

RESTING CYSTS FROM COASTAL MARINE PLANKTON

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Abstract

Coastal plankton show fluctuations in abundance and species composition. Resting stage (cyst) production is a common strategy adopted by hundreds of plankton species to ensure reproduction and to avoid adverse conditions. During the resting period, these species are normally absent from the water column, and cysts produced in the plankton accumulate in the sediment where they wait for the return of suitable conditions. A portion of the cyst bank does not hatch, instead undergoing a dormancy that may extend for decades. Confined coastal areas accumulate cysts in sediment due to one or more possibilities, including reduced water movement/hydrodynamics, high population density, abundance of cyst-producing species, and the absence or scarcity of possible cyst consumers in the benthos. The pelagic-benthic nexus, which affects both the sediment and the water column (and possibly sea ice) is still poorly understood. In fact, the presence of cysts in the life cycle of organisms is likely to have considerable consequences for the ecology of coastal plankton, as well as the evolution and biogeography of species. This review aims to depict the presence (and even abundance) of resting stages in marine environments and their impact on ecosystem functioning. The review starts with a description of encysted resting stages in all marine planktonic taxa, listing a total of 500 species with known cysts, and methods and tools for their collection and study. The physiology and timing of the rest period is then described for various taxa, followed by a discussion of the evolutionary implications of resting. The presence of encysted stages in different realms and phyla of plankton suggests an ancient origin and a successive diversification of morphologies that, today, roughly characterise each taxa. Ecological and biogeographical implications stem from this general framework and support the hypothesis of seasonal occurrences of planktonic life in ecosystems where productivity is suspended for a long time (e.g. in polar seas). The potential to suspend or resume life has implications for human activities, such as the risk of translocations through ship ballast water and contamination of water and seafood with toxins but also the benefit of cysts for the production of aquaculture feed. The review concludes with perspectives on present knowledge and outstanding questions to address in future studies.

Introduction

Plankton dynamics are commonly affected by periodicity (seasonality in temperate areas). A holistic approach that is useful for developing and assessing simplified models of pelagic food webs considers plankton as a single entity, with total demographic oscillations that are clearly linked to

environmental variability and nutrient availability, particularly in coastal areas (e.g. Ji et al. 2010). It is very important to consider that holoplankton are not a single entity, but rather a community of organisms. By definition, these organisms spend their entire life in the water column. The species structuring such a complex community do not undergo simultaneous demographic variations, but adopt different and competitive life-history strategies (Giangrande et al. 1994). Demographic variations also include the possibility of a species completely disappearing from the water column. Cycles of species' absence or presence (or even abundance) are linked to (or affected by) external and internal factors that also can stimulate or inhibit the demography of other species' populations (Nybakken 1997).

The number of species in plankton communities is so surprisingly high that it led Hutchinson (1961) to write a scientific article in which he urged biologists to think about the reasons for the apparently illogical coexistence of so many species in an apparently isotropic water volume.

Certain species are perennial and always present, albeit with variable abundances. Other species, referred to as *seasonal*, show periods of absence that are sometimes longer than the periods when they are present. The periodicity of species in collected samples can have various causes:

1. *A by-product of the failure to collect species that are rare and/or patchily distributed in the habitat.* In this case, the periodicity of the species is likely a consequence of the sampling methodology.
2. *The result of a species disappearing from the sampled area.* The periodicity of the species is due to its periodical migration, i.e. to its changeable spatial distribution on large geographic scale.
3. *The seasonal presence of a species.* This condition is linked to its rarefaction and/or disappearance from the water column, not in space but in time.

Nevertheless, planktonologists readily admit the weakness of their methodologies; for example, they are not able to collect rare species or they work only on small, unrepresentative portions of the geographic distribution of a species.

Cause 1 is indirectly sustained by the theory of flush and crash (Carson 1975), with species commonly undergoing periods of abundance (flush) and rarity (crash). During the crash period, the species is partitioned into a number of small populations separated in space, a condition that enhances intraspecific variability. Each flush episode, even when affecting a single population, has the effect of reconnecting the isolated populations and sharing any genetic positive novelty, thus giving the species an evolutionary advantage. Such developments are not the rule in the seasonality framework because they are based on random factors and are irregular and unpredictable (unlike the seasons).

Regarding both causes 2 and 3, the disappearance of holoplankton species should be done, more than to the migrating behaviour, with the existence in their life cycles of resting stages that sink to the bottom and wait for the return of suitable pelagic environmental conditions. The existence of such a strategy for many planktonic taxa is well known in both freshwater and marine ecosystems but has not been studied much. The recognition that species can have resting stages in their life cycles is a potentially important contributor to understanding the periodic disappearance of species from the plankton. The ecological role of cysts is still underestimated in marine biology textbooks, up to the point that terms like *cyst*, *resting*, and *diapause* are absent from the list of arguments at the end of each volume (among the most recent examples of this, see Valiela 1995, Barnes & Hughes 1999, Levinton 2001, Kaiser et al. 2005, Speight & Henderson 2010, Mladenov 2013, and Castro & Huber 2016).

While the production of encysted resting stages is typical of unicellular organisms (Protista), it is not the only way to rest. For example, planktonic Metazoa, in addition to resting eggs, can enter a lethargic stage as larvae, juveniles or adults (see Williams-Howze 1997, Baumgartner & Tarrant 2017, for marine copepods). The marine dormant stages of hundreds of species of Protista and

Metazoa, however, are unified in a few typical morphologies (mostly spherical and spiny) and are equally affected by the dynamic processes of sea-bottom sediments, making it possible to develop common methodologies for their study. Nevertheless, resting stages are considered responsible for many of the intermittent occurrences of species and for their abundance/rarity cycles in the coastal marine environment (Boero 1994, Boero et al. 1996, Giangrande et al. 1994).

The germination of active stages from bottom sediment was named “resurrection ecology” by Kerfoot & Weider (2004) and, in contrast to supply-side ecology, where propagules for new populations arrive from adjacent areas (Gaines & Roughgarden 1985, Lewin 1986), it features a great novelty: species subtract themselves from plankton functioning, but their (inactive) cysts remain sympatric with active forms.

In recent years, another element has been added to the plankton ecology picture—the discovery of resting stages that are contained within ice formed in periodically frozen seas (Horner et al. 1992, Brierley & Thomas 2002). When the ice melts, the resting stages may germinate to seed a new plankton population (Rozanska et al. 2008).

In this review, the term *cyst* will be used to refer to all resting stages, according to Belmonte et al. (1995), even though we are conscious that different terminologies are currently in use to refer to some plankton groups that may be related to their functions and modalities of formation. In addition, the world of cysts links marine ecology to other subjects, such as sedimentology, palaeontology and even forest ecology, thus enhancing the presence of different terminologies in the same fields of study. Notwithstanding that cysts from planktonic organisms were recognised as viable resting stages by marine paleosedimentologists more than 50 years ago (Wall & Dale 1966), the approach to marine cyst banks as inactive communities has still more to develop from the work of terrestrial botanists and studies on the ecology of soil seed banks (Leck et al. 1989).

Considering all these aspects, the aims of the present review are:

- To summarise the state of knowledge on the role of encysted stages in the life cycles of marine holoplankton, about 50 years from their recognition (Wall & Dale 1966, for phytoplankton, Sazhina 1968, for zooplankton), in order for them to be correctly considered in models each species population dynamics
- To point out, on the basis of the rich amount of literature available, the ecological role, evolutionary importance and biogeographical implications of the presence of resting stages in marine plankton taxa and communities
- To propose a unifying approach with the presentation of various methodologies and terminologies used to study the world of cysts from marine holoplankton
- To propose a functional role for the bottom sediment cyst bank, in relation to the processes of recruitment, survival/mortality, and export, examined with a focus on the sediment community (although dormant) and not the water column.

Resting stages in planktonic taxa

Currently, the production of resting stages is known to be a common life-cycle trait for hundreds of coastal plankton organisms belonging to various realms (see Belmonte & Rossi 1998, Lennon & Jones 2011; also see Plate 1). Among the marine Protista, the most studied are Bacillariophyceae and Dinophyceae. As a consequence, these groups comprise the majority of cyst-producing taxa known to date; many are listed by McQuoid & Hobson (1996) and Head (1996), together with dozens of Ciliophora (Reid & John 1983). Marine Metazoa that produce cysts include Rotifera (Gilbert 2004), Cladocera (Onbé 1974) and Copepoda Calanoida (Mauchline 1998). In the published lists, taxa for which the correspondence active/resting stage is not demonstrated are often reported. To address this issue, we have compiled lists for each group, including species where cyst formation and/or theca/cyst correlations have been confirmed by encystment/germination experiments or by observing living

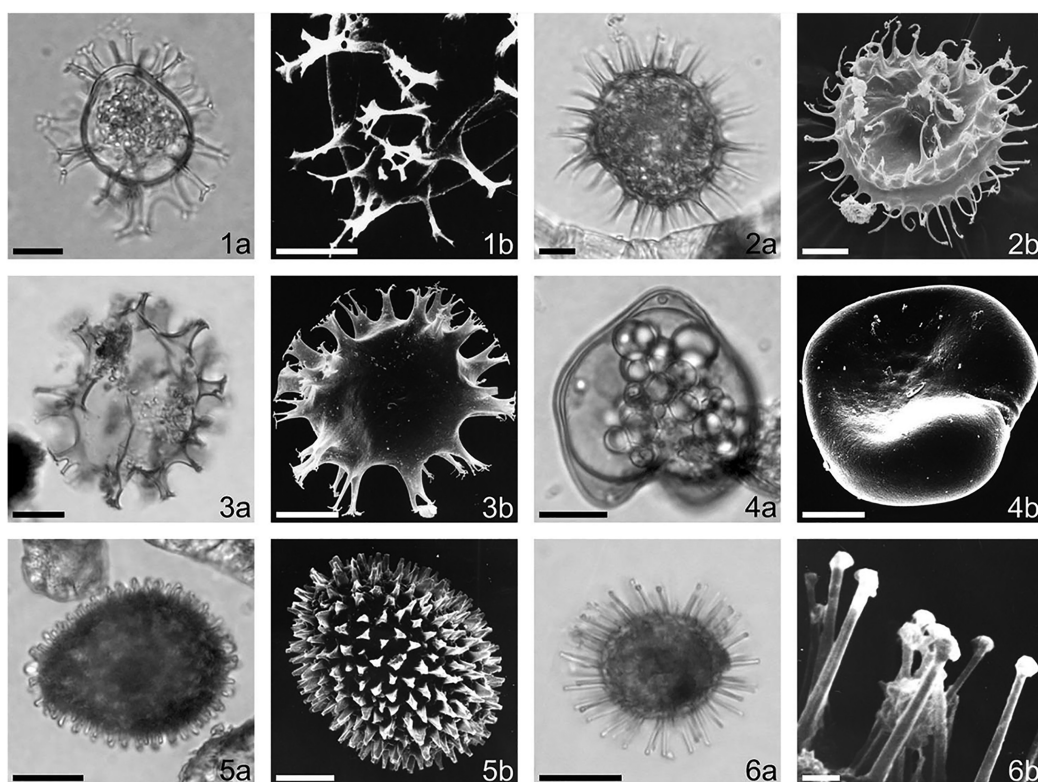


Plate 1 Photographs of some plankton cysts under (A) light microscopy and (B) SEM. Scale bars = 20 μ m unless otherwise specified. Details of the species, the location, year and method of collection (or the publication reference) are as follows: (1) *Gonyaulax* sp. (a) Mar Piccolo of Taranto, Ionian Sea, 2002; sediment trap; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (1b scale bar = 10 μ m.) (2) *Protoperidinium conicum* (a) Mar Piccolo of Taranto, Ionian Sea, 2012; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (3) *P. divaricatum* (a) Mar Piccolo of Taranto, Ionian Sea, 2002; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (4) *P. oblongum* (a) Mar Piccolo of Taranto, Ionian Sea, 2012; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (5) *Scrippsiella acuminata* (a) Mar Piccolo of Taranto, Ionian Sea, 2006; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (6) *S. ramonii* (a) Mar Piccolo of Taranto, Ionian Sea, 2002; sediment trap; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (6b scale bar = 5 μ m). (Continued)

cysts within the parental individual. An analysis of the published literature on the topic allowed us to report a total of 501 species among the so-called holoplankters (see Supplementary Material 1–4).

Bacillariophyceae

Bacillariophyceae (best known as diatoms) are photosynthetic eukaryotic organisms that live in marine environments worldwide (Vanormelingen et al. 2008). In spite of the high number of species described, many of their bioecological features, including life-history strategies, remain unknown (Chepurnov et al. 2004).

All diatoms are diplonts (Kaczmarska et al. 2013), spending the majority of their life history undergoing mitotic asexual division. The cell is constrained inside a rigid silicified frustule made up of two valves that resemble a box with a lid, or a Petri dish. Through binary fission, two new cells are formed within the parental theca. Each daughter cell receives one parental cell valve as its epitheca, and the cell division is terminated by the formation of a new hypotheca for each of the new cells.

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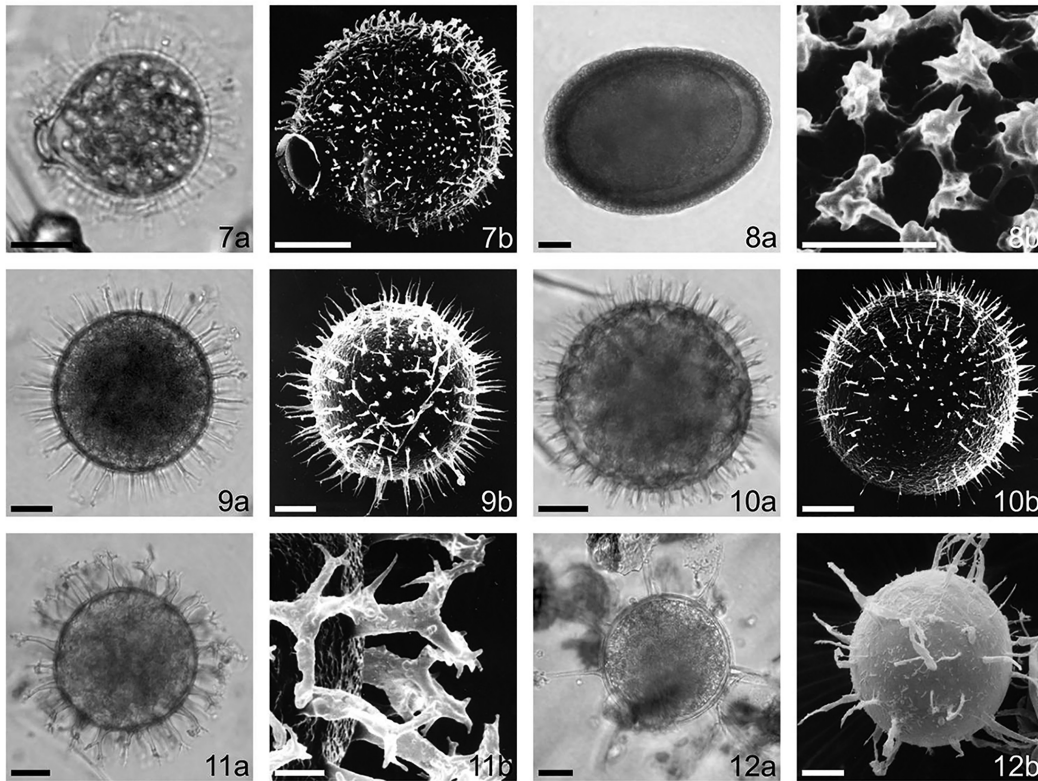


Plate 1 (Continued) Photographs of some plankton cysts under (A) light microscopy and (B) SEM. Scale bars = 20 μm unless otherwise specified. Details of the species, the location, year and method of collection (or the publication reference) are as follows: (7) *Laboea strobila* (a) Port of Haifa, Israel, 2011; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (8) *Synchaeta* sp. (a) Port of Ashdod, Turkey, 2004; Surface sediments; (b) North Adriatic Sea (From Rubino, F. et al. 2000.) (8b scale bar = 5 μm). (9) *Paracartia latisetosa* (long spines morphotype) (a) Mar Piccolo of Taranto, Ionian Sea, 2012; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (10) *P. latisetosa* (short spines morphotype) (a) Black Sea, 2013; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (11) *Pteriacartia josephinae* (a) Black Sea, 2013; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (11b scale bar = 5 μm); and (12) *C. typicus* (a) Mar Piccolo of Taranto, Ionian Sea, 2002; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000.) (12b scale bar = 5 μm).

One daughter cell, which receives the epitheca of the parental cell, has an identical size to the parent, while the other daughter cell, whose epitheca is formed from the hypotheca of the parental cell, is slightly smaller (see Hense & Beckmann 2015 for further details). As an immediate consequence, the mean population cell size decreases. This reduction is accompanied by changes in shape and valve outline complexity (Stoermer & Ladewski 1982) that further complicate classification and identification (Mann 2001). Size restoration is enabled via the auxosporulation phase, which may take place as a vegetative event or, more rarely, as the result of sexual reproduction. This process begins with the shedding of the theca and the formation of a large sphere, the auxospore, in which a new frustule of maximal size is formed, restarting the vegetative cycle (Hense & Beckmann 2015). Thus, in contrast to many other algal groups, sexual reproduction among diatoms is a mechanism for size restoration more than it is a factor in resting stage production or dispersal, as is the case for Dinophyceae (see Edlund & Stoermer 1997, for exceptions). Size reduction is not the only factor that can induce sexual reproduction in diatoms. Environmental conditions such as temperature, light,

nutrients, trace metals, organic growth factors and osmolarity might induce gametogenesis and fertilisation (see Schmid 1995, for a review). Sugie & Kuma (2008) showed that nitrogen depletion is responsible for resting spore formation in the whole population of *Thalassiosira nordenskiöldii*.

Three types of resting stages can be observed in diatom life cycles: resting (durable) spores, resting (perhaps temporary) cells and winter cells (McQuoid & Hobson 1996, Kaczmarek et al. 2013). They differ in terms of both morphological and physiological features. Resting spores show thick and heavily silicified frustules and a dense, dark cytoplasm. In some genera (e.g. *Chaetoceros* and *Rhizosolenia*), they are morphologically very different from vegetative cells, so that they can be wrongly described as different species or even new genera, as happened in some of the earlier studies (see Hendey 1964; also see Figure 1).

In contrast, in cysts produced by *Eucampia* or *Thalassiosira* species, for instance, the shapes and valvae patterns are similar to those of the active stages. Generally, resting spores have a thicker and more intensely siliceous frustule than active cells, and this favours their sinking towards the bottom sediment. The thick protection, however, also enables the spore to survive the digestive juices of copepod guts (Kuwata & Tsuda 2005).

Resting spores usually germinate before cell division occurs (Smetacek 1985), although in some species, they can divide to form more cells. This behaviour, unusual for a resting stage, is considered

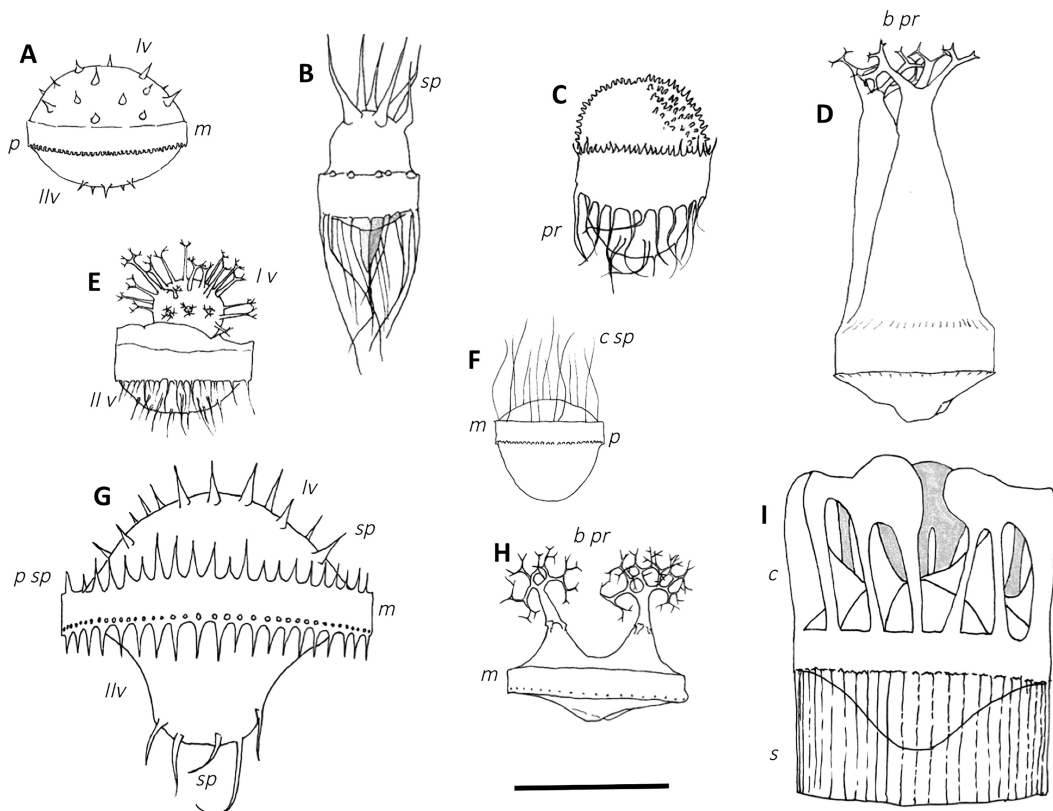


Figure 1 Sketches of resting spores of the genus *Chaetoceros*, as a representative of the Bacillariophyceae. (A) *Chaetoceros affinis*; (B) *C. lauderi*; (C) *C. brevis*; (D) *C. mitra*; (E) *C. seiracanthus*; (F) *C. diadema*; (G) *C. siamense*; (H) *C. elegans*; (I) *C. coronatus*. Scale bar = 20 μ m. (Abbreviations: *Iv*, primary valve; *IIV*, secondary valve; *b pr*, branched processes; *c*, crest; *c sp*, capillate spines; *m*, mantle; *p*, puncta; *p sp*, palisade spines; *s*, sheath; *sp*, spines.) (Modified from Ishii, K.-I. et al. 2011.)

to be evolutionarily advanced (Syvertsen 1979). Moreover, resting spore morphology is a fairly constant feature of the species and has great taxonomic value (Hasle & Syvertsen 1996), particularly for *Chaetoceros* species (Figure 1), where structures such as spines, crests and valve sheaths are highly species-specific (Ishii et al. 2011).

