A. Zingone. 2007. A taxonomic review of the genus *Phaeocystis*. *Biogeochemistry* 83: 3–18.
- MEDOC. 1970. Observation of formation of deep water in the Mediterranean Sea. *Nature* 227: 1037–1040.
- Millot, C. 1987. Circulation in the Western Mediterranean Sea. *Oceanol. Acta* 10: 143–149.
- Millot, C. 1999. Circulation in the Western Mediterranean Sea. *J. Mar. Syst.* 20: 423–442.
- Montresor, M., A. Zingone and D. Sarno. 1998. Dinoflagellate cyst production at a coastal Mediterranean site. *J. Plankton Res.* 20: 2291–2312.
- Nikolaïdis, G. and M. Moustaka-Gouni. 1990. The structure and dynamics of phytoplankton assemblages from the inner part of the Thermaikos Gulf, Greece. I. Phytoplankton composition and biomass from May 1988 to April 1989. *Helgol. Meeresunters* 44: 487–501.
- Novarino, G. 2005. Nanoplankton protists from the western Mediterranean Sea. II. Cryptomonads (Cryptophyceae = Cryptomonadea). *Sci. Mar.* 69: 47–74.
- Novarino, G., I.A.N. Lucas and S. Morrall. 1994. Observations on the genus *Plagioselmis* (Cryptophyceae). *Cryptogam. Algal.* 15: 87–107.
- Novarino, G., D.K. Millis and F. Hannah. 1997. Pelagic flagellate populations in the southern North Sea, 1988–89. I. Qualitative observations. *J. Plankton Res.* 19: 1081–1109.
- Okada, H. and A. McIntyre. 1977. Modern coccolithophores of the Pacific and North Atlantic Oceans. *Micropaleontology* 23: 1–55.
- Parke, M. and P.S. Dixon. 1976. Checklist of British marine algae – 3rd revision. *J. Mar. Biol. Ass. UK* 56: 527–594.
- Parke, M., I. Manton and B. Clarke. 1955. Studies on marine flagellates. II. Three new species of *Chrysochromulina*. *J. Mar. Biol. Ass. UK* 34: 579–609.
- Pastoureaud A., C. Dupuy, M.-J. Chrétiennot-Dinet, F. Lantoine and P. Lioret. 2003. Red coloration of oysters along the French Atlantic coast during the 1998 winter season: implication of nanoplanktonic cryptophytes. *Aquaculture* 228: 225–235.
- Pavillard, J. 1905. Recherches sur la flore pélagique (phytoplankton) de l'Étang de Thau. *Mém. Univ. Montpellier* 2: 1–116.
- Pavillard, J. 1916a. Recherches sur les Périдиниens du Golfe du Lion. *Trav. Inst. Bot. Univ. Montpellier* 4: 9–70.
- Pavillard, J. 1916b. Recherches sur les diatomées pélagiques du Golfe du Lion. *Trav. Inst. Bot. Univ. Montpellier et St. Zool. Sète* 5: 7–62.
- Peragallo, H. and M. Peragallo. 1897–1908. *Diatomées marines de France et des districts maritimes voisins*. M.J. Tempère, Grez-sur-Loing. pp. 492.
- Pomroy, A.J. 1989. Scanning electron microscopy of *Heterocapsa minima* sp. nov. (Dinophyceae) and its seasonal distribution in the Celtic Sea. *Br. Phycol. J.* 24: 131–135.
- Proschkina-Lavrenko, A.I. 1961. Diatomeae novae e Mari Nigro (Ponto Euxino) et Azoviano (Maetico). *Notul. Syst. Inst. Cryptog.* 14: 33–39.
- Qi, Y. and Y. Yang. 2003. What the *Prorocentrum* species could be? A review in a *Prorocentrum* bloom species classification where it initiated in ECS. *Chin. J. Appl. Ecol.* 14: 1188–1190.
- Ribera d'Alcalà, M., F. Conversano, F. Corato, P. Licandro, O. Mangoni, D. Marino, M.G. Mazzocchi, M. Modigh, M. Montresor, M. Nardella, V. Saggiomo, D. Sarno and A. Zingone. 2004. Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. *Sci. Mar.* 68 (Suppl. 1): 65–83.
- Robinson, A.R. and M. Golnaraghi. 1995. The physical and dynamical oceanography of the Mediterranean sea. In: (P. Malanotte-Rizzoli and A.R. Robinson, eds) *Ocean processes in climate dynamics: global and Mediterranean examples*. Proceedings of NATO-ASI. Kluwer Academic Publishers, Dordrecht. pp. 255–306.
- Round, F.E., R.M. Crawford and D.G. Mann. 1990. *The diatoms. Biology and morphology of the genera*. Cambridge University Press, Cambridge. pp. 743.
- Samtleben, C. 1980. Die Evolution der Coccolithophoriden-Gattung *Gephyrocapsa* nach Befunden im Atlantik. *Paleontol. Z.* 54: 91–127.
- Samtleben, C. and A. Schröder. 1990. Coccolithophoriden Gemeinschaften und Coccolithen-Sedimentation im Europäischen Nordmeer. Zur Abbildung von Planktonzönosen im Sediment. *Ber. Sonderforschungsbereich, 313 Kiel* 25: 1–52.
- Samtleben, C., P. Schafer, H. Andrulleit, A. Baumann, K.H. Baumann, A. Kohly, J. Matthiessen and A. Schroderitzrau. 1995. Plankton in the Norwegian Greenland Sea – from living communities to sediment assemblages – an actualistic approach. *Geol. Rundsch.* 84: 108–136.