While to the human eye resting cells are generally not distinguishable from vegetative stages in terms of shape and frustule patterns, copepods are able to recognise and selectively prey on the vegetative stage, thus avoiding the resting spores, which contain low levels of nitrogen and are unsuitable for correct copepod growth (Kuwata & Tsuda 2005). Resting cells are characterised by the presence of a very dense cytoplasmic mass, usually in a central position (Sicko-Goad et al. 1989), and they have reduced physiological features, such as respiration rate and photosynthetic activity (Kuwata et al. 1993).

Resting cells are formed mainly by species within the Pennales group, whereas resting spores are common among Centrales species (Round et al. 1990). Some species are able to produce both vegetative and spore resting stages (Kuwata et al. 1993).

Winter cells are very similar to resting spores, as they are heavily silicified and morphologically different from vegetative forms. At the same time, they differ from resting spores because they are metabolically active. In fact, they can divide by binary fission and form colonies (Kaczmarek et al. 2013). Although this kind of resting stage has been observed only in an Antarctic species (namely, *Eucampia antarctica*), they might represent a more general adaptation of phytoplankton species living in polar seas (Fryxell & Prasad 1990).

As suggested previously, diatoms normally form resting stages in a vegetative way. Actually, very few species have been observed to form resting spores as part of the sexual phase (see McQuoid & Hobson 1996 and references therein). Whether reproduction is vegetative or sexual, resting stage formation can occur through three patterns: exogenous types that are completely released from the parent cell, so they are not in contact with it; endogenous types that are wholly enclosed within the parent cell frustules; and semiendogenous types that are attached to one of the two parent valves. The latter case could result from an intermediate pattern of development, with the spore actually being exogenous (Syvertsen 1979).

Not all cells in an active planktonic population produce resting stages. This needs to be taken into account when estimating the number of resting stages that are delivered to bottom sediment during each resting phase. The large number of diatom cells, however, allows the production of a numerically dominant presence of diatoms in bottom-sediment cyst assemblages.

Dinophyceae

Dinophyceae are widely distributed in all aquatic environments in both plankton and benthos. About half of the known species are photosynthetically active, many species are heterotrophic and some are mixotrophic, demonstrating the futility of efforts to class them as plants or animals (Fensome et al. 1996, Dale 2001).

Dinophyceae represent one of the most important groups of microplankton. They show postzygotic meiosis and a haploid life cycle. Reproduction occurs mainly in accordance with vegetative mechanisms (Pfiester & Anderson 1987), leading to high population growth rates. In some cases/species, such a feature leads to dense blooms (red tides) that disturb entire ecosystems (Hallegraeff 2003).

Dale (1983) and Taylor (1987) assumed that 13%–16% of the roughly 2000 species described produce a benthic dormant stage (cyst), which corresponds to the condition of a hypnozygote (sensu Head 1996). Our literature survey produced a list of 182 species for which the production of a resting stage has been demonstrated (Suppl. Mat. 2), but this number is rapidly increasing, thanks to the intensification of studies on this topic. This hypnozygote has no flagella, produces a robust external wall and sinks to the bottom as an inert particle. Due to this wall, cysts of some species can fossilise, and hence they represent an important element in paleoecological investigations (Dale 1996, Pielou 2008).

Although the fossil record indicates that Dinophyceae became common only 245 million years ago (Fensome et al. 1996), a Precambrian origin for the taxon has been proposed on the basis of both comparative morphology and the molecular phylogeny of cysts (Knoll & Walter 1992). Indeed, studies on cysts started with fossils assigned to the *Peridinium* genus that were first observed by Ehrenberg (1838) in siliceous rocks of the Cretaceous period.

The studies by Deflandre (1935), Eisenack (1938) and Evitt (1961), among others, showed the organic nature of the cyst wall and led to the description of new fossil genera of the family Peridineae (Bujak & Davies 1983).

Wall & Dale (1968a,b) established the correspondence between cysts and active stages for a large number of species of the order Peridiniales. These pioneering studies described the most important morphological traits of Dinophyceae cysts, which are still useful today for their identification (Stover 1973, Lentin & Williams 1976):

- General shape
- Tabulation scheme, with indication of the presence/absence of the cingulum
- Archaeopyle position, shape and size
- Wall sculpture (shape and nature of processes)
- Size and position of endocyst in relation with pericyst

Considering the general morphology, the cyst shape shows a narrower range of diversity than the motile forms. This is more evident in living species than in fossil ones (Sarjeant et al. 1987). The general shape of cysts goes from simple spheres or ovoids, with no processes or other structures on the wall, to more complex and distinctive peridinioid (pentagonal) shapes, passing through regular outlines ornamented with columnar processes, crests, septa, horns and spines (Figure 2). Regardless of ornamentation, body shape is considered the most conservative of the cyst features (Dale 1983), generally falling into two distinct categories: either similar to the shape of the motile cells or, more typically, simpler and generally spherical.

Depending on where they are formed inside the planozygote, Dinophyceae cysts are typically classified into three main categories: proximate, chorate and cavate. Starting from the consideration that cysts are always smaller than the motile cells, at least during the zygote stage (because they form inside them), Downie & Sarjeant (1966) proposed that cysts could be grouped according to the degree of difference with respect to the parent cell, which affects their general appearance. Thus, proximate cysts are those that correspond most closely to the morphology of motile forms, about one-half to one-third of the original volume, they also bear signs of cingulum, sulcus and tabulation. Chorate cysts are smaller still (less than one-third of the original) and generally have processes or crests whose height, according to Sarjeant (1982), can exceed 30% of the shortest diameter of the central body. Finally, in cavate cysts, the cellular content is surrounded by two or more walls with spaces between them. For specific terminology and more accurate descriptions, see Williams et al. (2000).

Most Dinophyceae cysts have organic walls that are usually structured with one to three or four layers and are chemically similar to the exine of spores and pollen grains (sporopollenin) of higher plants (Bujak & Davies 1983; Kokinos et al. 1998). This material, which is destroyed only by strong oxidising agents, makes the cysts very resistant over time. In the family Thoracosphaeraceae, the outer layer is of calcium carbonate, imparting a distinctive appearance and colouration to the cyst surfaces. This calcareous outer layer also makes them distinguishable by their birefringence under polarised light down a microscope (Elbrächter et al. 2008). Recent studies have demonstrated that the ultrastructure of this layer is very complex, with the calcite crystals varying in terms of shape and orientation—a characteristic considered to be genetically derived and of high taxonomic value (Elbrächter & Hoppenrath, 2009). In addition to smooth and unornamented walls, as in many *Protoperidinium* species, Dinophyceae cyst coverings are characterised by a great variety of processes and ornamentations, many of them direct consequences of their formation.

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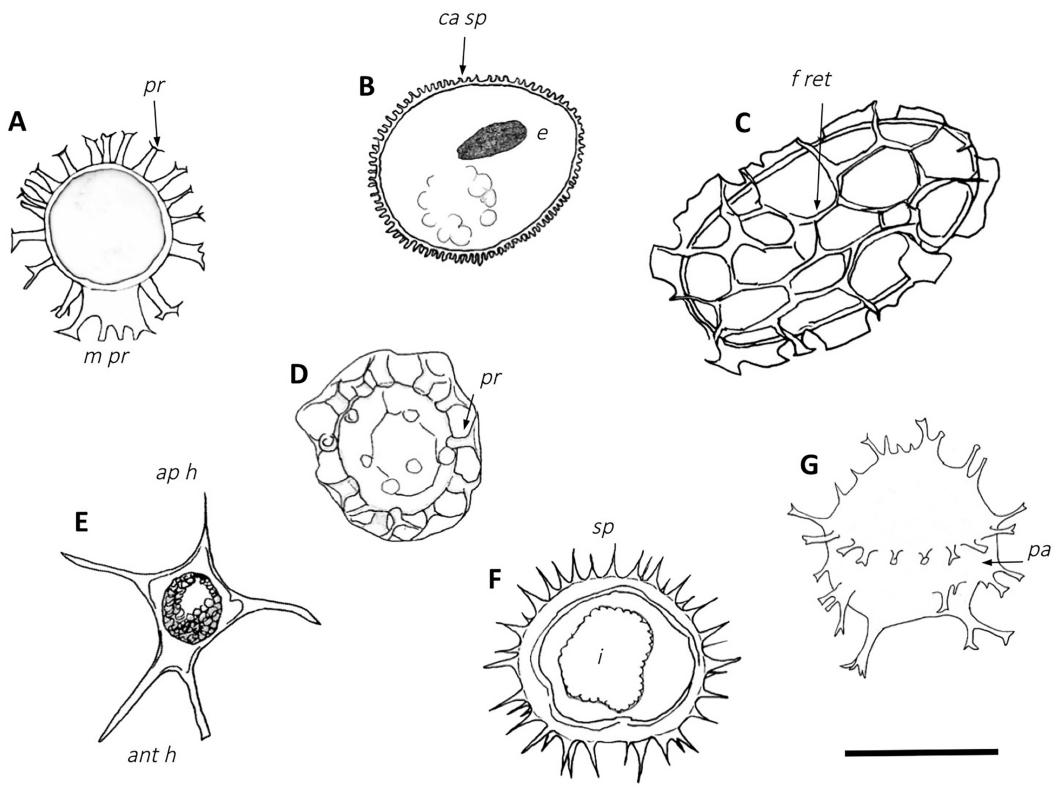


Figure 2 Sketches of Dinophyceae cysts from the order Peridiniales (original drawings from authors' cysts collection). (A) *Gonyaulax* sp.; (B) *Scripsiella acuminata*; (C) *Polykrikos schwartzii*; (D) *Pyrophacus steinii*; (E) *Protoperidinium stellatum*; (F) *P. conicum*; (G) *P. divaricatum*. Scale bar = 40 μm . (Abbreviations: *ant h*, antapical horn; *ap h*, apical horn; *ca sp*, calcareous spines; *e*, eyespot; *f ret*, fibrous reticulate layer; *i*, inner protoplasm; *m pr*, membranous process; *pa*, paracingulum; *pr*, processes; *sp*, spines.)

In many cases, the type of wall processes is distinctive in a species and may be considered a taxonomic feature. This notwithstanding, *Lingulodinium polyedrum* and *Protoceratium reticulatum* show great variability in lengths and ultrastructures of processes within the same population, due to the intrinsic variability of the species or the changing environmental conditions affecting their formation (Kokinos & Anderson 1995; Mertens et al. 2011, 2012). The complex species *Gonyaulax spinifera* is reported to produce 16 morphologically different cysts (Head 1996) probably representing several pseudocryptic species (Mertens et al. 2017), even though for 9 of them, the correspondence between theca and cyst has been proven.

Dale (1983) distinguishes ridges from processes. Ridges are often related to the tabulation pattern of the theca, reflecting the position of the sulcus and cingulum or plate boundaries, while processes may or may not be linked to the tabulation (see the discussion that follows for more detail on paratabulation).

Processes are essentially columnar or spinelike, hollow or solid. Distally, they may have pointed, bulbous or capitate endings, or else they may be intricately branched or interconnected.

Following Evitt et al. (1977), all the features of the cysts reflecting those of the theca are indicated by the prefix *para-*, from the Greek $\pi\alpha\rho\alpha-$ (= near, beside). Thus, paratabulation is, according to Lentin & Williams (1976, p.173), 'the pattern or arrangement of the constituent para-plates in a Dinophyceae cyst'. Just as tabulation is used in the identification of modern motile Dinophyceae taxa,

paratabulation is used to distinguish cyst species. Sometimes, even among thecate taxa (i.e. with a well-defined theca), paratabulation is incomplete, with the only evidence of it in cysts being the archaeopyle or the paracingulum, although the presence of these features is sufficient for taxonomic identification. For more details about tabulation, tabulation systems and tabulation formulae in both active cells and cysts, see de Verteuil & Norris (1996).

The archaeopyle is probably the most important feature of the cyst wall, playing a key role in taxonomic identification for both organic and calcareous types (Streng et al. 2004). It was originally defined by Evitt (1961, p. 389) as the ‘opening...formed by the release of a single plate or group of plates’ and subsequently by Lentin & Williams (1976) as an opening in a Dinophyceae cyst through which the active stage emerges.

Wall & Dale (1968a) observed that the position, shape and number of paraplates involved in the archaeopyle opening are very conservative in the order Peridiniales. This has been shown to be true for other thecate taxa, but not for species lacking thecal plates. Consequently, Matsuoka (1985) proposed a new terminology and new archaeopyle types that also include athecate taxa.

Little information on the structure and chemical composition of the cyst inner protoplasm is available, mainly because the wall is impervious to fixing and staining (Binder & Anderson 1990). As a general rule, the protoplasm undergoes a contraction and a reduction in the number and size of subcellular structures. Typical features of encysted protoplasm include granular starch bodies and lipid droplets, together with one or more orange/red-pigmented bodies (Dale 1983). These latter are often called *red eyes* or *accumulation bodies* due to their possible function as photoreceptors or storage structures. What is known so far is that they are produced by autotrophic species during the cyst formation process and sometimes continue to be present in the active cell for a short time after germination.

A very interesting unresolved issue is the attribution of many cyst morphotypes to a single species (heterospory), as in the case of *Gonyaulax spinifera* (Head 1996). However, it is unclear whether this indicates genuine heterospory or cyst overclassification (Taylor & Gaines 1989, Rochon et al. 2009). This perceived heterospory has stimulated the description of new species, together with the investigation of the correspondence between active and resting stages in other species of the genus *Gonyaulax* (Lewis et al. 2001, Ellegaard et al. 2003, Rochon et al. 2009, Mertens et al. 2015, 2017). In any case, heterospory may simply be an aspect of variability within species and an important strategy (see the section entitled “Evolutionary implications of rest traits”) to ensure the persistence of the species in the environment. Experimental evidence comes from recent studies of athecate species such as *Gymnodinium impudicum* (Rubino et al. 2017).

Among Dinophyceae, a distinction exists between temporary, ecdysal and pellicle cysts (see Bravo et al. 2010 for a detailed description of the differences and similarities of these cysts) and resting cysts. These two types mirror the distinction between quiescence and diapause (see the section entitled “Types and physiology of rest” for more details).

Temporary cysts are produced as a consequence of sudden environmental changes (e.g. temperature and salinity variations) and thus represent a rapid response to unpredictable variations. Normally, the theca is shed and the protoplasm of the vegetative cell contracts, becoming rounded or oval within a thin wall. As soon as conditions are favourable again, temporary cysts rapidly germinate a new active stage.

In contrast, resting cysts are normally the result of sexual reproduction, and generally their production is colligated with the arrival of adverse conditions. In some species, a transition from temporary to resting cysts has been observed. If favourable conditions do not return within a given time period, temporary cysts can produce a cyst wall, thereby transforming themselves into resting cysts (Rubino, personal observation).

Practically all planktonic dinoflagellate species are believed to produce temporary cysts. The differing physiological, biological and ecological features of temporary and resting cysts are also reflected in morphological differences.

Dinophyceae cysts can reach high abundances in the sediments of protected bays. Matsuoka et al. (2003) reported values up to about 8000 cysts per gram of dry weight sediment in Tokyo Bay. Godhe et al. (2001) measured a maximum flux of 2.7 million cysts m²/day towards the bottom and a cyst peak in the sediment that did not correspond to the active stage peak in the plankton, but probably to a progressive accumulation with time in the absence of germination.

Ciliophora

Ciliophora of the Tintinnina order and the Strombididae family (order Oligotrichida) are important heterotrophic and/or mixotrophic components of marine microplankton in oligotrophic waters (Stoecker et al. 1996). Most studies on the encystment-germination cycle of Ciliophora focus on soil and/or freshwater species (see Corliss & Esser 1974 and references therein); hence, they may be extended to marine species only with caution.

Encystment is considered as a regular trait of the ciliate life cycle, but of 141 described species of aloricate Oligotrichida of marine and brackish waters, only a few are known as cyst producers (see Suppl. Mat. 3). Until recently, knowledge of the marine ciliate encystment-germination cycle was limited to only three species: *Strombidium oculatum* (Fauré-Fremiet 1948, Jonsson 1994, Montagnes et al. 2002), *Helicostomella subulata* (Paranjape 1980) and *Cyrtostrombidium boreale* (Kim et al. 2002).

S. oculatum lives in rocky pools, and its encystment-germination cycle is correlated with tides (Montagnes et al. 2002). The other two species live in the sea and produce cysts in accordance with a seasonal rhythm. For some other species, such as *S. conicum* (Kim & Taniguchi 1995, 1997), *Strombidium crassulum* (Reid 1987) and some species of *Tintinnopsis* genus (Kamiyama & Aizawa 1990), only one of the two mechanisms (encystment or germination) has been described.

Ciliate cysts are not easily found in plankton samples, probably because of their high sinking speed or the shortness of the period during which they are produced (Reid 1987). In the literature are reported samples characterised episodically by ciliate cysts, as in the case of those collected by Meunier (1910) in the Kara and Barents seas in 1907 (but see also the case presented in Paranjape 1980 for the tintinnid *Helicostomella subulata*).

Tintinnina cysts are typically contained within the lorica of the organism. They are spherical or elliptical in shape. Hypotrichida cysts are spherical. The cysts of Heterotrichida and Oligotrichida are characterised by the presence of an apical bubblelike cap on the apical opening from which the active stages emerge at the end of their dormancy (Figure 3).

The presence of this cap and their flasklike shape (30–140 µm in length) make these cysts unmistakable (Reid & John 1983). These cysts were named Papulifera by Meunier due to the presence of this ‘bubble’ (= papula, in Latin) on their apex. Meunier’s ‘bubbled’ cysts were grouped according to their shape under the names *Fusopsis* (spindlelike), *Piropsis* (pearlike) and *Sphaeropsis* (spherical or ovoid) (Reid & John 1978). The papula is considered an archaic feature because it is very common among cyst-producing taxa.

However, like Tintinnina cysts, Papulifera cysts can be identified with certainty in many cases only after germination (Kim & Taniguchi 1995). Papulifera cysts often have spines or wrinkles on their outer covering, and the type of ornamentation has been the subject of studies concerning the phylogenesis of these ciliates (Reid & John 1983). Foissner et al. (2007) report that surface ornamentation rarely exists among Ciliophora cysts. When surface ornamentations are present, they can be delicate and tiny, and thus invisible under a compound microscope and/or easily eliminated during treatments applied before observation.

The cysts of the Oligotrichida *S. crassulum* have been described in detail by Reid (1987). The apex closed by the papula narrows into a neck about 14 µm in diameter (the cyst itself has a transversal diameter of about 50 µm). The external membrane is thin and bears tiny spines that make it look like velvet. The underlying layer is the thickest and is composed of calcium carbonate and phosphate, immersed in an organic matrix. This layer is seen to be multistratified when observed

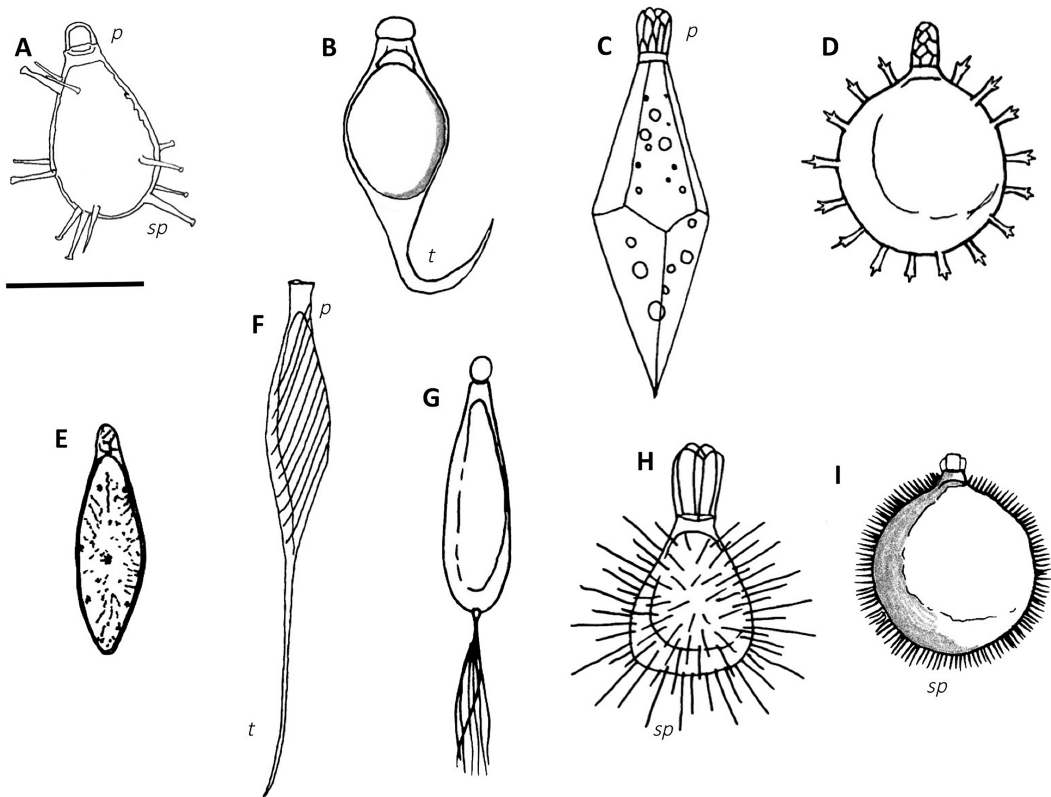


Figure 3 Sketches of Ciliophora cysts. (A) *Strombidium biarmatum*. (Redrawn from Agatha, S. et al. 2005.) (B) *Cyrtostrombidium boreale*. (Redrawn from Moscatello, S. et al. 2004.) Cysts attributed to Ciliophora (Redrawn from Meunier 1910), but waiting to be linked to a motile stage (the terminology of Meunier 1910 is used); (C) *Fusopsis polyedra*; (D) *Sphaeropsis echinata*; (E) *F. pauperata*; (F) *F. spiralis*; (G) *F. flagrifera*; (H) *Piropsis acineta*; (I) *S. brevisetosa*. Scale bar = 40 μm . (Redrawn from Agatha, S. et al. 2005.) (Abbreviations: p, papula; sp, spines; t, tail.)

by transmission electron microscopy (TEM). A thin inner membrane encloses an undifferentiated granular cytoplasm.

The three layers (moving from the outside inwards) are named *ectocyst*, *mesocyst* and *endocyst*.

Foissner et al. (2005, 2007) report that the chemical composition of this multilayer includes various types of carbohydrates, proteins and glycoproteins. The same authors distinguish spines (if formed by the ectocyst) from thorns (if formed by the mesocyst) and lepidosomes or scales (if formed in the cytoplasm and successively transferred to the external surface). In any case, it seems that the strength of the cyst wall in some way requires the cyst to reduce its volume to the minimum. In many freshwater species, this sensible reduction of the final volume to 3%–5% of the active stage volume is probably obtained with a subtraction of water more than a deprivation of cytoplasm and organelles (Verni & Rosati 2011).

Hyperhaline habitats host ciliates (e.g. those of the *Fabrea* genus) with apparently smooth cysts.

The sediments of lagoons and bays sometimes host rich assemblages of such cysts (Moscatello & Belmonte 2004). Their number does not depend on the production rate of the active stages, as in the case of Metazoa. In fact, each active stage produces only one cyst because it simply encysts itself generally after an act of two-cell fusion (sexual reproduction). The number of cysts

found in sediments is consequently a simple reflection of the abundance of active stages in the water column just before cyst formation. Nothing can be said about the length of the resting (which could be responsible for the accumulation of ungerminated cysts); in any case, Doherty et al. (2010) established that the cyst bank of sediment may contain only a few ciliate cysts, due not only to the mechanism of production, but also to their relatively short period of rest.

Other Protista

Unicellular organisms of marine plankton, which are different from Bacillariophyceae, Dinophyceae or Ciliophora, are only rarely considered in ecological studies on rest and resting stages, although they are well known in studies of single species. *Chattonella marina* and *Heterosigma hakashiwo* (Raphidophyceae) are probably emblematic examples, being unicellular algae responsible for noxious blooms in coastal areas and whose cysts capture scientists' attention with the hope of understanding their cyclical appearance (Imai 1989, Kim et al. 2015). Never dominant, but sometimes common, are morphotypes such as *Radiosperma corbiculum* and *Hexasterias problematica*, classified as palynomorphs (Price & Pospelova 2011) or as other algae (Candel et al. 2012) (Figure 4).

Very recently, *Hexasterias problematica* (syn. *Polyasterias problematica*) has been recognised as the cyst of a Ciliophora (order Prorodontida), together with *Halodinium verrucatum*, both sharing close relationships with *Radiosperma*, suggesting the latter should be a ciliate and not an alga (Gurdebeke et al. 2018).

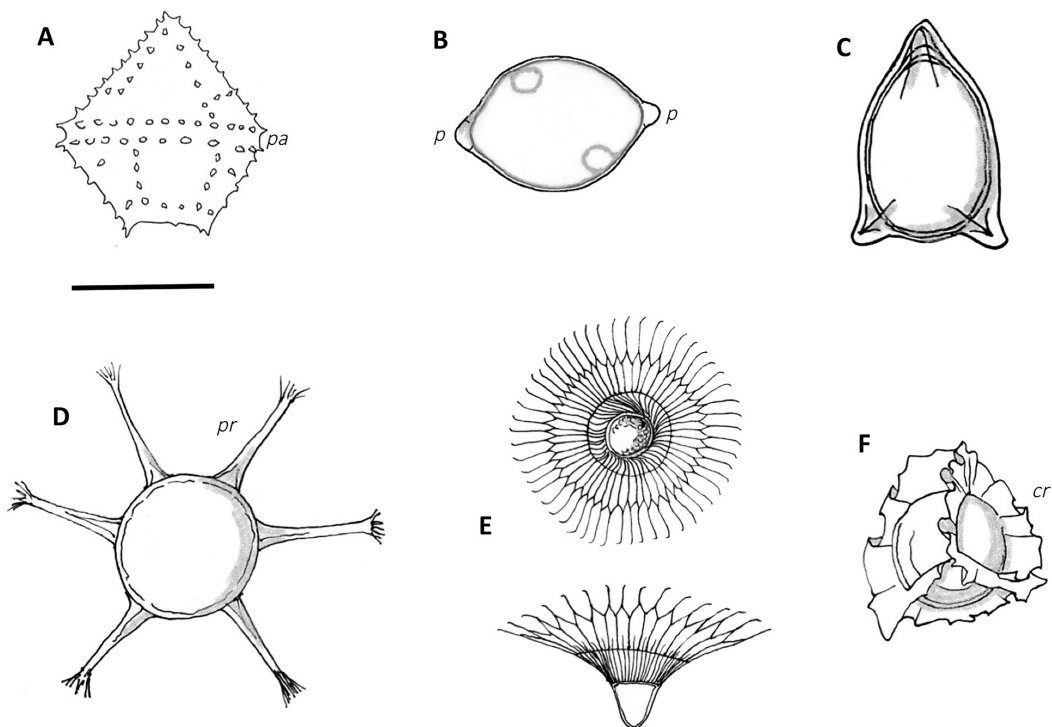


Figure 4 Cyst morphologies of other Protista, including some palynomorphs of micropalaeontologists. (A) *Protoperidinium* sp. (Dinophyceae) (original drawing from authors' cysts collection). (B) Ciliophora (unidentified) with a double papula. (Drawn from Rubino et al. 2013.) (C) *Favella* sp. (Ciliophora). (Redrawn from Reid & John 1983). (D) *Hexasterias problematica* (Ciliophora) (original drawing from authors' cysts collection). (E) *Radiosperma* in polar and side view. (Redrawn from Meunier 1910.). (F) *Pterosperma*. (Redrawn from Meunier 1910.) Scale bar = 50 μ m. (Abbreviations: cr, crest; p, papula; pa, paracingulum; pr, processes.)

Other resting stages, of unknown systematics, are commonly reported from coastal or neritic habitats by palaeontologists. The list, continuously updated by micropalaeontologists, includes hundreds of organic-walled microfossils recognised during the last 50 years and generally included under the term palynomorphs. Most of them have been attributed to known taxa on the basis of some distinctive characters (e.g. the paratabulation or the archeopyle for Dinophyceae and the papula for Ciliophora cysts), but many still wait for a final identification in the frame of an intricate network of competences (i.e. palynology, sedimentology, planktonology, and palaeontology).

Generally, open-sea and/or oceanic unicellular organisms show the presence of resting stages in their life cycle, but probably with no interaction with the bottom and no obvious similarities with those of coastal species. Encystment is common in many oceanic Acantharia and involves a complete reorganisation of the architecture of the mineral skeleton, other than a series of mitotic and meiotic divisions (Bernstein et al. 1999). The process, clearly active and efficacious for a rapid sinking, is not reversible, as happens in many planktonic Protista. Being that this is the way to produce thousands of gametes, cysts in Acantharia are not true resting stages, but rather a necessary step for their reproduction (Decelle et al. 2013). The cyst formation in this taxon is thus typical of the open ocean—it does not involve the sediment, there is not a true rest period and it does not show a germination moment.

Rotifera

The Rotifera phylum is not well represented in marine plankton. Its ecological importance grows as it goes from marine to brackish and fresh waters, with some species (e.g. those of the genera *Brachionus*, *Synchaeta* and *Trichocerca*) common in the neritic microzooplankton (de Smeets et al. 2015).

The production of cysts (resting eggs) is documented for all freshwater Rotifera (for a review, see Ricci 2001), and it is generally associated with the sexual phase of the life cycle. Often this occurs only after many parthenogenetic generations. According to Gilbert (2007), this life-cycle trait evolved to achieve the maximum production of resting eggs, which wait for the return of favourable conditions to ensure the persistence of a species. Indeed, when the population deriving from parthenogenesis reaches its maximum density, it induces meiosis in oogenesis (Gilbert 2004), giving rise to haploid males that are able to fertilise the bulk of available haploid eggs, thus determining the formation of diploid, fertilised eggs destined to become resting stages (the so called male-female encounter hypothesis of Serra et al. 2004). Commonly, the resting eggs of marine Rotifera are ovoid (80–150 µm in length) and easily recognisable in the cyst assemblages of bottom sediment (Marcus 1990, Viitasalo & Katajisto 1994, Belmonte et al. 1995) (Figure 5).

Unlike subitaneous eggs, the surface of resting eggs is often sculptured, rough or both (at least in marine species). However, the surface features never assume the shape of long spines. The cyst is spherical and smooth in species found in continental habitats, even those that are hyperhaline (Ricci 2001).

The internal embryo is often seen to be partially detached from one side of the cyst wall. This forms an empty space accounting for up to 25% of the total cyst volume. In freshwater *Brachionus*, when this space is more than 25%, it means that the embryo is not viable (García-Roger et al. 2005). In *Synchaeta* and *Brachionus*, birth occurs through a narrow hole that opens like a door in one of the extremities of the cyst wall (Piscia et al. 2016).

Each female produces only one or two resting eggs, and Rotifera account for only a small number of species in the marine plankton. Consequently, the abundance of resting eggs in sediment cyst assemblages is numerically inferior to that of unicellular organisms and comparable with that of other Metazoa (e.g. Rubino et al. 2013).

Crustacea, Cladocera

Although Cladocera, like Rotifera, account for only a few species in the marine zooplankton, in some cases they are reported in such high numbers (as in the north Adriatic and Baltic seas) that

RESTING CYSTS FROM COASTAL MARINE PLANKTON

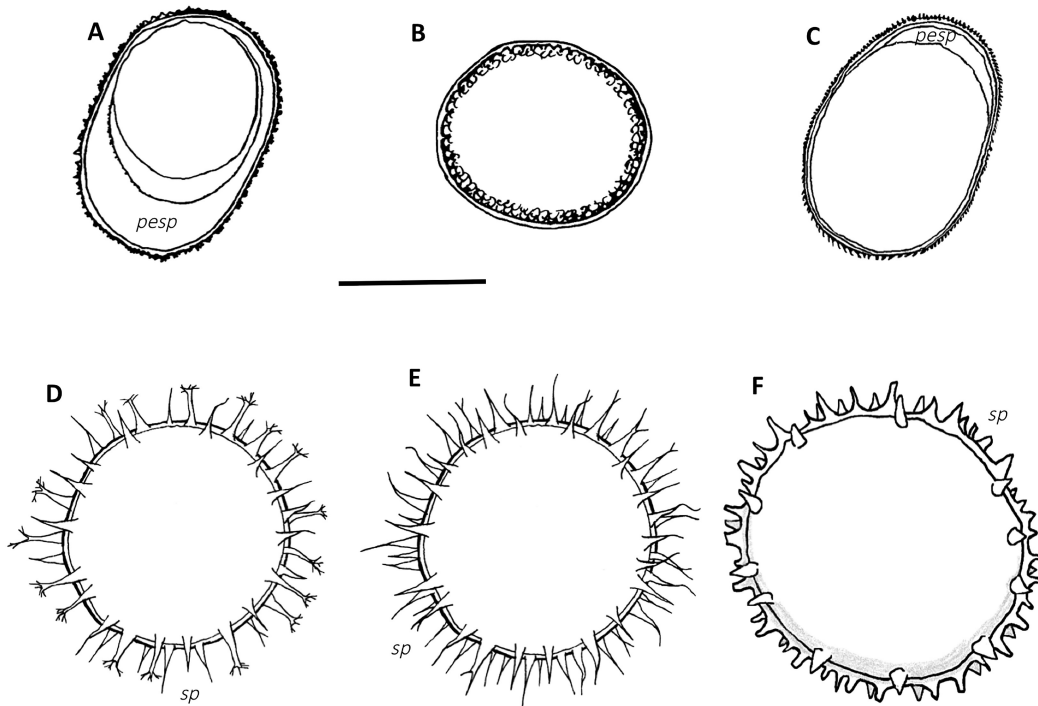


Figure 5 Sketches of resting eggs of planktonic Metazoa (A, B, C = Rotifera; D, E, F = Copepoda Calanoida); (original drawings from authors' cysts collection). (A) *Brachionus* sp.; (B) *Exarthra* sp.; (C) *Synchaeta* sp.; (D), (E) *Acartiidae* spp.; (F) *Pontellidae* sp. Scale bar = 50 μm . (Abbreviations: *pesp*, periembrionic space; *sp*, spines.)

they characterise local communities (Egloff et al. 1997, Guglielmo et al. 2010, Viitasalo 2012). Reproduction is parthenogenetic during most of the year, and each female produces a relatively high number of parthenogenetic eggs (generally incubated in a dorsal chamber named *ephippium*). The appearance of males in the population follows the same pattern as Rotifera and seems to be directly induced by the numerical growth of populations just before the arrival of the unfavourable season (Aleksseev 2007). The fertilised eggs are resting (diapausal) and appear in small numbers (1–2 per female). The appearance of males in the population seems directly connected with the strategy of producing fertilised/diapausal eggs. Indeed, Miyashita et al. (2011) demonstrated that local populations can completely lose their males for years.

In marine Cladocera (8 species in total, belonging to the orders Onychopoda and Ctenopoda), the diapause egg is abandoned in the water column, together with the exuvia of the moulted females or the bodies of the dead ones. Saito & Hattori (2000) described a vertical distribution of the various stages of the marine Cladocera *Podon leuckarti*, with gamogenic females persisting near the bottom, even when the remaining population migrates to subsurface layers during the daytime.

The low number of diapause eggs produced by each female practically corresponds to the egg production rate of Rotifera. However, egg abundance in the sediment assemblages is dependent on the site and the period, with Cladocera being particularly abundant only for short periods and commonly in neritic waters. This leads to a low numerical importance of Cladocera eggs in the sediment of confined environments, although their weight may be important due to their relatively larger size compared to other cyst-producing organisms (average diameter = 150–300 μm).

The diapause eggs of Cladocera are easily distinguishable in the sediment assemblages because they are generally larger than all the other resting eggs (Onbé 1985, 1991). They can be spherical, as in *Evadne* and *Podon*, or ovoid and typically concave on one side, as in *Penilia*. Indeed, such eggs

are the largest ones found in sediment cyst assemblages (Marcus 1990, Viitasalo & Katajisto 1994, Belmonte et al. 1995, Madhupratap et al. 1996).

The eggs may also exhibit calcification of the external layer, which results in a higher sinking rate (Braiko 1966). At the same time, this layer enables them to better resist pressure and/or scraping.

Most of the Cladocera resting eggs have a smooth external wall. In addition, they exhibit a multilayered envelope, which is typically thick. The robust external covering is probably a defence against predators. Indeed, the *Mysis* shrimps of the northern Baltic Sea feed selectively on the eggs of *Bosmina longispina maritima* (contained in an ephippium) and ignore the eggs of *Podon polyphemoides* (not ephippiated), which have a thicker external covering (Viitasalo & Viitasalo 2004, Viitasalo 2007).

Crustacea, Copepoda

Copepoda are the most diverse and abundant Metazoa taxon in the marine mesozooplankton. Many orders contribute to species assemblages in the water column, but those belonging to Calanoida are certainly the most representative and the best adapted to a holoplanktonic life in the sea (Huys & Boxshall 1994). In order to overcome adverse periods, species of the superfamily Calanoidea enter a lethargic phase as juveniles (copepodids I–V), while species of the superfamily Diaptomoidea commonly produce resting eggs (see Mauchline 1998 for a review on the rest of the species among Calanoida).

Sazhina (1968) was the first to report the existence of a marine Calanoida resting egg (with delayed hatching) that was morphologically different (it showed a spiny surface) from the subitaneous ones (with a hatching time of 1–2 days), observed in the life cycle of two species (*Pontella mediterranea* and *Centropages ponticus*) from the Black Sea.

Since that time, the list of marine *Calanoida* species that can produce resting eggs has been repeatedly updated (Uye 1985, Williams-Howze 1997, Engel 2005), and today includes at least 54 species (Suppl. Mat. 4). However, the list contains only coastal species, and they are all phylogenetically cognate (belonging to the same superfamily, Diaptomoidea). This suggests that this life cycle trait favoured the adaptation of Diaptomoidea to coastal environments, where abiotic conditions are more variable than in the open sea.

All freshwater Calanoida species belong to this superfamily, and the presence of a resting stage in their life cycle was proposed as being responsible for the adaptation of this marine taxon to freshwater habitats (Lindley 1992, Belmonte 1998c, but see Belmonte 2018 for a more recent interpretation)

The diapause eggs of Calanoida are generally spherical (diameter, 60–200 μm) and commonly show ornamentations on the surface.

Marine Diaptomoidea differ from freshwater species in that they lay eggs in the water column (they have no ovisacs) (Sazhina 1987), and such eggs inevitably sink to the sea bed. In detail, the sinking rate of smooth eggs is higher than that of spiny eggs. According a normal embryo development time (1–2 days), a smooth egg of *Calanus finmarchicus* hatches after a 40-m sink and the spiny egg of *C. ponticus* after a 8-m sink from the mother position (Sazhina 1987). The spine length on eggs of *Centropages typicus* has been found to be inversely correlated with the water temperature and directly with water density, thus suggesting this retarding role (Gaudy 1971). This allows the hypothesis of spines acting as a device for the egg to impede retard reaching the bottom in coastal areas. At all temperate latitudes (where seasonality is evident), it is common to find that coastal sediments of shallow areas contain Calanoida eggs, and that they are more abundant than on open- and deep-sea beds. In addition, egg abundance in the sediments is often higher than that of active stages in the water column (Uye 1985, Belmonte et al. 1995, Dahms et al. 2006).

Calanoida populations can be very abundant in coastal areas, but it should be noted that only a small portion of the population (adult females) is involved in egg production. Nevertheless, egg production can be high and continuous over many days. Indeed, unlike Rotifera and Cladocera, the number of Calanoida resting eggs in the sediment is higher because it is conditioned by the fact that

fertilised females lay eggs throughout their life span (25–45 days), at a rate that can reach 100 eggs per day in *C. typicus* (Ianora 1998). More commonly, the egg production rate of species in coastal-confined habitats ranges from 0 to 78 eggs per female per day (Belmonte & Pati 2007, Drillet et al. 2008b) independent of whether they are subitaneous or resting. This is enough to make the Calanoida eggs (about 104–106 m⁻² of bottom area) more abundant than those of Rotifera (about 104 m⁻²) and Cladocera (about 103–105 m⁻²) in sediment assemblages (Hairston 1996).

Among some marine Calanoida, the eggs that are genetically programmed to rest (diapause eggs) are sometimes indistinguishable from subitaneous ones, as is commonly the case among freshwater species. Grice & Marcus (1981) suggested that in such cases, resting eggs can be identified only by their typical delayed hatching, which they show even if exposed to suitable conditions. Uye (1985) based the identification of egg types in *Acartia clausi* (which does not have resting eggs morphologically different from subitaneous ones) on this approach. However, Belmonte (1998a), Castro-Longoria Williams (1999) and Castellani & Lucas (2003) detected chorionic structures (tubercles, ridges or both) on apparently smooth resting eggs of neritic Diaptomoidea, albeit only observed by scanning electron microscopy (SEM). In any case, many marine Diaptomoidea produce diapause eggs that are morphologically distinct from the subitaneous ones (e.g. Sazhina 1968, Santella & Ianora 1990, Ianora & Santella 1991, Belmonte 1992, 1997, Belmonte & Puce 1994, Castro-Longoria Williams 1999, Onoué et al. 2004).

In these more common cases, diapause eggs show spines and evident processes on the surface (the chorion). Many species also show evident chorionic processes in some subitaneous eggs of their clutches (Hansen et al. 2010), but generally the diapause eggs are never smooth. In one case, smooth diapause eggs of *Paracartia latisetosa* have been reported among the more common spiny ones by Posi & Belmonte (2011), but the authors demonstrated that this was due to a tendency of some diapause eggs, laid as spiny, to lose their external spiny covering in the environment. Morphological processes on the chorion of subitaneous eggs include small tubercles that are invisible under a compound microscope in the case of *Pteriacartia josephinae* and *Acartia adriatica*, short and tiny spines in *Paracartia latisetosa* and *Acartia tonsa*, long and thin spines in *Acartia italica* and long, thick and branching spines in *C. typicus*. In all these species, however, the general rule is that there are more abundant and robust spines on the chorion of diapause eggs than on subitaneous ones (see Belmonte 1997, and Plate 2)

Subitaneous and diapause eggs do not differ in terms of morphology alone. Wang et al. (2005) noted that the dry weight of subitaneous eggs in *Centropages tenuiremis* was substantially less than that of diapause eggs, as was the lipid, protein and carbohydrate content. The levels of aspartic acid, glutamic acid, glycine, methionine, isoleucine, leucine, norleucine, lysine, ammonium chloride and arginine were significantly higher in diapause eggs than in subitaneous ones.