- Saugestad, A.H. and B.R. Heimdal. 2002. Light microscope studies on coccolithophorids from the western Mediterranean Sea, with notes on combination cells of *Daktylethra pirus* and *Syracosphaera pulchra*. *Plant Biosyst.* 136: 3–28.
- Schiller, J. 1925. Die planktonischen Vegetationen des adriatischen Meeres. A. Die Coccolithophoriden-Vegetation in den Jahren 1911–14. *Arch. Protistenkd.* 53: 59–123.
- Schiller, J. 1933. *Dinoflagellatae (Peridineae) in monographischer Behandlung I. Teil*. Akademische Verlagsgesellschaft, Leipzig, pp. 617.
- Siano, R., W.H.C.F. Kooistra, M. Montresor and A. Zingone. 2009. Unarmoured and thin-walled dinoflagellates from the Gulf of Naples, with the description of *Woloszynskia cincta* sp. nov. (Dinophyceae, Suessiales). *Phycologia* 48: 44–65.
- Silva, P., J. Throndsen and W. Eikrem. 2007. Revisiting the nomenclature of haptophytes. *Phycologia* 46: 471–475.
- Siokou-Frangou, I., U. Christaki, M.G. Mazzocchi, M. Montresor, M. Ribera d'Alcalà, D. Vaqué and A. Zingone. 2010. Plankton in the open Mediterranean Sea: a review. *Biogeosciences* 7: 1543–1586.
- Sur, H.I., E. Ozsoy and U. Unluata. 1993. Simultaneous deep and intermediate depth convection in the Northern Levantine Sea, winter 1992. *Oceanol. Acta* 16: 33–43.
- Takahashi, K. 1981. *Vertical flux, ecology and dissolution of Radiolaria in tropical oceans: implications from the silica cycle*. PhD Thesis, Massachusetts Institute of Technology/Woods Hole Oceanographic Institution. pp. 461.
- Takano, H. 1981. New and rare diatoms from Japanese marine waters. VI. Three new species in Thalassiosiraceae. *Bull. Tokai Reg. Fish. Res. Lab.* 105: 31–43.
- Taylor, F.J.R. 1967. Phytoplankton of the south western Indian ocean. *Nova Hedwigia* 12: 433–476.
- Taylor, F.J.R. and R.E. Waters. 1982. Spring phytoplankton in the subarctic North Pacific Ocean. *Mar. Biol.* 67: 323–335.
- Thomsen, H.A. 1986. A survey of the smallest eukaryotic organisms of the marine phytoplankton. *Can. Bull. Fish. Aquat. Sci.* 214: 121–158.
- Throndsen, J. 1969. Flagellates of Norwegian coastal waters. *Nytt. Mag. Bot.* 16: 161–216.
- Throndsen, J. 1997. The planktonic marine flagellates. In: (C.R. Tomas, ed) *Identifying marine phytoplankton*. Academic Press, San Diego. pp. 591–729.
- Travers, M. 1971. Diversité du microplankton du Golfe de Marseille en 1964. *Mar. Biol.* 8: 308–343.

- Travers, M. 1975. Inventaire des protistes du Golfe de Marseille et de ses parages. *Ann. Bot. Fenn.* 51: 51–75.
- Vaulot, D., W. Eikrem, M. Viprey and H. Moreau. 2008. The diversity of small eucaryotic phytoplankton ($\leq 3 \mu\text{m}$) in marine ecosystems. *FEMS Microbiol. Rev.* 32: 765–820.
- Velasquez, Z.R. and A. Cruzado. 1995. Inventory of the diatom flora of the NW Mediterranean Sea. *Vie Milieu* 45: 249–263.
- Williams, P.J.I.B. 1998. The balance of plankton respiration and photosynthesis in the open ocean. *Nature* 394: 55–57.
- Winter, A., Z. Reiss and B. Luz. 1979. Distribution of living coccolithophore assemblages in the Gulf of Elat (Aqaba). *Mar. Micropaleontol.* 4: 197–223.
- Winter, A., B. Rost, H. Hilbrecht and M. Elbrächter. 2002. Vertical and horizontal distribution of coccolithophores in the Caribbean Sea. *Geo-Mar. Lett.* 22: 150–161.
- Worden, A.Z., J.K. Nolan and B. Palenick. 2004. Assessing the dynamics and ecology of marine picophytoplankton: the importance of the eucaryotic component. *Limnol. Oceanogr.* 49: 168–179.
- Yoshida, M., M.-H. Noël, T. Nakayama, T. Naganuma and I. Inouye. 2006. A haptophyte bearing siliceous scales: ultrastructure and phylogenetic position of *Hyalolithus neolepis* gen. et sp. nov. (Prymnesiophyceae, Haptophyta). *Protist* 157: 213–234.
- Young, J.R., M. Geisen, L. Cros, A. Kleijne, C. Sprengel, I. Probert and J.B. Østergaard. 2003. A guide to extant coccolithophore taxonomy. *J. Nanoplankton Res. Spec. Issue 1*: 1–132.
- Zingone, A., M.-J. Chrétiennot-Dinet, M. Lange and L. Medlin. 1999. Morphological and genetic characterization of *Phaeocystis cordata* and *Phaeocystis jahnii* (Prymnesiophyceae), two new species from the Mediterranean Sea. *J. Phycol.* 35: 1322–1337.

Received 31 May, 2010; accepted 3 February, 2011