Belmonte et al. (1997) noted that spines are typical of marine species (being absent in freshwater ones) and suggested that this trait could be an adaptation to marine coastal habitats. First, unlike freshwater species, most marine Diaptomoidea have no ovisacs and lay their eggs individually and directly in the water. Spines on the chorion could have evolved to retard the sinking on the bottom (often hypoxic) water layers commonly found in confined coastal environments (Gaudy 1971, Sazhina 1987). This delay favours the early embryonic development, which needs oxygen, before entering the insensible diapause state. The hypoxic conditions recurring in bottom mud and water of confined environments are not suitable for embryonic development or for egg hatching (Lutz et al. 1992). A delayed sink may allow the spiny eggs to complete early embryonic development and to enter diapause before reaching the anoxic bottom. Here, the resting eggs can wait for the seasonal restoration of oxygen concentrations suitable for hatching. In addition, chorionic spines of diapause eggs can protect the egg surface from scraping by mineral particles in the sediment, enlarge the communication surface between the inside and outside of the egg and probably avoid ingestion and wall damage by predatory species (Belmonte et al. 1997).

As already reported for Ciliophora (Foissner et al. 2007) and some Dinophyceae (Kokinis & Anderson 1995, Mertens et al. 2011), the number and length of spines are not constant, even within the same species. Among Calanoida, there is a continuum of measurements between the minimum

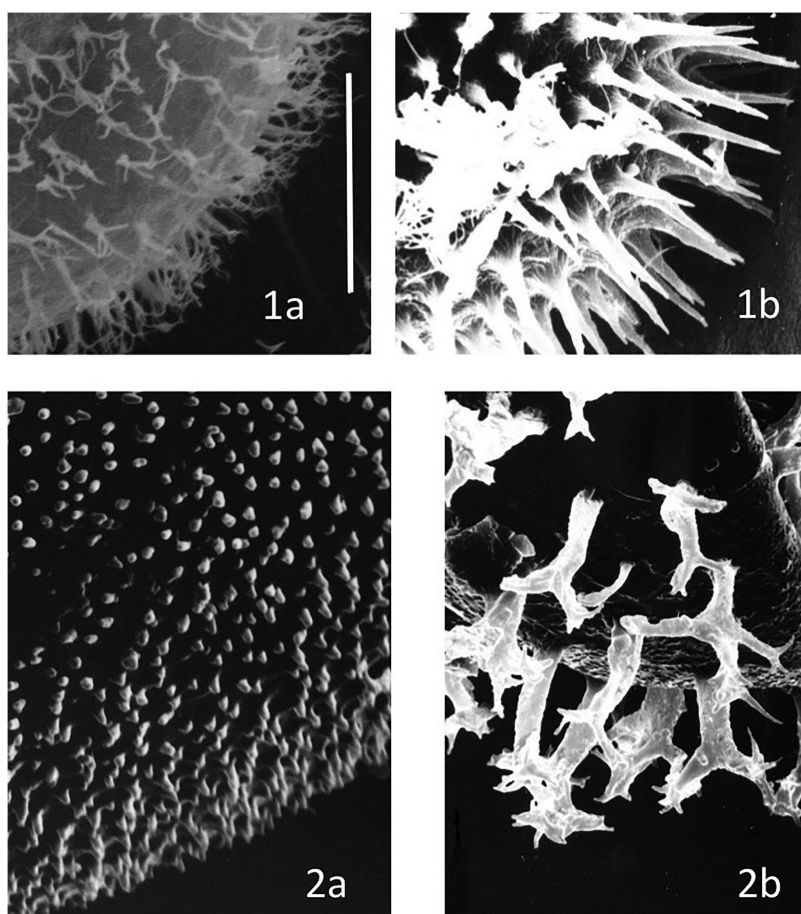


Plate 2 Surface sculptures of Calanoida resting eggs (original photographs, coastal basin of Acquatina, South Adriatic Sea, 2002). (1) *C. ponticus* (a) subitaneous egg; (b) resting egg; (2) *P. josephinae* (a) subitaneous egg; (b) resting egg. Scale bar 20 = μm .

and the maximum extremes, which generally correspond to various development destinies (see Belmonte 1992, Hansen et al. 2010).

Due to the spines, Calanoida eggs in recent marine sediment were initially interpreted by micropalaeontologists as fossil cysts of Dinophyceae, and for this reason, they were reported as ‘hystrichospheres’ (West 1961). The birth of Calanoida nauplii from these cysts (McMinn et al. 1992), however, has definitively resolved this puzzle.

On hatching, Calanoida eggs (both subitaneous and diapausal) open along an equatorial fracture line, producing two hemispherical parts. The fracture of the outer envelope happens as a consequence of enhanced internal hydrostatic pressure and is not due to mechanical action by the organism within, because the nauplius is still enveloped in a thin birth membrane when it exits the egg envelope.

Due to intraspecific morphological variability, it is still difficult to identify what species resting eggs belong to. In fact, some spiny patterns are not as typical as proposed (e.g. Belmonte et al. 1997, Belmonte 1998a,b), but rather vary with each species (or even each clutch), as reported also in other taxa (Mura 1986, Foissner et al. 2007), and appearing as adaptive and even inducible by the environment (Dumont et al. 2002). Spines, however, are never rigid, and Santella & Ianora (1992) demonstrated that they elongate themselves on the chorion surface only after laying eggs.

Methods of collection, identification and investigation

Although plankton cysts were already known from the open ocean (Meunier 1910, Reid 1978), their accumulation in bottom sediments suggests that it is fundamental to consider such a compartment in any study on plankton demographic fluctuations. Reid (1978) reported interesting abundances of cysts in the open sea with the Continuous Plankton Record program, but the low species richness and abundance of specimens allowed him to admit that the large aggregations of cysts in bottom sediments are the result of unknown mechanisms being not explainable by the low number found in the plankton. Among the bottom sediments, those richest are mainly from confined coastal areas, where weak horizontal transport of water masses allows the rapid sedimentation of newly produced resting stages (or the deposition of those transported from elsewhere) towards fine sediment bottoms (see Lindley 1990, Genovesi et al. 2013, as an example). As a general rule, the finer the sediment, the more abundant the cyst assemblages are. This is because in the water column, cysts behave like the finest sediment particles: they are incapable of active movement and tend to settle towards the bottom in weak hydrodynamic conditions (Anderson et al. 1985b). Sinking cysts replenish the cyst bank, ensuring the persistence of the species in the environment (see section “Ecological implications: resurrection ecology” of the present review, for more information). An effective study of the cyst bank of an area, therefore, must take account of the granulometric features of the sediment, possibly with reference to previously conducted surveys, in order to select the best sites to investigate.

Several tools can be used to collect sediment (Figure 6). The choice depends on the aims of the study. Box-corers, multicorers or gravity-corers must be used for taking quantitative samples, limiting the use of grabs to qualitative sampling and germination experiments. In shallow basins, SCUBA diving can be very effective because it enables direct observation of the sea floor, with the

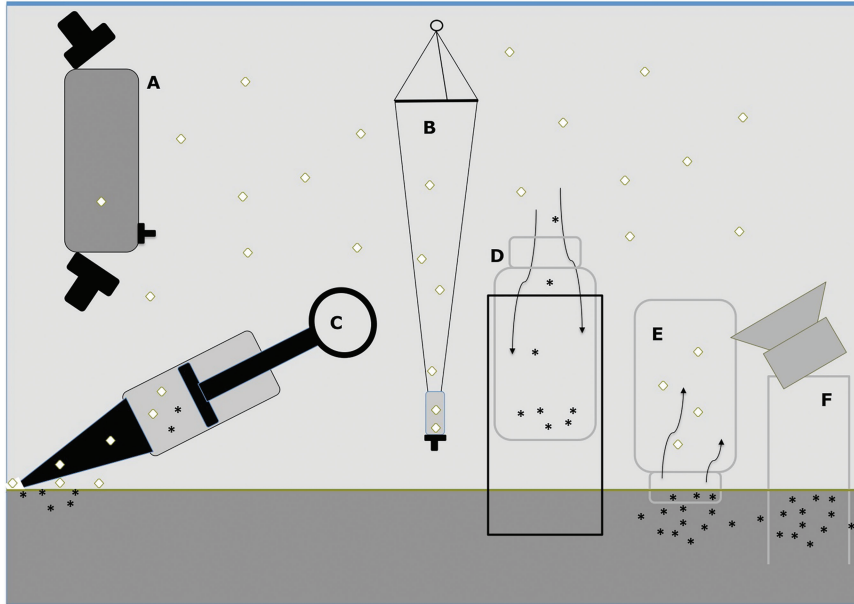


Figure 6 Sampling devices (exemplified) for collection of marine plankton (white rhombi) and their resting stages (black asterisks). Each device is accompanied by (in brackets) the material collected. Marine plankton: (A) Niskin bottle (Phytoplankton); (B) plankton net (Zooplankton). Resting stages: (C) sucking device for sediment-water interface (hyperbenthos); (D) sediment trap (sinking material); (E) inverted traps (hatchlings and organisms leaving the sediment); (F) sediment corer (sediment with resting stages inside). (A) & (B) also collect resting stages in the water column if the collection is carried out during their production.

only consideration being the need to avoid sediment resuspension (Fleeger et al. 1988). Box-corers, multicorers and gravity-corers are obviously needed in the case of deep basins, and hand-corers in shallow basins, in particular for stratigraphic studies. After collection, sediment must be stored at low temperature in the dark until it can be processed in the laboratory, in order to avoid uncontrolled germinations.

A method that helps to minimise the presence of mineral particles, as well as providing an indication of the flow rate of cysts toward the bottom, is the use of sediment traps. These are positioned well below the water surface in order to collect the production of the overlying water column, but well above the bottom, to avoid collecting resuspended material (for an example, see Price & Pospelova 2011).

Concerning the extraction of cysts from sediment, a great variety of methods have been tested, and again, the choice depends on the aims of the study. For example, when detailed information on the structure of the cyst bank is needed, it is better to adopt simple procedures, such as the use of ultrasound to disrupt sediment particles, followed by fractionated filtration to separate the size classes, roughly corresponding to Protista (20–75- μm) and Metazoa (75–200- μm) cysts (see Rubino et al. 2000).

When the study requires high taxonomical resolution, filtration can be combined with density gradient centrifugation (see Bolch 1997 for dinoflagellates; Onbé 1978 for copepods). Lukic et al. (2016) demonstrated that the sugar flotation method has no effect on the hatching success of Cladocera resting eggs. Notwithstanding, any nonvisual extraction of cysts from sediments always leaves the possibility that the final data on cyst concentration has been modified by this method and does not reflect reality. In some cases, chemicals of varying efficacy are used in order to dissolve sediment particles and obtain a clean assemblage of benthic microorganisms and cysts, at least those with organic walls (Matsuoka & Fukuyo 2000). However, the density gradient centrifugation method probably removes cysts from the final sample portion, which is to be analysed, and the use of chemicals can destroy the wall of many cyst types. Acids especially destroy calcareous cysts, but they may reveal the presence of an inner, organic wall. Yamaguchi et al. (1995) showed that Dinophyceae cysts are best identified under epifluorescence microscopy, without density gradient centrifugation, after fixation of natural sediment samples with glutaraldehyde and methanol and subsequent staining with the fluorochrome primuline. Ichinomiya et al. (2004) found that Ciliophora cysts were clearly distinguished by epifluorescence in natural sediment after simple fixation with glutaraldehyde. However, the fixative makes it impossible to investigate cyst germination and is useful solely for the numerical evaluation of cyst assemblages.

Analyses of encysted communities may also be carried out without extracting cysts from the sediment, but instead waiting for them to germinate from sediment that can be incubated as a slurry after sonification and sieving (Lewis et al. 1999, Persson 2001). This method enables the size of the viable fraction of cysts in the sediment to be determined and rare species to be discovered. Quantitative data on the potential for recolonisation of the pelagic compartment by different species (Rubino et al. 2017) may also be obtained.

Methods used to capture newly produced cysts involve the collection of sinking material from the water column. In this case, sediment traps make it possible to estimate the flow rate of cysts sinking towards the sediment over varying time periods. Ning et al. (2008) proposed a Coconut Fibre Mat (CFM) to capture zooplankton resting stages. According to these authors, the method guarantees clean samples of resting stages that are immediately identifiable under a microscope and ready for rearing and hatching purposes.

Given the interest in the ecology of benthic-pelagic coupling, many researchers have used inverted traps, not to collect particles sinking downwards, but to capture hatchlings derived from sediment cyst assemblages (e.g. see Ishikawa et al. 2007 for microalgae; and Naess 1991, Jiang et al. 2004, Engel 2005, and Sichlau et al. 2011 for Calanoida).

Although they do not seek to establish the actual derivation of the nauplii (nauplius dormancy is never considered, and it is assumed that they result from egg hatching in all cases) these methods give an accurate estimate of the rate of naupliar recruitment per time unit. At present, only Harpacticoida and Cyclopoida (among Copepoda) are thought to enter diapause or dormancy as juveniles or nauplii in the sediments. The possibility of Calanoida nauplii slowing or stopping their development due to unfavourable conditions after hatching has not been demonstrated.

Raw analysis of samples, for both qualitative and quantitative purposes, is carried out under conventional light microscopy (i.e. bright-field, differential interference contrast and phase contrast) but polarised light microscopy also has been proposed as being useful in the identification of dinoflagellates (Reid & Boalch 1987). A 200×–320×–400× magnification is commonly used for Protista cysts, and a 100 × magnification is used for Metazoa resting eggs. Confocal laser scanning microscopy (CLSM) and digital optical microscopy (DOM) have been applied to cyst analysis only recently. They allow researchers to better investigate morphological features and provide high quality and high resolution digital images together with 3-D reconstructions of resting stages. Lastly, SEM and TEM provide far more information, although the equipment and analysis costs are high.

Cyst types can also be identified by molecular tools. In a comparative study of morphological and molecular methods, the diversity of marine Ciliophora was found to be higher when using the latter (Doherty et al. 2010). Montero-Pau et al. (2008) declared as easy and inexpensive the DNA extraction from plankton resting stages, with HotSHOT for polymerase chain reaction (PCR) amplification. Lindeque et al. (2013) defined as easy the recognition of morphologically nondistinguishable eggs of Acartiidae in the sediments of Tau Lagoon (France), if based on the description of the common metazoan DNA barcoding gene mtCOI.

In addition, the presence of resting stages in the life cycle of many toxic Dinophyceae species has led to the development of PCR assays, in order to monitor the presence of cysts in the surface sediments of areas impacted by harmful algal blooms (HABs). Erdner et al. (2010) obtained results with this technique that was comparable to those derived from primuline staining, but only for very recent cysts (those present in the first 1–2 cm of sediment). For deeply buried cysts, PCR gave significantly less information about the cyst assemblage. The method remains encouraging, however, because it can simultaneously identify and count cysts, producing a significant time gain.

It should be considered, however, that molecular methods, at present, give a result relative to the diversity of just one gene (e.g. the mtCOI), and this is unlikely to correspond to the species richness of a community because each taxon is expected to show a different degree of variability for the same gene.

In many cases, identification to the species level is possible only by observing the active stage. Moreover, the direct link between active and resting stages is critical for understanding the life cycle of each species. Germination and encystment experiments are useful in order to demonstrate this link and to confirm the identification, whether this is done by observing the cyst or the active stage. In unicellular organisms, the cyst hatches a motile cell that is generally identifiable without waiting for its development. However, a rearing experiment makes it possible to produce cysts from active stages and thus confirm species identification by completing the full life cycle. In the case of Metazoa, with the exception of Rotifera, the resting egg hatches into a motile stage (juvenile or larva, according to the type of postembryonic development), which is not immediately identifiable at the species level. In such cases, identification may require up to 1 month of rearing in the laboratory (as in the case of Calanoida).

On the other hand, single specimens (females) may be reared independently to obtain resting eggs for descriptive purposes. Suitable females can be obtained in any period of the year. If they are gathered in the pre-diapause season, resting eggs can be obtained without stimulation (Belmonte 1992, Belmonte & Pati 2007); otherwise, females can be artificially induced to produce resting eggs by varying the photoperiod, the temperature or the quality and quantity of their food.

In many cases, the search for resting stages has revealed the existence of species never before reported for that site. Orlova et al. (2004) added 15 species to the list of Dinophyceae found along the east Russian coast, simply by isolating and waiting for the germination of cysts collected from the sediment of that area.

Whatever approach is used to ascertain the size of cyst assemblages, water column sample collection should not be neglected. Indeed, species producing resting stages represent a variable percentage of the plankton assemblages (depending on the degree of confinement of the coastal system), but never the totality. In addition, although alternative findings of the same species as both active forms (in the water column) and cysts (in the sediment) in successive seasons are possible, they are rare, and an integrated sampling approach to establishing the species richness of each area is recommended (Moscatello et al. 2004, Rubino et al. 2009).

Rest features

Types of rest

According to Gyllström & Hansson (2004), rest (also known as *dormancy*) encompasses both diapause (stopped development) and quiescence (delayed development). In our opinion, these are the correct terms to use, distinguishing between two aspects of a single phenomenon—that is, dormancy (Figure 7). *Aestivation, hibernation, lethargy* and other similar terms are common; they refer mainly to induced rest, when an unsuitable situation occurs and is adopted in different ways based on the taxa involved. Phytoplanktonologists use the word *dormancy* as a synonym for *diapause* (e.g. Bravo & Figueroa 2014, for Dinophyceae), inheriting it from the terminology used for higher plants (see Baskin & Baskin 1989). The term *diapause*, originally created for insects (Wheeler 1893), could be usefully adopted to refer to all planktonic cyst-producers, including phytoplankters, to indicate a genetically programmed phenomenon, characterised by two periods: insensitive and competent (Mansingh 1971; Grice & Marcus 1981). The former is considered necessary for the completion of physiological maturation (Pfiester & Anderson 1987), and its length is species-specific, varying from hours to months, at least for Dinophyceae. During this time period, the organism does not perceive external stimuli and rests even if external conditions become appropriate for active life. During the second period, the resting organism can awake in the presence of positive external stimuli (Rathaille & Raine 2011).

According to Hallegraeff et al. (1998), there may be two kinds of diapause. A long-term diapause, acting as a true overwintering strategy (dependent on the astronomical date and not on climate) controlled by an endogenous clock, and a short-term rest (not properly diapause), acting as a rapid-response strategy to deal with sudden changes in the environment, allowing the species to shift quickly between pelagic and benthic habitats. The former could be used by species living in deep waters, where cysts must face more constant temperatures and light conditions (Anderson 1998),

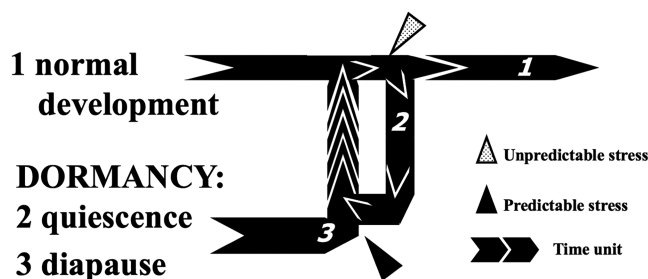


Figure 7 Graphical comparison between quiescence (path 2) and diapause (path 3). Quiescence is a response to a stress situation. Diapause anticipates the occurrence of a stress situation. (Modified from Giangrande et al. 1994.)

while the latter may be more advantageous for neritic strains that need to be able to perceive stimuli in a more competitive way. This is the case of the Dinophyceae species *Alexandrium catenella*, whose mandatory dormancy period ranges from 24 h to months, depending on the water depth and latitude (Hallegraeff et al. 1998, Figueroa et al. 2005, Tobin & Horner 2011).

In contrast, in the case of quiescence, encystment is triggered by exogenous factors—that is, adverse environmental conditions—and the organism's development or some vital functions slow down. Unlike diapause, this state is immediately reversed by the restoration of suitable conditions (see Giangrande et al. 1994, and Figure 7). In this context, each species can undergo a quiescent stage in any moment of its life cycle, while as a general rule, diapause is associated with precise stages (cysts and spores among Protista, and embryonic early stages among the most common planktonic Metazoa) (Alekseev 1990).

Currently, however, a more complex picture is emerging, at least for Bacillariophyceae and Dinophyceae. Indeed, most Bacillariophyceae resting spores are produced asexually (McQuoid & Hobson 1996) and show high respiration rates and photosynthetic activity when suddenly exposed to light after a period spent in the dark (e.g. in the case of resuspension from the sediment and subsequent resinking) (French & Hargraves 1980). In addition, they do not have a mandatory, insensitive resting period (Hargraves & French 1983). On the other hand, among Dinophyceae, there are species that asexually produce true resting stages (Kremp & Parrow 2006) and species that are capable of sexually forming cysts with a short rest (Figueroa et al. 2006), in response to an increase in temperature and shortage of nutrients.

Triggering of rest initiation (encystment)

Many cues can induce dormancy, depending on the season, but the only one common to all cyst-producing groups seems to be day length (i.e. photoperiod) (see Alekseev 1990, 2007 for Crustacea; Kamiyama et al. 1995 for Ciliophora; McQuoid & Hobson 1996 for Bacillariophyceae; Sgrosso et al. 2001 and references therein for Dinophyceae).

Bacillariophyceae enter dormancy under conditions of nutrient depletion, particularly when this concerns nitrogen. However, *Chaetoceros pseudocurvisetus* can form resting spores only if a large amount of silica is available (Kuwata & Takahashi 1990), because these dormant stages have heavily silicified frustules, otherwise a part of the population forms resting cells (Kuwata & Takahashi 1999). *C. anastomosans* requires high salinity (Oku & Katamani 1997).

In cultures, Dinophyceae show very complex interactions involving at least three factors: temperature (for which there may be a narrow optimal window) (Anderson 1998, Ellegaard et al. 1998), day length and nutrient concentration, of which the latter seems to be by far the most important (Sgrosso et al. 2001, Nagai et al. 2004, Kremp et al. 2009). Indeed, in this group of planktonic Protista encystment is normally a consequence of the induction of sexual reproduction (von Dassow & Montresor 2011) and in most species this is triggered by nutrient shortages, normally at the end of maximum asexual reproduction in the water column. Many studies based on laboratory experiments have shown a species-specific response to Nitrogen and/or Phosphorus limitation that includes the production of hypnozygotes (Shikata et al. 2008). Figueroa et al. (2006), in a very fascinating study, demonstrated that Dinophyceae life cycles could be considerably more complex than the oversimplified holoplanktonic scheme classically described in textbooks. The sexually produced planozygotes of *Alexandrium taylorii* can evolve into short-term or long-term cysts or undergo direct division depending on the relative concentrations of nitrates and phosphates in the culture media.

Other exogenous factors may play important roles in the encystment of Dinophyceae, most importantly shifts in temperature (Anderson et al. 1985a), but also salinity (Zonneveld & Susek 2007), oxygen, iron (Doucette et al. 1989), bacteria (Adachi et al. 1999, Mayali et al. 2007), overcrowding and chemical pollution as well (Triki et al. 2017; Rubino et al. 2017). Many studies have focussed on the possible concomitant role of these factors, and the picture is further complicated by evidence of contrasting ecotype behaviours in different environments (e.g. in coastal versus deep oceanic waters)

and at different latitudes (Bravo & Anderson 1994, Ichimi et al. 2001). In any case, according to Figueroa et al. (2011), the reality emerging from field studies could be even more complex than the virtual situation inferred from laboratory cultures. Recently, the use of sediment traps to catch newly produced cysts has allowed the monitoring of cyst production over time. Evidence of continuous encystment, albeit at low densities, by *Alexandrium minutum* (Garcés et al. 2004) suggests that nutrient dynamics is not a major factor inducing dormancy in this species. Moreover, the results of other studies have demonstrated that encystment is favoured by good growth conditions (Olli & Anderson 2002, Figueroa et al. 2005) and, because it occurs at the end of the population bloom (Rengefors 1998), it suggests that it is caused by life-cycle transitions rather than exogenous factors. Kremp et al. (2009) distinguish between triggers (the proximate causes) and stressors (the ultimate causes) of encystment. The former is a signal of the advent of the latter, such as the increase in temperature which heralds the arrival of spring with low nutrient conditions, which, for a coldwater species, represents the unfavourable season. This topic is directly related to the concept of an endogenous clock—that is, a genetically controlled mechanism capable of activating diapause (Boero, 1994; Anderson, 1998).

Among Rotifera Monogononta, overcrowding (which raises the concentration in the water of chemicals produced by the organisms) seems to be just as important as external cues (Gilbert 1974, 1992, 2007). Indeed, the diapause eggs are only the fertilised ones, and sexually active female Rotifera appear in the population only during periods of high concentrations of parthenogenetic generations. In such cases, the production of diapause eggs is sustained by high food availability and allows the mothers to store high lipid content in the eggs. Due to the extremely reduced metabolism of the diapause eggs, lipid storage is clearly an ideal endowment for the hatchlings. This rule is also valid for Copepoda, at least in the case of *Eurytemora affinis*, whose females produce resting eggs in overcrowded conditions (Ban 1994). In Dinophyceae, only the production of temporary cysts (quiescence) in *Scrippsiella acuminata* is reported as due to allelopathic effects (Fistarol et al. 2004; Tillmann & Hansen 2009), while hypnozygotes (diapausal) are produced by *S. acuminata* and *Gyrodinium instrianum*, and temporary cysts by *Heterocapsa circularisquama* as a response to overcrowding (i.e. cell contacts) (Uchida 2001).

Other than single stimuli, synergistic effects have to be considered. Among Crustacea, photoperiod seems to combine its role with that of temperature and overcrowding (Alekseev 1990).

The start of the diapause can be a clearly identifiable moment during the year (as in *Labidocera aestiva*; see Marcus 1982), or it may be characterised by such a high level of variability that a genetic programme should not be considered responsible. In many species of the copepod family Acartiidae, each single female can produce subitaneous and diapause eggs contemporaneously (Onoué et al. 2004, Pati & Belmonte 2007), and females of the same population show oscillations in the relative abundances of the two types of eggs over a relatively long period (e.g. some months).

Even among Rotifera, the message deriving from the number of asexually produced generations may not be completely obeyed by all parthenogenetic females within the same population, although they perceive the same stimuli. These observations suggest that the genetic character of the phenomenon is subjected to high variability to allow the populations to better adjust physiologically to unpredictable environmental variations.

The hostile period can be either in summer or winter, and it depends on the geographical location (Marcus 1979, Uye 1985). Some species are seasonally present only at certain latitudes and present year round at others. At latitudes where the unfavourable season is completely absent, some of these species maintain the ability to produce resting eggs, while other species lose this trait (Marcus 1979, Ohman et al. 1998).

Triggering of germination (excystment)

Given the presence of a period of obligatory dormancy (the refractory phase), diapause in resting eggs should be considered as part of their unchangeable destiny. However they are able to perceive

the moment of their reactivation, which is stimulated by external environmental factors (Kasahara et al. 1974, Uye 1985, Marcus 1987, Alekseev 1990). This sensitivity is activated only after the refractory phase is concluded. From this point of view, there are similarities with quiescence eggs (for terminology differences, see Grice & Marcus 1981), which, in contrast, are not programmed to require a resting period but can rest if unfavourable conditions require it.

In Dinophyceae, the exit from diapause and consequent germination are controlled or regulated by both exogenous and endogenous factors (Tobin & Horner 2011). The latter includes a mandatory dormancy period and the presence of a biological clock (Castell-Perez et al. 1998, Rengefors & Anderson 1998), which is incapable of triggering germination but capable of preventing it during untimely periods (Matrai et al. 2005). Both exogenous and endogenous factors may be related to variables such as their belonging to a particular geographical strain and the depth of the water where the cysts germinate.

Among the exogenous factors acting on germination, temperature and photoperiod seem to be the most important (Itakura & Yamaguchi 2001, Kim et al. 2002), but some uncertainty exists as to the exact nature of their action. Notwithstanding some studies showing contradictory results, many data generally indicate temperature as having the greater impact on germination rate, and temperature and photoperiod as enhancing development once germination succeeds (Kirm et al. 2005, Rathaille & Raine 2011). In polar and subpolar areas, due to low light conditions and sea-bottom temperature, *in situ* cyst beds could represent situations without a future, i.e. cysts have not the possibility to germinate. Richlen et al. (2016) hypothesised that in this case, blooms may be derived from advected populations, originating from nearby fjords and bays.

Raphidophyta and Bacillariophyceae appear to differ from Dinophyceae in this regard, although few field studies are available, and thus any attempt to define a general rule may be premature. Cyst germination in the Raphidophyta *Heterosigma ahashiwo* is strongly controlled by temperature (Shikata et al. 2007), while a photoperiod plays a role in controlling the fate of the inoculum once germinated. Indeed, cysts can germinate in the dark, but the survival of the new active cells greatly decreases. For resting cells of the Bacillariophyceae *Skeletonema costatum* and *Leptocylindrus danicus*, the pattern seems to be the opposite; a photoperiod is the trigger of germination (Hollibaugh et al. 1981, Shikata et al. 2008), while temperature influences the survival of the new planktonic cells (von Stosch & Fecher 1979, Shikata et al. 2008).

Salinity (Kim et al. 2002, McQuoid 2005), oxygen (Keafer et al. 1992, Kirm et al. 2005), nutrients (Binder & Anderson 1987, Figueroa et al. 2005), turbulence (Kremp 2001, Kirm et al. 2005) and bacteria (Adachi et al. 1999) can also play a role in germination in Dinophyceae, but, as seen with encystment, they interact, creating many scenarios for the various species. This picture is similar for the other main plankton groups.

Engel (2005) discussed the role of temperature, photoperiod and dissolved oxygen on the hatching of Calanoida eggs. He found inhibition of hatching in many cases but was never convinced of an effective triggering action, which appeared to be relatively independent of external conditions. Kamiyama et al. (1995) showed a rare example of irradiance being responsible for the germination of Tintinnina cysts. However, this observation needs to consider the not-infrequent case of cysts sinking to a dark bottom or being covered by sediment particles, which makes useless this sensitivity and suggests, as for Calanoida, the existence of an internal trigger independent from external stimuli.

Timing and duration of rest

Given the passivity of diapause eggs, the duration of rest is likely to be determined by the cyst-producing organism (the grandmother among Rotifera and Cladocera, the mother among Copepoda, and the active stage among Protista). Among Metazoa, the maternal role in reactivation automatically derives from the programming of the refractory phase duration. In such cases, external stimuli

merely play an interfering role (e.g. as reactivation inhibitors), which affects but not determines an already-programmed reactivation time (Marcus 1987; Ban 1992; Belmonte & Pati 2007). Marcus (1987) found different diapause durations in eggs produced by co-specific females in different seasons. Ban (1992) was the first to clearly speak of a 'mother effect' in *E. affinis*, finding that ovogenesis of potentially fertile females were affected by temperature and photoperiod when they were still at the nauplius stage.

In *Paracartia latisetosa*, Belmonte & Pati (2007) demonstrated that the mother sets the clock for the duration of diapause in each egg. Diapause eggs obtained in the laboratory from mature females were maintained under constant conditions until hatching. Hence, no temperature or photoperiod variation could affect their diapause termination. Eggs produced in August and December both hatched on average in the same period, thus suggesting that diapause interruption and synchronous hatching could not have been induced by environmental conditions. The environment role is one possibility to prohibit egg hatching at the end of diapause, but the hatching moment remains genetically programmed and independent from external conditions.

Regardless of the season (mainly photoperiod and temperature) or overcrowding that determines the start and duration of diapause, resting eggs hatch at the end of their refractory phase in the presence of adequate oxygen concentration. Calanoida diapause eggs do not hatch in hypoxic environments even if the refractory period has terminated. Furthermore, oxygen seems to be absolutely essential for the complete development of embryos (Lutz et al. 1992, Engel 2005).

Cysts and resting eggs may accumulate on the bottom of water basins where the photoperiod cannot be perceived and where temperature variations may be insignificant. Such sea beds, especially in deep and confined coastal sites, may be periodically hypoxic or anoxic due to the absence of water mixing and photosynthesis (oxygen-producing), at least in some periods of the year. This, as a consequence, can inhibit the resumption of the oxidative metabolism of embryos that are awaking from diapause but have not hatched yet. In this framework, the spiny surface of resting eggs has been considered as useful for the entrance into diapause. Indeed, by delaying egg sinking, the parachute effect determined by the presence of spines could allow each egg to reach the bottom only after the embryo initial development, which needs high oxygen levels. This hypothesis is suggested by a study on Calanoida, where Lutz et al. (1992) demonstrated that low oxygen concentrations (typical of bottom mud in confined areas) during initial embryonic development impede correct entrance into diapause.

In addition to low oxygen concentration, egg hatching can be inhibited by temperature (the case of Cladocera in the Onagawa Bay is described by Komazawa & Endo 2002). However, synchronous hatching can be triggered by external stimuli, as in the case of Cladocera eggs in the Guanabara Bay (Mugrabe et al. 2007), but it can be delayed or staggered (nonsynchronous), also for endogenous reasons (Marcus et al. 1994). This might even be the result of a deliberate strategy by the species, which engineers non-synchronous hatching of the cysts so as to distribute the risk of unsuccessful hatching over time.

Notwithstanding the rest period, the metabolism of Rotifera cysts is not completely depressed, and embryo cells profit from the resting period by repairing damaged portions of DNA, thus obtaining hatchlings with greater fitness than that of the generation they derive from (Ricci & Fontaneto 2009). Tunnacliffe et al. (2005) found that these freshwater Rotifera undergo dehydration/vitrifying by producing small hydrophilic proteins. This type of metabolic vitrifying, however, has not been ascertained in the diapause of marine species, which never leave the water.

Among Crustacea, the metabolism of cysts in the refractory phase is at undetectable levels. This is obtained by deep dehydration of the embryo and/or substitution of water molecules with trealose. Clegg (1997) attributed the phenomenon in *Artemia* to the presence of endocellular chaperon proteins that vitrify the entire molecular apparatus with reversible alterations.

In both Rotifera and Crustacea, the molecules involved are simple, they are not exclusive to particular taxa, and chaperon proteins are a common molecular tool in living organisms.

Passive defence

Generally, the cyst wall is thicker and more resistant than the covering of the corresponding active stage. This is considered sufficient to protect the diapause subject, although Stabili et al. (1999) found lysozimelike and trypsinlike activity on the cyst wall of *Artemia franciscana*, highlighting the existence of passive immunity, as well as mechanical defence, in that particular resting stage. In addition to the physical barrier and the possible immunological defence, the environment could contribute to the preservation of resting stages. A chemically reducing and anoxic environment (such as the muddy bottoms of confined coastal areas), is hostile to the majority of living organisms, thus preventing other species from damaging or preying on cyst assemblages (Persson, 2000), while the chemical aggression of such an environment does not in itself damage cysts.

The resistance capability of resting stages (and the duration of their rest period) has been ascertained in many cases. Pati & Belmonte (2003, 2007) showed that the most common disinfectants (such as those typically used in aquaculture) have only a partial effect on cyst germination in certain species of Dinophyceae, Ciliophora, Rotifera and Crustacea. Raikow et al. (2006) found SEACLEAN® (menadione) to be effective in impeding cyst germination, but the sensitivity of the product to light and its ineffectiveness on cysts buried in the sediment mean that it is still far from being a comprehensive threat.

Due to their generalised resistance, cysts can pass throughout the gut of Metazoa with no consequences for their viability. Cysts and resting eggs have been hatched in the laboratory after passage through the gut of birds (Figuerola & Green 2002), polychaetes (Marcus 1984, Kremp et al. 2003), fishes (Redden & Daborn 1991) and small crustaceans (Montresor et al. 2003, Kuwata & Tsuda 2005).

The survival capacity of cysts in bottom sediment has been evaluated as decades in Copepoda (Marcus et al. 1994, Jiang et al. 2004, Dahms et al. 2006), with some Protista cysts able to hatch after 100 years (Belmonte et al. 1999, Härnström et al. 2011, Ribeiro et al. 2011, Ellegaard et al. 2016) and some freshwater Calanoida eggs after 300 years (Hairston et al. 1995).

Evolutionary implications of rest

As a life-history trait, reproductive plasticity is fundamental for survival in variable environments. The shift from the production of normal to diapause eggs can be considered an indicator of phenotypic plasticity (Giangrande et al. 1994). In a study of 167 Crustacea, Hairston & Càceres (1996) proposed that diapause is more common among species inhabiting variable or temporary environments (such as inland waters) than among species in stable, large environments. Inland, temporary waters have been conquered by primitive Crustacea, whilst more recently evolved ones remain in the open sea. Hairston & Bohonack (1998) considered the production of resting eggs among Calanoida as a key tool in the conquest of inland freshwater. This claim, however, is not consistent with the fact that all the other freshwater Copepoda (Harpacticoida and Cyclopoida) do not appear to have resting eggs but are able to rest during other life-cycle stages (i.e. larva, juvenile, adult). Thus, the resting cyst/egg is not the solution, but the rest capacity per se. Marine Calanoida, also have a rest capacity in a copepodite or adult condition (Baumgartner & Tarrant 2017). In freshwater Crustacea (that have incubating devices as egg sacs and ephippia), the resting capacity may be coupled with a form of parental care as a successful adaptation to freshwater. This character may also be responsible for the general absence of spiny surfaces on freshwater eggs. In fact, resting eggs of Centropagoidea are free laid and spiny in marine and smooth in freshwater (Belmonte, 2018).

Cohen et al. (2009) suggested interpreting the organic walled spiny resting stages of early marine Metazoa—the large ornamented Ediacaran microfossils (LOEM) of about 600 million years ago—as spiny resting stages in their life cycle. They also suggest that this feature is truly primitive and would have been indispensable for survival in the shallow hypoxic seas of the Pre-Cambrian era.

Thus, the fact that many phyla show resting stages with spiny surfaces (Belmonte et al. 1997) may be the result not of evolutionary convergence, but of plesiomorphy, if this feature was widely present and common in early Metazoa. The loss of spines, conversely, might be considered a consequence of the evolution of parental care. In fact, it seems that spiny surfaces are particularly common among the cysts or eggs laid free in the water, and they are not common if cysts are contained in specially developed structures (egg sacs in Calanoida, ephyppia in Cladocera or lorica in Tintinnina), carried by the mother (as in Rotifera) or both. However, this is just a suggestive interpretation that needs confirming opinions of many researchers of different taxa.

Undoubtedly, the loss of spines (or their shortening) could also be due to a general size diminution. Oxygen ($\delta^{18}\text{O}$) enrichment, as well as the climate in general, were suggested by Finkel et al. (2007) to be responsible for an observed reduction in size of fossil phytoplankton and their cysts from the Cenozoic to the present day. The largest median size corresponds to the warm and highly $\delta^{18}\text{O}$ -rich Eocene period, and the smallest sizes to the glacial Pleistocene. In addition to a hypothetical anti-sinking role, the morphological differences detectable among the surface features of modern resting eggs may represent the result of the evolutionary divergence of taxa.

The cyst banks in sediment contain cysts derived from overlapping generations of free-swimming organisms. For this reason, at any one time, cyst banks host a wider genetic diversity than is found in water column communities (Gyllström & Hansson 2004). Cyst banks actually produce a generation overlap which, together with environmental fluctuations, can maintain species coexistence in a different interpretation of the so-called Storage Effect of Chesson & Warner (1981).

Rich cyst banks, together with the existence of an extralong diapause (ELD), increase the resilience of each population and enhance the community variability. ELD opens up genetic flows between generations living at distant times. For this reason, it has been described as a delaying factor in the species' evolutionary process (Hairston & De Stasio 1988). When cysts germinate, they introduce genetic variability comparable to immigration from an external source (the 'evolutionary information from the past' of Templeton & Levin 1979, p. 246). Bohonack et al. (2006) confirmed the idea of delayed evolution and suggested that this could result in higher genetic uniformity across populations in each region.

An ELD of phytoplankton cysts can be a powerful strategy for the permanent residence of a population of a species in a region. Estimated as more than 100 years by Ribeiro et al. (2011), an ELD has been proposed as a possible way that photosynthetic marine communities recovered after the asteroid impact at Chixculub-Yucatan and the resulting period of prolonged darkness that occurred about 65.5 million years ago at the Cretaceous-Tertiary transition.

An ELD is the consequence of both environmental conditions and genetic programming. In basins with variable water volumes (mainly freshwater), Ellner et al. (1999) found that the timing of diapause and success of germination from the cyst bank more strongly affects the plankton population than any selective factor acting directly on the active stages. Càceres & Tessier (2003), studying freshwater species, reported that only a portion of cysts produced every year (from 6% to 50% in *Daphnia*) germinate at the first suitable opportunity. The remaining cysts are dormant for varying lengths of time, allowing the population to take advantage of future scenarios. Even smaller percentages of germination (3.5%) were found by Glippa et al. (2014) in the egg bank of three copepods in the Seine estuary (France). This bet-hedging strategy of variable timing of hatching pays off in habitats where conditions occasionally are so bad that recruitment totally fails from the dormant stage pool (Cohen 1966, Seger & Brockmann 1987, Philippi & Sen 1989). Tarazona et al. (2017) demonstrated empirically the existence of the bet-hedging strategy in resting egg production and hatching of the rotifer *Brachionus plicatilis*. In this recent study, populations experiencing unpredictable environmental variations showed an earlier start to resting egg production and a smaller fraction hatched, in comparison to populations reared under predictable variations.

In this framework, diapause duration may simply represent the average value of a distribution (wide or narrow) of many time values, some of them potentially very far apart. ELD is probably

responsible for decadal survival (Marcus et al. 1994, Dahms et al. 2006, Sichlau et al. 2011), or multicentennial (Hairston et al. 1995) in the case of Calanoida. In any case, the existence of cyst banks and possible successive injections of propagules of the same population is responsible for the adaptive success of ELD (Hairston 1996). The most adapted genotypes (the ones that produce the most cysts) are repeatedly proposed, even in the absence of suitable conditions, as a means of ensuring the survival of active stages and results in the coexistence of many potentially competitive species (Hairston & Fox 2010).

According to Warner and Chesson (1985) the Storage Effect based on resting stages offers a possible explanation for the coexistence of many species in a single aquatic environment, the need for which had already been highlighted by Hutchinson (1961). Interestingly, both the Hutchinson hypothesis (proximity of bottom and sinuosity of lake shorelines) and the random injection of propagules cited by Hairston & Fox (2010) indicate a need to extend the research field to the benthos, to solve the paradoxical coexistence of many species in the plankton.

Any understanding of the mechanisms of adaptation to variable environments (such as confined coastal waters), as well as the correct interpretation of plankton community dynamics, must take account all the biological aspects of benthic-pelagic coupling. For this to be achieved, the traditional compartments separating scientists of plankton from those of the benthos has to be overcome (Boero et al. 1996, 2004).

Ecological implications: resurrection ecology

The presence of plankton species in a resting form in ecological compartments different from the water column and yet sympatric with their own active stages, is fundamental to understanding the dynamics of single populations and that of the whole plankton community.

Bottom sediments seem to be the obvious site for accumulation of cysts from the overlying water column, but in cold seas, cysts could also be trapped in a sympagic habitat of the surface ice. Both the benthic and the sympagic compartments are the object of studies due to the existence of complex autochthonous communities (meiobenthos within sediments, sympagic biota within ice), although the nonactive biological components have been disregarded in the past. Dormant biotic pools should instead represent an essential link between activity seasons and are responsible for biomass and energy transfer between ecological compartments.

In both the meiobenthos and sympagic biota, the attention of researchers in the past has mostly focussed on exclusive or typical taxa (i.e. those that are perfectly adapted to local conditions). Pati et al. (1999), however, found that the abundance of cysts in sediment may be even greater than the active components of the meiofauna and proposed the term *Inactive Temporary Meiobenthos* to refer to this fraction. Such abundant, yet disregarded, organisms allowed Marcus & Boero (1998) to propose the term *Supply-Vertical-Ecology* to refer to the processes and implications of recruitment and biomass transfer, mediated by plankton cysts, between the water column and sediments. Such a term was inspired by the supply-side ecology of Lewin (1986) (see also Underwood & Fairweather 1989). That term was successively replaced with the more impactful *resurrection ecology*, proposed by Kerfoot & Weider (2004) (Figure 8).

Confined coastal areas are able to capture and accumulate large numbers of resting stages in their sediment (Belmonte et al. 1995). Cyst production and accumulation are particularly evident during the abundance peaks of plankton populations. Cyst production is likely a consequence of nutrient subtraction from the water during periods of rapid phytoplankton growth. Peak abundances in the water and sediment, however, are always separated by a time lapse, with cyst peaks delayed by 1–2 months with respect to the active stage (Chen et al. 2009).

It is not entirely clear whether the richness of confined coastal areas derives from the abundance of cyst producers that bloom in these areas, or to an accumulation effect of small particles due to the low hydrodynamism, or even to the lack of benthic predators. In open neritic habitats,

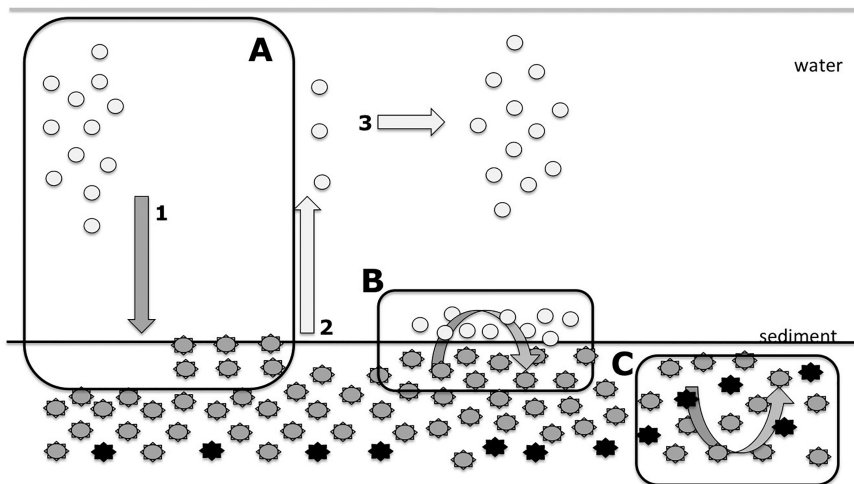


Figure 8 A schematic diagram of the dynamic interactions of resting stages between the water column and sediment cyst bank. (A) possibly long-lasting exchange; (1) supply from the water column (production by plankton); (2) subtraction in favor of water column (germination); (3) multiplication of active stages (potentially producers of resting stages). (B) Tight and fast exchange; supply-removal (encystment-germination) from/to hyperbenthos. (C) Mixing within the bottom cyst bank.

cyst-producing species are present, but this sediment tends to be coarser (i.e. the area is subjected to high hydrodynamism) and have numerically poorer cyst assemblages. In contrast, confined coastal areas, although with a shallower water column and less oxygenated sediments (due to their limited hydrodynamism), show high concentrations of cysts in sediment. This links the cyst abundance to the size of sediment particles.

According to Cohen et al. (2009), the abundance of cysts in confined environments also could be enhanced by the absence of potential predators, which are poorly adapted to hypoxic sediments. Scheef & Marcus (2010, 2011) found an abundance of resting stages in bottom seagrass beds. In such habitats, the low oxygen content, high summer temperature (which enhances the decomposition of organic matter) and low hydrodynamism (the vegetation acts as a drag on water movements) greatly favour cyst accumulation. It should be pointed out that some spatial situations, not properly identifiable as confined (and thus not typically hypoxic), such as the German Bight and Kiel Bay, show rich assemblages of cysts in sediment (Madhupratap et al. 1996, Engel 2005). Moreover, even in sediment that is hypoxic, cyst assemblages are not necessarily abundant.

Modig & Ólafsson (2001) demonstrated that the amphipod *Monoporeia affinis* can rework sulphide sediment and thus reoxygenate them to a depth of 10 mm, thereby playing an indirect role (through oxygenation and bioreworking) in the germination of cysts. *M. affinis* was cited by Albertsson & Leonardsson (2000) as possibly affecting the recruitment of active stages to the water column because its burrowing activity can drive resting eggs deeper into the sediment. More recently, Viitasalo & Viitasalo (2004) and Viitasalo (2007) demonstrated that *Mysida* feed selectively only on certain cyst types, thus possibly affecting plankton composition by differentiated subtraction of propagules. Interestingly, the indicated *Mysida* are planktivorous and probably exploit cyst banks when active stages of their prey are absent from the water column.

In many cases, however, cysts pass through the gut of deposit feeders without consequences for their viability. Marcus (1984) showed that both subitaneous and diapause eggs produced by the copepod *L. aestiva* were capable of surviving passage through the gut of two benthic Polychaeta. Redden & Daborn (1991) even proposed that being preyed upon (with a consequent passage through

the gut) could be a strategy for egg-carrying copepods to enhance their reproductive success at the population level because embryos contained in the egg sac of *Eurytemora herdmanni* are not digested by the fish *Menidia menidia*. Finally, the selective predation of egg-carrying females enhances the likelihood that nonmature females will survive and produce their own clutch of eggs.

Bacillariophyceae resting spores have been found undamaged, and even viable, in faecal pellets of Calanoida (Hargraves & French 1983). It is likely that their highly silicified frustules are indigestible to copepods, which may even avoid them during their filter feeding, selectively preferring active cells (Kuwata & Takahashi 1999, Kuwata & Tsuda 2005). Dinophyceae cysts have repeatedly been found in faecal pellets from Polychaeta and Bivalvia (Ichimi & Montani 2001, Tsujino et al. 2002). Kremp et al. (2003) found that gut passage and pelletisation do not substantially reduce the germination rates of Dinophyceae cysts, and may even enhance them. Montresor et al. (2003) even found that passage through the gut of a copepod functioned as a trigger for hatching of Dinophyceae cysts.

Limicole Polychaeta rework sediment, with substantial implications for the overlying water column, similar to the impact of soil reworkers on seed banks in terrestrial forests (Meysman et al. 2006). For example, Giangrande et al. (2002) found that such Polychaeta rework sediment particles (and Dinophyceae cysts that these authors used in the experiments) down to 7 cm below the sediment surface. This reworking leads to rapid burial of newly arrived cysts, but at the same time allows the uplift of deeply buried cysts to the surface.

This reworking of the sediment can also be produced by human activities. Although this field has not been extensively studied, some data (Giannakourou et al. 2005, Siokou-Frangou et al. 2005) suggest that trawling causes the resuspension (and consequently germination) of cysts in the Gulf of Thermaikos. This aspect of the interaction between fishery and cyst banks not only involves resuspension and possible germination of cysts, but also their damage (e.g. the reduction of their germination rate), as demonstrated by Drillet et al. (2014).

Whatever the destiny of cysts in the superficial sediment layer (whether or not they are digested by a cyst consumer), the mechanisms of their subtraction (e.g. germination) are responsible for the characteristic vertical profile of their abundance in the sediment column. Indeed, abundance peaks are typically found just below the most superficial layer (Hairston & Fox 2010, Sichlau et al. 2011). Some findings of abundance peaks at the sediment surface, on the contrary (Dahms et al. 2006), can easily be attributed to a proxy period/episode of massive production from the plankton. In any case, the top layer of sediment is what is most relevant to encystment/germination dynamics, showing strong fluctuations in cyst abundance according to the season (Rubino et al. 2016).

Resurrection ecology is at the basis of the functioning of confined environments (sensu Guelorget & Perthuisot 1992). Although such environments are known to be the most productive on the planet (Odum 1971), for a long time they were believed to depend on marine vivification (sensu Sacchi 1985) for the restoration of biological communities seasonally suppressed by environmental stress. The marine vivification hypothesis assumed the colonisation of a highly productive, although stressed, area from a less productive one, whose biota is not biologically adapted to habitats with such high availability of resources, although periodically stressed.

Today, Resurrection Ecology may explain the reappearance of species in accordance with the seasons; that for many species, they do not depend on neighboring environments (supply=side ecology) but mainly on the bottom sediments of a confined area where they spent the adverse season. Resurrection ecology in confined areas is a typical example of ecological resilience. The plankton of confined environments appear to be autochthonous, and the presence of similar species in neighboring neritic areas is now believed to be the consequence of the export of a species from the assemblages of a confined area, the exact opposite of what was thought some time ago (Figure 9).

The export of cysts from production areas involves other marine habitats as well. In fact, cysts have been detected in deep-sea sediment (Dale & Dale 1992) or captured by deep sediment traps (Rynearson et al. 2013), and studies have even proposed a role for cysts via coastal-deep sea connections. Della Tommasa et al. (2004) showed that cysts, mainly produced by coastal species,

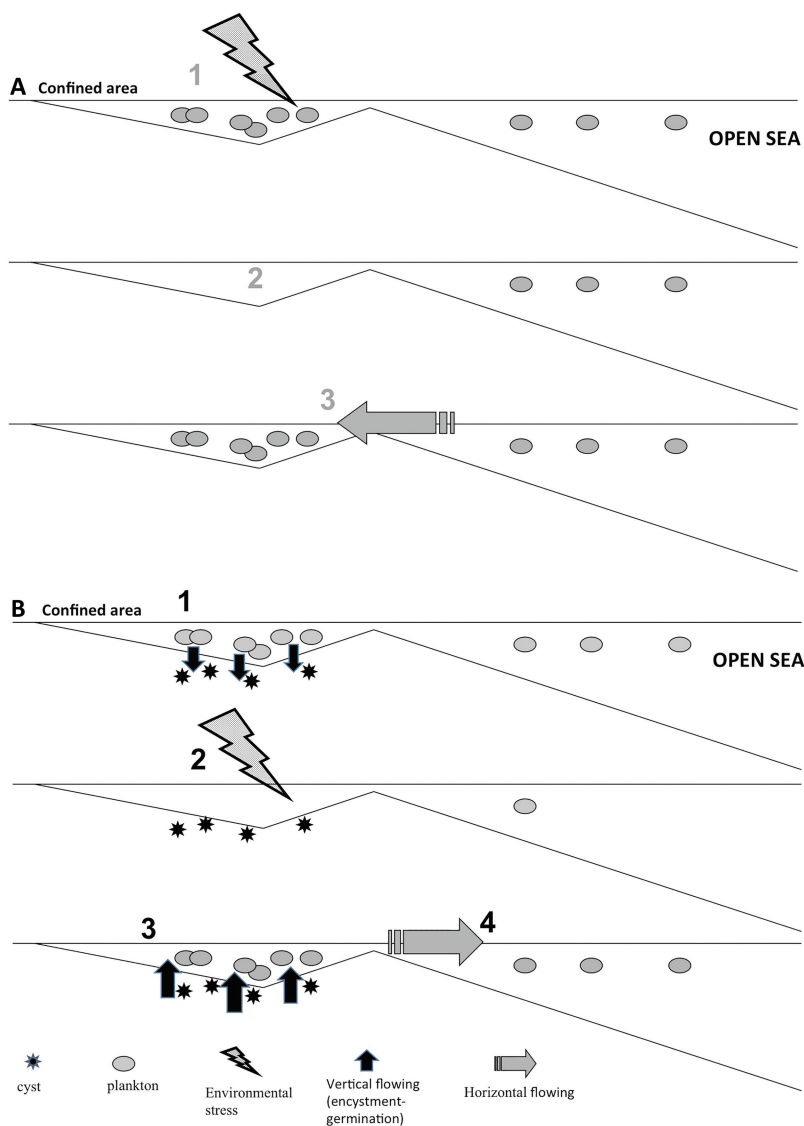


Figure 9 (A) The marine vivification theory elaborated for coastal confined environments: for the restarting of confined plankton communities. (1) occurrence of harsh environmental conditions; (2) disappearance of a confined plankton community; (3) restoration of the confined plankton community by recruitment from the adjacent sea. (B) The resurrection ecology theory for the restarting of confined plankton communities. (1) production of cysts before the occurrence of harsh environmental conditions; (2) occurrence of harsh conditions after the disappearing of confined plankton community from the water column; (3) restoration of the confined community by the sediment cyst bank; (4) spill over and export of propagules and biomass in the adjacent open sea.

accumulate in deep-sea sediment off the mouth of the Foix canyon (Spain), and suggested that such bottom morphologies play a role in the ecology of coastal areas. In fact, during the periodical upwelling of deep-sea waters which at times occurs in such canyons, cysts deposited in the deep sea may be redistributed to the marine neritic areas from which they originally came.

In the last 20 years, scientists have suggested that ice habitats also provide a biological reservoir for the plankton community in cold seas (Gradinger 1999, Brierley & Thomas 2002). The trapped

plankton organisms, both as a planktonic stage and cysts, may remain dormant in the ice during the adverse season and repopulate the water column when the ice melts. Although scientists admit the data need confirmation, they consider the biodiversity found as sufficient to hypothesise that cysts provide an injection to initiate plankton blooms at the start of each ice-melting season. Gradingier (1999) also reported: ‘In some cores (e.g. Station 204 of ARK 10/1) cysts of unknown origin, which were not attributed to either diatoms or flagellates, contributed a high proportion of the algal abundance’.

The overwintering of plankton species within ice is an admitted possibility (see Horner 1985, for a review of sea-ice communities) and Heikkilä et al. (2016) propose the rich number of cysts collected by their sediment traps as coming (at least partly) from the melt-mediated release of sea ice-dweller cysts to the water column in Hudson Bay. Further research is needed to clarify where the rich assemblages of sympagic benthic species originate, when the sympagic assemblages appear in the ice formation and where the organisms go when the ice melts.

Taxa potentially able to produce cysts are well represented in the sea-ice biota, and together with taxa found in that habitat, some papers (Buck et al. 1992, Ikavalko & Thomsen 1997, Gradingier 1999, Ikavalko 2001) list unspecified cysts. Other studies (Garrison & Buck 1989, Schnack-Schiel et al. 2001, Meiers et al. 2002, Ikavalko et al. 2004) have recognised planktonic taxa in the sea ice biota, and Friedrich & De Smet (2000) have reported the production of cysts, but before the melting period, by species commonly active in the ice during the winter. The extreme conditions present within the ice during the long-lasting polar winters (low temperature, low light or complete darkness and high salt concentration in liquid water segregated in ice crevices) suggest the suitability of a resting strategy for at least generalist species (Thomas & Dieckmann 2002, Werner et al. 2007). However, again, little attention has yet been paid to this particular aspect of polar sea ecology.

The sea-ice biota is a peculiar compartment where planktonic species, trapped during the autumn in the forming ice, may have evolved the possibility of producing cysts to survive the extreme winter conditions. Conversely, it may be that specialised ice species survive in the sympagic biota and produce cysts after the ice melts to wait for the formation of a new ice cover (Ratkova & Wassmann 2005). In any case, the presence of cysts could allow the immediate restoration of planktonic communities when favourable conditions return (Figure 10).

As with terrestrial forest seed banks, in order to make a decisive contribution to our understanding of plankton functioning in coastal areas, the ecology of marine cyst banks must evaluate input

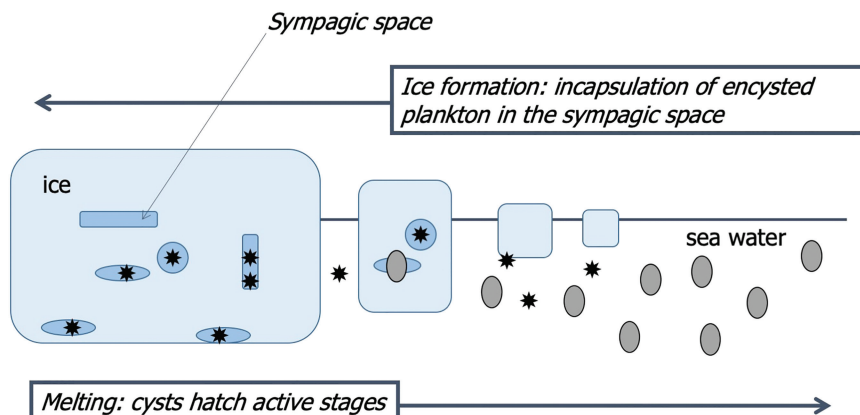


Figure 10 Resurrection ecology applied to sea ice. At the beginning of winter, plankton produce cysts that do not sink to the bottom, but rather are entrapped in sympagic spaces within the ice as it forms. As the season warms from spring, melting of the ice frees resting stages that germinate, restarting the plankton community.

(fecundity/fertility, import), storage (short and long term) and subtraction (death, predation, recruitment, export) for each of the species involved. Persson & Rosenberg (2003) demonstrated that the relative abundance of a cyst type is affected by the composition of the predator community that feeds on cysts in sediment. If the whole community is considered, such grazing mortality is likely to affect the size and viability of a seeded plankton community (Persson 2000). Kamiyama (2013) suggested that the existence of short resting periods (e.g. in Tintinnina) might be responsible for reduced numbers of cysts in sediment of species that are abundant in the plankton. Broman et al. (2015) called for a consideration of cyst germination within the context of the carbon biological pump, which until now has been focussed on pelagic-benthic fluxes and does not take into account any back flow from sediment to the water column.

Viitasalo (2007) examined the complex network of interactions which could play a role in the population dynamics of the cladoceran *Bosmina longispina maritima* in Baltic Sea plankton. The polychaete *Marenzelleria* sp. is believed to be responsible for the upward transfer of deeply buried ephippia in the sediments. In contrast, the amphipod *M. affinis* and the bivalve *Macoma baltica* may be responsible for their transfer downwards in the sediment. Upward transfer (carried out by the polychaete) exposes the ephippia to predation by the mysidacean *Mysis mixta* (which cannot prey on ephippia buried under 1 cm of sediment). The bivalve probably ingests part of the ephippia that it moves. Hence, the bivalve and the amphipod subtract recruits from the plankton and/or preys for the mysidacean. This framework (even when based on only four actors) clearly demonstrates the complexity of interactions in the sediment cyst assemblage, which represents a real challenge for marine plankton ecologists.

Biogeographic implications

According to Fenchel (1993, p. 375), 'smaller organisms tend to have wider or even cosmopolitan distributions, a higher efficiency of dispersal, a lower rate of allopatric speciation, and lower rates of local and global extinction than do larger organisms'. Wilkinson (2001) confirmed that organisms smaller than 150 μm are generally cosmopolitan because their low body mass facilitates aerial dispersal. Finlay (2002) attributed this lack of biogeographical separation to the large number of individuals. A high percentage of microorganisms in a natural system are inactive (from 20% to 80%, according to Lennon & Jones 2011), and dispersal of dormant stages may contribute to the apparent cosmopolitan distributions of taxa. Among freshwater Protista and small Metazoa at least, the capability to produce resting stages facilitates dispersal by air, dust and migrating animals (but see the critical review of Foissner 2006). However, the low species richness that should derive from this situation contradicts May's (1986) rule, which posits the existence of a higher number of small species than large ones.

Modern methodological approaches such as molecular biology and genetics have shown that the number of ubiquitous species is smaller than usually thought, even among smaller species (see Ricci & Fontaneto 2009, for Rotifera). This, however, cannot exclude the large dispersal potential that resting stages give to species. Although endemics have been recorded among marine Protista (see Taylor & Pollinger 1987, for Dinophyceae), it is presumed as obvious that while biogeographical limits generally affect large organisms, they do not apply to microorganisms.

Although sceptical of the cosmopolitanism of microorganisms, Foissner (2006) admits that the geographical distribution of Protista species is in any case broader than that of multicellular organisms. The presence of cysts, in this framework, both enables and enhances the dispersal capacity of species.

The ability to avoid being affected by adverse conditions automatically allows cysts to pass barriers that are both geographical and ecological for the active stages. The composition of the cyst wall and the physiology of the encysted organisms, still poorly understood, may be closely connected to the species' geographical distribution (Foissner 1997, Foissner et al. 2002).

The possibility of seed transfers between separate water bodies by passive transport in the gut of fishes swallowed by migrating water birds was proposed by Darwin (in Reznick 2011, p. 334) to explain the wide distribution of freshwater organisms. More recently, Figuerola & Green (2002) reported the possibility that cysts could also be exchanged between different environments in birds' guts. Indeed, the digestive enzymes of birds were found to affect neither the viability nor the hatching of cysts.

This framework has yet to be verified for marine environments, where birds cannot play the same role as in brackish waters or flooded plains. However, as already mentioned, benthic detritivores as well as fishes can be vectors of plankton species whose cysts are resistant to digestion and can survive in the gut of a fish for days before being expelled in faeces.

Flinkman et al. (1994) found similar hatching success for *Eurytemora* eggs taken from the faeces of Baltic herring. Indeed, the vulnerability of ovisac-bearing females probably reduces the chances of immature females being preyed upon and, as already reported, Kremp et al. (2003) demonstrated that passage through a polychaete gut actually ameliorates the hatching rate of resting eggs.

All these cases demonstrate that cysts can be transported long distances from their deposition site in the gut of vagile, or even swimming organisms. The shape of the resulting dispersal kernel depends on the mobility of the swallowing animal, its behaviour (migratory or sedentary), the time spent by cysts in its gut and its own trophic destiny—that is, whether it becomes the prey of other species. Consequently, cyst distributions in space are the result of a complex set of linked processes.

Being inactive, cysts simply sink to the bottom sediment when produced. Once there, they may be transferred up and down within the sediment as a consequence of the actions of limivorous organisms, leading either to their subtraction from or their injection into bottom water currents (Meysman et al. 2006).

The sculptures on the surface of the majority of marine cysts have been interpreted as being useful for many purposes (Belmonte et al. 1997). One of these is possibly to favour their attachment to floating or moving objects. This form of dispersal may account for the geographic distribution of species, including their appearance in previously unreported sites. If an extra long diapause (ELD) is added to the framework of geographic distribution, it is not obvious that a new record in an area corresponds to a nonindigenous species (NIS). In fact, the newly appearing species might derive from the germination of ELD cysts, thereby introducing a species from a different time (the past), but from the same site. In any case, although the possibility cannot be excluded, the majority of NISs in the world today are attributed to dispersion via human vectors, such as in the ballast waters of ships navigating between continents. The latter mechanism is believed to have been responsible for about 400 NISs present today along the marine coasts of the United States (Ruiz et al. 1997), and about 4000 NISs (most of them planktonic) have been dispersed throughout the world in this way (Carlton & Geller 1993; Ruiz et al. 2000).

As cysts, the majority of these stowaways survive the adversity of a long period in the ballast tanks, where they accumulate in the bottom sediments and rest for long periods (Bailey et al. 2003; Wonham et al. 2005). Although a true ecological community of active stages has been described as functioning in such tanks during the period of navigation (Galil & Hulsemann 1997), cysts represent the best way to travel. Ballast waters are the most extensively studied and verified of these vectors, partly due to the fear that toxic organisms may be transferred this way (e.g. Lacasse et al. 2013) and the ecological risks connected to the new arrivals (e.g. Seebens et al. 2013).

The dispersal of mesozooplankton species in accordance with the abovementioned mechanisms is still limited in comparison to the huge knowledge that is available for freshwater habitats. According to Bollens et al. (2002), (relative to coastal brackish waters), current knowledge about marine mesozooplankton dispersal is based on about 100 papers, referring to 32 species worldwide.

Data from Hallegraeff and Bolch (1992) suggested that such worldwide circulation might damage local biodiversity, in addition to distributing species that contain toxins. Hallegraeff (1998) advised aquaculture farmers to avoid establishing their farms near the ballast water charge-discharge sites

of oceanic ships. Only recently have attempts been made to conduct research on biocides that can be applied to resting stages contained in ballast waters or their residue (Raikow et al. 2006, Fahnenstiel et al. 2009). Considering that ballast waters are responsible even for transcontinental transfer, they represent for marine biogeography what birds represent for wetlands biogeography.

When new species are recorded in ports, it is highly likely that they arrived with ships. The calanoid *Paracartia grani*, well known from the North Atlantic, was first reported in the Mediterranean in the port of Malaga in the late twentieth century (Rodrigues & Vives 1984). Subsequent reports of the species (Lakkis & Zeidane 1990), in other Mediterranean ports, were associated with its capacity to produce resting eggs (Guerrero & Rodrigues 1998), supporting the hypothesis of dispersal via ships (Belmonte & Potenza 2001).

Navigation also seems to be the cause of dispersal for species living in apparently isolated habitats. The cladoceran *Podon polyphemoides* and the calanoid *Acartia clausi* have been reported in the Caspian Sea (an enclosed sea) since 1957 and 1984, respectively. Their arrival in that sea has been attributed to its navigable connection, via the Volga-Don canal, with the Azov-Black Sea system (Zaitsev & Ozturk 2001).

Navigation via the Volga-Don-Neva has also been definitively accepted as responsible for the transfer of fauna from the Ponto-Caspian system (Black, Azov and Caspian Seas) to the Baltic Sea along a “trans-Sarmatian route”, now believed to be an important channel of geographic dispersal. Although some species that have recently invaded the Baltic Sea from the Caspian (such as the cladoceran *Cercopagis pengoi*, first reported in the Baltic by Leppäkoski & Olenin 2000) are known to be highly tolerant of the fresh waters of rivers, they appear to have crossed the Sarmatian plain and invaded the Baltic Sea only recently. The construction of canals and the beginning of their navigation provides the best explanation for the recent northward dispersal of many species.

The Sarmatian route is not only a conduit for northward dispersal. In the case of the calanoid *A. tonsa*, southward dispersal has been recorded, apparently bucking the current climate change trend, which is expected to drive species poleward. *A. tonsa* was first reported in the Baltic Sea by Smirnov (1935), just a few years after it was first recorded in European Atlantic waters (Remy 1927 in Brylinski 1981). The species was reported in the Mediterranean basin more than 50 years later (Gaudy & Viñas 1985, Farabegoli et al. 1989), and in the Black Sea later still (Belmonte et al. 1994), allowing Belmonte & Potenza (2001) to hypothesise penetration through the Gibraltar Strait. Recently, however, it was ascertained that samples from the Black Sea studied by Belmonte et al. (1994) were taken in 1976 (see Zaitsev & Ozturk 2001, p. 89–94); hence, the species was already in the Black Sea before its appearance in the Mediterranean Sea. Although its arrival in the Bay of Sevastopol (the Crimea and Black Sea) could be attributed to any incoming ship, the Sarmatian route, direct from the Baltic, is also a possibility.

Hence, the river connection over the Sarmatian plain carries species in both directions, towards either the Baltic or the Black-Caspian basins. Although noncyst producing organisms (such as the ctenophoran *Mnemiopsis leydi*) also use this route, the resting eggs of *C. pengoi* and *A. tonsa* better enable them to survive the adverse conditions that they face along this 1000-km river journey.

Plankton cysts and humans

Resting stages are used as feed in aquaculture, partly because they lend themselves to transport and storage. Both *Artemia* (Anostraca) and *Brachionus* (Rotifera) cysts are widely used by specialised rearing enterprises, although the hatchlings of the former are too large and those of the latter are too small for some specific developmental stages of fish. Thus, Calanoida nauplii have been proposed as a living food of intermediate size (Støttrup 2000), and the use of potentially storable resting eggs has been explored (Marcus & Murray 2001), including attempts to obtain them on an industrial scale (Murray & Marcus 2002, Jo & Marcus 2004, Sedlacek & Marcus 2005). At the same time, there also have been attempts to harvest and store eggs laid spontaneously by copepods

in nature. Calanoida nauplii have the advantage of having high nutritional content, in addition to their intermediate size (between that of Rotifera and Anostraca hatchlings). Drillet et al. (2006) demonstrated that the subitaneous eggs of *A. tonsa* can remain quiescent if stored cold (2°–3°C), without severe effects on the viability of hatchlings even after 11 months. Cold storage, however, is not useful for all geographical populations of the species and can be ameliorated with chemicals such as antibiotics (Drillet et al. 2007, 2008a).

In addition, the generally high tolerance of cysts to chemicals (as demonstrated by Pati & Belmonte 2003, 2007) allows the use of disinfectants that both ameliorate cyst-hatching success and prevent the transfer of pathogens to rearing pools by means of the living food supply. *Brachionus* cysts maintain their hatchability even after lyophilisation (i.e. freeze-drying) and canning at various atmospheric pressures, a procedure that has been considered as effectively guarding against microbial attack (Balompapueng et al. 1997).

The same resistance of cysts to disinfectants must also be taken into account in treatments of aquaculture tanks or ponds after algal blooms. The disinfectant concentrations, exposure times used or both may not succeed in eliminating undesirable or toxic microalgae, with an impact on production in terms of both quality and quantity.

The attention received by cysts from the aquaculture community is probably the maximum level of voluntary human interaction with plankton resting stages. A review by Drillet et al. (2011) lists a series of aspects (production methodology upgrading, conservation and shipping and commercialisation strategy) to be taken into account, which insert the cysts problem into a human economic dimension.

The toxicity of some cyst-producing species poses a contamination risk not only for aquaculture species, but also for water and food used by humans. Indeed, many toxic organisms can be reactivated by resuspension processes (e.g. port-dredging activities), potentially contaminating the trophic chain up to the final human consumers. In this respect, the trawl fishery has already been shown to actively resuspend cysts from the sea bed (Siokou-Frangou et al. 2005), and infrequent nonroutine dredging of ports (i.e. carried out after many years) may be responsible for a large resuspension of cysts (Belmonte et al. 1995). It has been demonstrated that aquaculture farms set up in bays may negatively affect the survival of sediment cyst banks (Wang et al. 2016). This study suggested that fish and shellfish mariculture may be responsible for a reduction in the numbers and hatching success of resting eggs.

Among the involuntary consequences of human activities, ballast water release from shipping in geographically distant ports has been recognised as a major factor in the transport of NISs around the world. Such introductions lead to ecological imbalances, and potentially to the introduction of harmful algae and the development of toxic planktonic blooms.

Sanitary aspects of mariculture represent an important element in the frame of resting stage–human interactions.

HABs are produced by many species that can produce cysts (Bacillariophyceae, Dinophyceae, Haptophyta and Raphidophyta), inhabiting coastal areas where they cause harm to humans and other organisms (Faust & Gullede 2002, Hallegraeff et al. 2003). HABs have a direct impact on human health, with negative influences on human wellbeing and the economy (with consequences to fisheries, tourism and recreation) (Falconer 1993). Anthropogenic pressures in coastal areas possibly favour HABs, and their impacts on human life is becoming a more pressing public health issue (Berdalet et al. 2015, and references therein). Humans may be influencing algal blooms by increasing nutrient availability via runoff, sewage, fertilisers, microclimate change, remixing of coastal sediments or merely by infecting new areas by transferring new species (as resting stages) from infected areas by a ship's ballast waters. Marine biotoxins produced by HABs can accumulate in marine animals (molluscs and fish) that can enter into the human diet. HAB toxins are distinguished in water- and fat-soluble molecules, all showing acute toxicity, but still little knowledge is available about the consequences of chronic exposition. Symptoms for humans may vary from minor to severe

gastrointestinal intoxication to neurological disorders. Monitoring of HAB species should be regularly implemented and include assessments of the viability and size of cyst banks, in order to obtain more reliable estimates of potential impacts from HAB (Visciano et al. 2016, and references therein).

Perspectives and challenges

Not all plankton groups, even in highly variable environments, produce encysted and/or recognisable resting stages, and hence this trait cannot be considered as the only mechanism that protects species against environmental change. Consequently, a cyst-based strategy to survive unfavourable periods is part of a general framework of species and community dynamics, with different strategies for each site or species.

The strategy used by many seasonal species or groups is still not known, although this may simply mean that resting stages have yet to be discovered, as suggested by the recent impressive increase of knowledge registered for dinoflagellate life cycles. On the other hand, species that are dormant as larvae or juveniles deserve to be considered in this framework. Notwithstanding the growing interest in resting stages in coastal habitats, there is little understanding of the rest in species that do not produce specialised cysts or resting eggs. Not all recorded resting stages are easily assignable to a taxon, and much effort is still required to resolve this simple descriptive question of who is who.

Cyst production and settling involves conspicuous biomass transfer from the water column to the benthos, and yet the potential consumers of this resource are still largely unknown. *Mysis relicta*, in the Baltic Sea, has been identified as one such consumer, but whether a species guild based mainly on this energy supply exists in the benthos—or indeed, whether such a guild is even possible—is unknown. The research is made more difficult by the proven ability of cysts to pass through the gut of animals without consequence. Hence, it is insufficient to identify who eats the cysts; who actually uses them as an energy source for their own metabolism must be found as well. This is of paramount importance for the ecology of coastal environments because the population dynamics of plankton may depend partially or totally on such benthic predators.

A suggestion that has emerged from the studies conducted over the last 25 years (still awaiting definitive confirmation) is that the abundance of cyst bank assemblages is directly correlated with the instability of the environment. Indeed, in such environments, the investment of species in the future may be higher. In stressed situations, species could be induced to invest more in the long-term future by means of diapause and a bet-hedging strategy (as in seed banks) than in creating the next generation. In temporary waters, species that produce cysts to rest and not to hatch immediately are common. Such species (including Anostraca, Cladocera and Calanoida) produce just one generation per year. The difficulty of obtaining larvae from eggs of the previous generation is responsible in part (if at all) for the population in the following year.

Most cysts are designed to ‘travel in time’, each clutch hatching in small percentages every year for many years. This is consistent with the general impression of the numerical predominance of cysts over active stages in the species of very temporary environments, but studies explicitly concerned with this topic are still rare.

One of the most interesting issues that deserve attention is sediment dating. Although some work has already been done, it is evident that dating of layered sediments, coupled with a knowledge of species that produce cysts and their biology, is a powerful tool in the reconstruction of the history of plankton communities. In the present period of global climate change, this has importance to what constitutes change, and what is the effect of long-term resilience.

Sediments are not the only place where cysts may be found. Sea ice may also act as an important cyst reservoir, which plays a fundamental role in the reappearance of polar plankton at the return of sunlight to polar areas. It is still to be ascertained if cysts can be trapped in the surface film in the open sea, from which currents and wind may disperse them in any direction, not only within polar latitudes.

Finally, there is a pressing need for a unification of the terminology used to describe and measure various cysts and eggs. Methods need to be shared, and an integrated approach adopted for the study of dormant resting cysts and eggs that is relevant to studies of the plankton and benthos, but also sedimentology, palaeontology, microbiology, environmental chemistry and marine coastal management.

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Supplementary Material 1

List of modern species of planktonic marine Bacillariophyceae producing resting stages.

Modern taxon	Type	References
<i>Actinocyclus curvatulus</i> Janisch (1878)	RS	Piredda et al. (2017)
<i>Actinoptychus senarius</i> (Ehrenberg 1838) Ehrenberg (1843)	RC	Ishii et al. (2012)
<i>Amphora coffeaeformis</i> (Agardh) Kützing	RC	Anderson (1975, 1976); McQuoid & Hobson (1996)
<i>Arcocellulus mammifer</i> Hasle, von Stosch & Syvertsen (1983)	RS	Piredda et al. (2017)
<i>Asterionellopsis glacialis</i> (Castracane 1886) Round (1990)	RS	Montresor et al. (2013)
<i>Bacteriastrum delicatulum</i> Cleve (1897)	RS	Hargraves (1976); McQuoid & Hobson (1996)
<i>Bacteriastrum furcatum</i> Shadbolt (1854)	RS	Karsten (1905); McQuoid & Hobson (1996)
<i>Bacteriastrum hyalinum</i> Lauder	RS	von Stosch & Fecher (1979); McQuoid & Hobson (1996); Bosak et al. (2015a)
<i>Bacteriosira bathyomphala</i> (Cleve 1883) Syvertsen & Hasle (1993)	RS	McQuoid & Hobson (1996); Hasle & Syvertsen (1996)
<i>Biddulphia alternans</i> (Bailey 1851) Van Heurck (1985)	RC	Ishii et al. (2012)
<i>Biddulphia tridens</i> (Ehrenberg 1838) Ehrenberg (1841)	RS	Piredda et al. (2017)
<i>Cerataulus smithii</i> Ralfs (1861)	RS	Piredda et al. (2017)
<i>Chaetoceros aculeatus</i> Makarova (1962)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros affinis</i> Lauder (1864)	RS	Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996)
<i>Chaetoceros anastomosans</i> Grunow (1882)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Oku & Kamatani (1997)
<i>Chaetoceros approximatus</i> Gran & Angst (1931)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros brevis</i> Schütt (1895)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros ceratosporus</i> Ostenfeld (1910)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Ferrario et al. (1998)
<i>Chaetoceros chinchae</i> Mereschkowsky (1899)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Suto (2005) (As <i>Vallodiscus chinchae</i>)
<i>Chaetoceros chunii</i> Karsten (1905)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros cinctus</i> Gran (1897)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Gaonkar et al. (2017)
<i>Chaetoceros compressus</i> Lauder (1864)	RS	Pitcher (1990); McQuoid & Hobson (1996); Rines (1999); Chamnansinp et al. (2015)
<i>Chaetoceros constrictus</i> Gran (1897)	RS	Pitcher (1990); Rines & Hargraves (1988); McQuoid & Hobson (1996)
<i>Chaetoceros contortus</i> Schütt (1895)	RS	McQuoid & Hobson (1996); Chamnansinp et al. (2015)
<i>Chaetoceros contortus</i> Schütt (1895) var. <i>ornatus</i> Chamnansinp, Moestrup & Lundholm (2015)	RS	Chamnansinp et al. (2015)
<i>Chaetoceros coronatus</i> Gran (1897)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros costatus</i> Pavillard	RS	Garrison (1981); Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros crinitus</i> Schütt (1895)	RS	Stockwell & Hargraves (1986)
<i>Chaetoceros criophilus</i> Castracane (1886)	RC	Fryxell (1989); McQuoid & Hobson (1996)

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Modern taxon	Type	References
<i>Chaetoceros crucifer</i> Gran (1931)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros curiosus</i> Makarova (1962)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros curvisetus</i> Cleve (1889)	RS	Hargraves (1979); Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros cylindrosporus</i> Makarova (1962)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros dayanensis</i> Li & Zhu (2015)	RS	Li et al. (2015)
<i>Chaetoceros debilis</i> Cleve (1894)	RS	Garrison (1981); Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros diadema</i> (Ehrenberg 1854) Gran (1897)	RS	Hargraves (1972); Garrison (1981); French & Hargraves (1985); Pitcher (1990); Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros dichatoensis</i> Gaonkar, Montresor & Sarno (2017)	RS	Gaonkar et al. (2017)
<i>Chaetoceros didymus</i> Ehrenberg (1845)	RS	Garrison (1981); Pitcher (1990); Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros difficilis</i> Cleve (1900)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros dipyrenops</i> Meunier (1913)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros distans</i> Cleve (1873)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros diversus</i> Cleve (1873)	RC	McQuoid & Hobson (1996)
<i>Chaetoceros dubius</i> Proschinka-Lavrenko (1955)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros eibenii</i> Grunow (1882)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros elegans</i> Li, Boonprakob, Moestrup & Lundholm (2017)	RS	Li et al. (2017)
<i>Chaetoceros elmorei</i> Boyer (1914)	RS	Rushforth & Johansen (1986); Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros exospermus</i> Meunier (1913)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros externus</i> Gran (1897)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros furcellatus</i> Yendo (1911)	RS	Stockwell & Hargraves (1986); Eilertsen et al. (1995); McQuoid & Hobson (1996)
<i>Chaetoceros gelidus</i> Chamnansinp, Li, Lundholm & Moestrup (2013)	RS	Degerlund et al. (2012) (as <i>Chaetoceros socialis</i> , northern strains); Chamnansinp et al. (2013)
<i>Chaetoceros heterovalvatus</i> Proschinka-Lavrenko (1953)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros hirtisetus</i> (Rines & Hargraves 1990) Chamnansinp, Moestrup & Lundholm 2015	RS	Chamnansinp et al. (2015)
<i>Chaetoceros hispidus</i> (Ehrenberg) Brightwell	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros holsaticus</i> Schütt (1895)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros horridus</i> Krasske (1941)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros incertus</i> Makarova (1962)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros ingolfianus</i> Ostefeld (1902)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros lacinosus</i> Schütt (1895)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros laevisporus</i> Li, Boonprakob, Moestrup & Lundholm (2017)	RS	Li et al. (2017)
<i>Chaetoceros lauderi</i> Ralfs (1864)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Ishii et al. (2011)
<i>Chaetoceros longicornis</i> Makarova (1962)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros lorenzianus</i> Grunow (1863)	RS	Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996); Li et al. (2017)
<i>Chaetoceros melchersianus</i> Margalef (1967)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)

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Modern taxon	Type	References
<i>Chaetoceros millipedarius</i> Xu, Li & Lundholm (2019)	RS	Xu et al. (2019)
<i>Chaetoceros minimus</i> (Levander 1904) Marino, Giuffr�, Montresor & Zingone (1991)	RS	Marino et al. (1991); McQuoid & Hobson (1996)
<i>Chaetoceros mitra</i> (Bailey) Cleve (1896)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Li et al. (2017)
<i>Chaetoceros muelleri</i> Lemmermann (1898)	RS	Reinke (1984); Rushforth & Johansen (1986); Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros neglectus</i> Karsten (1905)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros neogracilis</i> (Sch�tt) van Landingham (1968)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros nipponica</i> Ikari (1928)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros paradoxus</i> Cleve (1873)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros paulsenii</i> Ostensfeld (1902)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros pavillardii</i> Ikari (1928)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros protuberans</i> Lauder (1864)	RS	Montresor et al. (2013)
<i>Chaetoceros pseudocrinitus</i> Ostensfeld (1901)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros pseudocurvisetus</i> Mangin (1910)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996);
	RC	Oku & Kamatani (1995); Kuwata & Takahashi (1999)
<i>Chaetoceros radicans</i> Sch�tt (1895)	RS	Syvrtsen (1979); Garrison (1981); Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996)
<i>Chaetoceros rigidus</i> Ostensfeld (1902)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros robustus</i> Makarova (1961)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros rotosporus</i> Li, Lundholm & Moestrup (2013)	RS	Li et al. (2013)
<i>Chaetoceros scabrosus</i> Proschinka-Lavrenko (1955)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros secundus</i> Cleve (1873)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros seiracanthus</i> Gran (1897)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros siamense</i> Cleve (1902)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros similis</i> Cleve (1896)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros simplex</i> Ostensfeld (1902)	RS	Rushforth & Johansen (1986); Stockwell & Hargraves (1986)
<i>Chaetoceros socialis</i> Lauder (1864)	RS	Garrison (1981); Pitcher (1990); Stockwell & Hargraves (1986); Eilertsen et al. (1995)
<i>Chaetoceros sporotruncatus</i> Gaonkar, Kooistra & Lange (2017)	RS	Gaonkar et al. (2017)
<i>Chaetoceros subcoronatus</i> Krasske (1941)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros subtilis</i> Cleve (1896)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros subtortilis</i> Proschinka-Lavrenko (1961)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996)
<i>Chaetoceros tenuissimus</i> Meunier (1913)	RS	Montresor et al. (2013)
<i>Chaetoceros teres</i> Cleve (1896)	RS	Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996)
<i>Chaetoceros throndsenii</i> Marino, Montresor & Zingone (1991)	RS	Marino et al. (1991); McQuoid & Hobson (1996)
<i>Chaetoceros vanheurckii</i> Gran (1897)	RS	Garrison (1981); Hollibaugh et al. (1981); Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996)

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<i>Chaetoceros vixvisibilis</i> Schiller (1930)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Hernández-Becerril et al. (2010)
<i>Chaetoceros wighamii</i> Brightwell (1856)	RS	Stockwell & Hargraves (1986); McQuoid & Hobson (1996) (as <i>Chaetoceros amanita</i>); Bosak et al. (2015b)
<i>Cylindrotheca closterium</i> (Ehrenberg 1839) Reimann & Lewin (1964)	RS	Montresor et al. (2013)
<i>Dactyliosolen blavyanus</i> (Peragallo 1892) Hasle (1975)	RS	McQuoid & Hobson (1996)
<i>Detonula confervacea</i> (Cleve 1896) Gran (1897)	RS	Hargraves (1976); Durbin (1978); McQuoid & Hobson (1996)
<i>Detonula pumila</i> (Castracane 1886) Gran (1900)	RS	Ishii et al. (2012)
<i>Ditylum brightwellii</i> (West 1860) Grunow (1883)	RS	Hargraves (1976); McQuoid & Hobson (1996); Riaux-Gobin (1996); Koester et al. (2007)
<i>Ditylum buchananii</i> von Stosch (1987)	RS	McQuoid & Hobson (1996)
<i>Eucampia antarctica</i> (Castracane 1886) Mangin (1915)	WS RS	Fryxell (1989) Hoban et al. (1980) as <i>Eucampia balaustium</i> Castracane (1886)
<i>Eucampia antarctica</i> (Mangin 1915) var. <i>recta</i> Fryxell & Prasad (1990)	RS	Fryxell & Prasad (1990)
<i>Fragilariopsis cylindrus</i> (Grunow 1883) Krieger (1954)	RS	McQuoid & Hobson (1996); Ferrario et al. (1998)
<i>Fragilariopsis oceanica</i> (Cleve) Hasle (1965)	RS	McQuoid & Hobson (1996); Hasle & Syvertsen (1996)
<i>Leptocylindrus danicus</i> Cleve (1889)	RS	Hargraves (1976); French & Hargraves (1985) (1986); Ishizaka et al. (1987); McQuoid & Hobson (1996)
<i>Leptocylindrus minimus</i> Gran (1915)	RS	Hargraves (1990); McQuoid & Hobson (1996)
<i>Lithodesmium variable</i> Takano (1979)	RC	Ishii et al. (2012)
<i>Melosira arctica</i> Dickie (1852)	RS	McQuoid & Hobson (1996)
<i>Melosira moniliformis</i> (Müller 1783) Agardh (1824)	RS	McQuoid & Hobson (1996)
<i>Minutocellus</i> cf. <i>polymorphus</i> (Hargraves & Guillard 1974) Hasle, Stosch & Syvertsen (1983)	RS	Montresor et al. (2013)
<i>Odontella aurita</i> (Lyngbye 1819) Agardh (1832)	RC	McQuoid & Hobson (1996)
<i>Odontella litigiosa</i> (van Heurck 1909) Hoban	RS	Hoban et al. (1980); McQuoid & Hobson (1996)
<i>Odontella longicuris</i> (Greville 1859) Hoban (1983)	RC	Ishii et al. (2012)
<i>Odontella mobiliensis</i> (Bailey 1851) Grunow (1884)	RC	Ishii et al. (2012)
<i>Odontella weissflogii</i> (Grunow 1882) Grunow (1884)	RS	Hoban et al. (1980); McQuoid & Hobson (1996)
<i>Papiliocellulus simplex</i> Gardner & Crawford (1992)	RS	Piredda et al. (2017)
<i>Paralia sulcata</i> (Ehrenberg 1838) Cleve (1873)	RS	McQuoid & Hobson (1996)
<i>Pauliella taeniata</i> (Grunow 1880) Round & Basson (1997)	RS	Hasle & Syvertsen (1996) (as <i>Achnanthes taeniata</i> Grunow 1880)
<i>Porosira glacialis</i> (Grunow 1884) Jørgensen (1905)	RS	Villareal & Fryxell (1990); McQuoid & Hobson (1996)
<i>Proboscia alata</i> (Brightwell 1858) Sundström (1896)	RS	McQuoid & Hobson (1996)
<i>Rhizosolenia braunii</i> Hustedt (1952)	RS	McQuoid & Hobson (1996)

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Modern taxon	Type	References
<i>Rhizosolenia formosa</i> Peragallo (1888)	RS	McQuoid & Hobson (1996)
<i>Rhizosolenia longiseta</i> Zacharias (1893)	RS	McQuoid & Hobson (1996)
<i>Rhizosolenia polydactyla</i> Castracane	RS	McQuoid & Hobson (1996); Hasle & Syvertsen (1996)
<i>Rhizosolenia setigera</i> Brightwell (1858)	RS	Hargraves (1976); McQuoid & Hobson (1996)
<i>Rhizosolenia sima</i> Castracane (1886)	RS	McQuoid & Hobson (1996)
<i>Sellaphora pupula</i> (Kützing) Mereschkovsky (1902)	RS	Piredda et al. (2017)
<i>Skeletonema costatum</i> (Greville 1866) Cleve (1873)	RC	Sakshaug & Andresen (1986); McQuoid & Hobson (1996)
<i>Skeletonema dohrnii</i> Sarno & Kooistra (2015)	RS	Piredda et al. (2017)
<i>Skeletonema menzelii</i> Guillard, Carpenter & Reimann (1974)	RS	Montresor et al. (2013)
<i>Skeletonema pseudocostatum</i> (Medlin 1991) Sarno & Zingone (2005)	RS	Piredda et al. (2017)
<i>Skeletonema tropicum</i> Cleve (1900)	RS	Montresor et al. (2013)
<i>Stellarima microtrias</i> (Ehrenberg 1884) Hasle & Sims (1986)	RS	Syvertsen (1985) (as <i>Coscinodiscus furcatus</i> Karsten 1905); Fryxell (1989); McQuoid & Hobson (1996)
<i>Stephanopyxis nipponica</i> Gran & Yendo (1914)	RS	Haga (1997); Ferrario et al. (2013)
<i>Stephanopyxis palmeriana</i> (Greville 1865) Grunow (1884)	RS	Drebes (1966); McQuoid & Hobson (1996)
<i>Stephanopyxis turris</i> (Greville & Arnott) Ralfs (1861)	RS	Hargraves (1976)
<i>Syringidium bicornis</i> Ehrenberg (1845)	RS	Hasle & Sims (1985); McQuoid & Hobson (1996)
<i>Syringidium simplex</i>	RS	Hasle & Sims (1985)
<i>Thalassionema nitzschioides</i> (Grunow 1862) Mereschkovsky (1902)	RS	Montresor et al. (2013)
<i>Thalassiosira allenii</i> Takano (1965)	RS	Piredda et al. (2017)
<i>Thalassiosira antarctica</i> Comber (1896)	RS	Doucette & Fryxell (1985); McQuoid & Hobson (1996)
<i>Thalassiosira antarctica</i> var. <i>borealis</i> Fryxell, Doucette & Hubbard (1981)	RS	Krawczyk et al. (2012)
<i>Thalassiosira australis</i> Peragallo (1921)	RS	Syvertsen (1985); McQuoid & Hobson (1996)
<i>Thalassiosira constricta</i> Gaarder (1938)	RS	Heimdal (1974); McQuoid & Hobson (1996)
<i>Thalassiosira</i> cf. <i>eccentrica</i> (Ehrenberg 1840) Cleve (1904)	RS	Piredda et al. (2017)
<i>Thalassiosira gravida</i> Cleve (1896)	RS	Krawiec (1982) (as <i>Thalassiosira rotula</i> Meunier 1910); McQuoid & Hobson (1996)
<i>Thalassiosira kushirensis</i> Takano (1985)	RS	Krawczyk et al. (2012)
<i>Thalassiosira mediterranea</i> (Schröder 1911) Hasle (1972)	RS	Montresor et al. (2013)
<i>Thalassiosira nordenskiöldii</i> Cleve (1873)	RS	Durbin (1978); Hollibaugh et al. (1981); McQuoid & Hobson (1996)
<i>Thalassiosira pseudonana</i> Hasle & Heimdal (1970)	RS	Piredda et al. (2017)
<i>Thalassiosira scotia</i> Fryxell & Hoban (1979)	RS	Fryxell et al. (1979); McQuoid & Hobson (1996)
<i>Trieres mobiliensis</i> (2013)	RS	Piredda et al. (2017)

Abbreviations: RS = resting spore; RC = resting cell; WS = winter stage.

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Supplementary Material 2

List of modern species of planktonic marine Dinophyceae producing resting stages.

Modern taxon	Paleontological taxon	References
Order <i>Prorocentrales</i> Lemmermann (1910)		
<i>Prorocentrum gracile</i> Schütt (1895)		Cannon (1993)*
<i>Prorocentrum leve</i> Faust, Kibler, Vandersea, Tester & Litaker (2008)		Mertens et al. (2017a)*
<i>Prorocentrum lima</i> Ehrenberg (1873) Dodge (1975)		Faust (1993)*
<i>Prorocentrum micans</i> Ehrenberg (1833)		Cannon (1993)*
Order <i>Dinophysiales</i> Lindemann (1928)		
<i>Dinophysis acuminata</i> Claparède & Lachmann (1859)		Bardouil et al. (1991) Hajdu & Larsson (2006)
<i>Dinophysis acuta</i> Ehrenberg (1839)		Moita & Sampayo (1993) Reguera et al. (1995)
<i>Dinophysis ovum</i> Schütt (1895)		Cannon (1993)*
<i>Dinophysis cf. tripos</i> Gourret (1883)		Moita & Sampayo (1993)
Order <i>Gymnodiniales</i> Lemmermann (1910)		
<i>Akashiwo sanguinea</i> K. Hirasaka (1922) Hansen & Moestrup (2000)		Tang & Gobler (2015)*
<i>Amphidinium carterae</i> Hulburt (1957)		Cao Vien (1967)*; (1968)* Sampayo (1985)*
<i>Amphidinium operculatum</i> Claparède & Lachmann (1859)		Barlow & Triemer (1988)* as <i>A. klebsii</i> (division cysts)
<i>Barrufeta bravensis</i> Sampedro & Fraga (2011)		Sampedro et al. (2011)*
<i>Barrufeta resplendens</i> Hulburt (1957) Gu et al. (2015)		Gu et al. (2015b)*
<i>Grammatodinium tongyeonginum</i> Li & Shin (2017)		Li et al. (2017)*
<i>Gymnodinium aureolum</i> Hulburt (1957) Hansen (2000)		Tang et al. (2008)*
<i>Gymnodinium catenatum</i> Graham (1943)		Anderson et al. (1988)* Ellegaard et al. (1994)* Gu et al. (2013b)*
<i>Gymnodinium corollarium</i> Sundström et al. (2009)		Sundström et al. (2009)*
<i>Gymnodinium impudicum</i> Fraga & Bravo (1995) G. Hansen & Moestrup (2000)		Sonneman & Hill (1997)* as <i>Gyrodinium impudicum</i> Kobayashi et al. (2001)* as <i>Gyrodinium impudicum</i> Rubino et al. (2010)* as <i>Gymnodinium impudicum</i> cyst type a

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Modern taxon	Paleontological taxon	References
<i>Gymnodinium inusitatum</i> Gu (2013)		Gu et al. (2013b)*
<i>Gymnodinium litoralis</i> A. Reñé et al. (2011)		Reñé et al. (2011)*
<i>Gymnodinium microreticulatum</i> Bolch & Hallegraeff (1999)		Bolch et al. (1999)* Gu et al. (2013b)*
<i>Gymnodinium nolleri</i> Ellegaard & Moestrup (1999)		Ellegaard & Moestrup (1999)* Figueroa & Bravo (2005a)* Rubino et al. (2010)*
<i>Gymnodinium trapeziforme</i> Attaran-Fariman & Bolch (2007)		Attaran-Fariman et al. (2007)*
<i>Gyrodinium undulans</i> Hulburt (1957)		Sonneman & Hill (1997)*
<i>Karenia brevis</i> Davis (1948) G. Hansen & Moestrup (2000)		Walker (1982)* as <i>Ptychodiscus brevis</i> Persson et al. (2013)*
<i>Katodinium fungiforme</i> Anissimova (1926) Fott (1957)		Spero & Morée (1981)*
<i>Katodinium rotundatum</i> Lohmann (1908) Loeblich III (1965)		Hamer et al. (2001)
<i>Levanderina fissa</i> Levander (1894) Moestrup et al. (2014)		Kojima & Kobayashi (1992)*; Uchida et al. (1996)*; Shikata et al. (2008)* as <i>Gyrodinium instriatum</i> Moestrup et al. (2014)*
<i>Margalefidinium polykrikoides</i> Margalef (1961) Gómez, Richlen & Anderson (2017)		Li et al. (2015a)*; Thoha et al. (2019)*
<i>Nematodinium armatum</i> Dogiel (1906) Kofoid & Swezy (1921)		Bolch (2001)* possible germination inferred from PCR amplification Rubino et al. (2017)* germination from incubation experiments
<i>Polykrikos hartmannii</i> Zimmerman (1930)		Matsuoka & Fukuyo (1986)*
<i>Polykrikos kofoidii</i> Chatton (1914)		Matsuoka et al. (2009)*
<i>Polykrikos schwartzii</i> Bütschli (1873)		Matsuoka et al. (2009)*
<i>Wangodinium sinense</i> Z. Luo et al. (2018), Y. Tang & H.F. Gu (2018)		Luo et al. (2018)*
<i>Warnovia</i> cf. <i>rosea</i> Pouchet (1897) Kofoid & Swezy (1921)		Ellegaard et al. (2002)*
Order Suessiales Fensome & al. (1993)		
<i>Biecheleria baltica</i> Moestrup, Lindberg & Daugbjerg (2009)		Moestrup et al. (2009)*
<i>Biecheleria cincta</i> Siano, Montesor & Zingone (2009) Siano (2012)		Siano et al. (2009)*
<i>Biecheleria halophila</i> Biecheler (1952) Moestrup, Lindberg & Daugbjerg (2009)		Kremp et al. (2005)* as <i>Woloszynskia halophila</i> Moestrup et al. (2009)*
<i>Biecheleriopsis adriatica</i> Moestrup, Lindberg & Daugbjerg (2009)		Kang & Wang (2018)
<i>Dactylocladus pterobelotum</i> Takahashi, Moestrup & Iwataki (2017)		Takahashi et al., in press*

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Modern taxon	Paleontological taxon	References
<i>Polarella glacialis</i> Montresor, Procaccini & Stoecker (1999)		Montresor et al. (1999)*
<i>Woloszynskia</i> sp.		Bolch & Hallegraeff (1990)*
Order Gonyaulacales F.J.R. Taylor (1980)		
<i>Alexandrium affine</i> Inoue & Fukuyo (1985) Balech (1995)		Fukuyo et al. (1985)*; Band-Schmidt et al. (2003)*
<i>Alexandrium andersonii</i> Balech (1990)		Montresor et al. (1998)*; Ciminiello et al. (2000)*
<i>Alexandrium catenella</i> Whedon & Kofoid (1936) Balech (1985)		Meksumpun et al. (1994)* Sonneman & Hill (1997)* Bravo et al. (2006)*
<i>Alexandrium compressum</i> Fukuyo, Yoshida & Inoue (1985) Balech (1995)		Matsuoka (1992)
<i>Alexandrium fraterculus</i> Balech (1964) Balech (1985)		Nagai et al. (2009)*
<i>Alexandrium fundyense</i> Balech (1985)		Anderson et al. (2014) Anglés et al. (2012a)*
<i>Alexandrium hiranoi</i> Kita & Fukuyo (1988)		Kita et al. (1985)* as <i>Goniodoma pseudogonyaulax</i> Kita & Fukuyo (1988) Kita et al. (1993)* Bravo et al. (2006)*
<i>Alexandrium kutnerae</i> Balech (1979) Balech (1985)		
<i>Alexandrium leei</i> Balech (1985)		Fukuyo & Pholpunthin (1990b)*
<i>Alexandrium lusitanicum</i> Balech (1985) Bolch et al. (1991)*		Blanco (1989a)*
<i>Alexandrium margalefii</i> Balech (1985)		Bravo et al. (2006)*
<i>Alexandrium minutum</i> Halim (1960)		Bolch et al. (1991)* Bravo et al. (2006)*; Anglés et al. (2012b)*
<i>Alexandrium monilatum</i> Howell (1953) Balech (1995)		Walker & Steidinger (1979)* as <i>Gonyaulax monilata</i>
<i>Alexandrium ostenfeldii</i> Paulsen (1904) Balech & Tangen (1985)		Mackenzie et al. (1996)* Jensen & Moestrup (1997)* temporary cysts
<i>Alexandrium pacificum</i> Litaker (2014)		Fertouna-Bellakhal et al. (2015)
<i>Alexandrium peruvianum</i> (Balech & Mendiola) Balech & Tangen		Bravo et al. (2006)* Figueroa et al. (2008)*
<i>Alexandrium pseudogonyaulax</i> Biecheler (1952) Horiguchi, Yuki & Fukuyo (1992)		Kita et al. (1985) formation of temporary cysts Montresor (1995a)*; Zmerli Triki et al. (2015)*
<i>Alexandrium tamarense</i> Lebour (1925) Balech (1995)		Anderson & Wall (1978)* as <i>Gonyaulax tamarensis</i> Blanco (1989a)*; Person et al. (2000)* Genovesi et al. (2011)*

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Modern taxon	Paleontological taxon	References
<i>Alexandrium tamiyavanichi</i> Balech (1994)		Fukuyo & Pholpunthin (1990a)*as <i>A. cohorticula</i> Godhe et al. (2000)
<i>Alexandrium tamutum</i> Montresor, Beran & John (2004)		Montresor et al. (2004)* Figueroa et al. (2007)*
<i>Alexandrium taylorii</i> Balech (1994)		Garcés et al. (1998)*; Giacobbe et al. (1999)*; Figueroa et al. (2006)* Steidinger (1975) in Head (1996)
<i>Fragilidium heterolobum</i> Balech ex Loeblich III (1965)		
<i>Fragilidium mexicanum</i> Balech (1988)		Orlova et al. (2004)* Selina & Orlova (2009)* Sonneman & Hill (1997)*
<i>Fragilidium subglobosum</i> von Stosch (1969) Loeblich III (1965)		
<i>Gonyaulax</i> cf. <i>alaskensis</i> Kofoid (1911)	<i>Spiniferites</i> sp.	Dobell & Taylor (1981)*
<i>Gonyaulax baltica</i> Ellegaard, Lewis & Harding (2002)	<i>Spiniferites bulloideus</i> Deflandre & Cookson (1955)	Ellegaard et al. (2002)*
	<i>Impagidinium caspiense</i> Marret (2004)	Marret et al. (2004); Mertens et al. (2017a,b)*
<i>Gonyaulax digitalis</i> Pouchet (1883) Kofoid (1911)	<i>Spiniferites bentorii</i> Rossignol (1962) Wall & Dale (1970)	Matsuoka (1985a); Wall & Dale (1968)* Orlova et al. (2004) Wall & Dale (1968)*
	<i>Spiniferites nodosus</i> Wall (1967) Sarjeant (1970)	
	<i>Bitectatodinium tepikiense</i> Wilson (1973)	Lewis et al. (2001)* Marret & Zonneveld (2003)
<i>Gonyaulax ellegardiae</i> Mertens et al. (2015)	<i>Spiniferites pachydermus</i> Rossignol (1964) Reid (1974)	Zonneveld et al. (2013) Mertens et al. (2015)*
<i>Gonyaulax elongata</i> Reid (1974) Ellegaard, Daugbjerg, Rochon, J.Lewis & Harding (2003)	<i>Spiniferites elongatus</i> Reid (1974)	Ellegaard et al. (2003)*; Van Nieuwenhove et al. (2018)
	<i>Spiniferites frigidus</i> Harland & Reid (1980)	Marret & Zonneveld (2003)
<i>Gonyaulax membranacea</i> Rossignol (1964) Ellegaard, Daugbjerg, Rochon, J.Lewis & Harding (2003)	<i>Spiniferites membranaceus</i> Rossignol (1964) Sarjeant (1970)	Ellegaard et al. (2003)*
<i>Gonyaulax scrippsae</i> Kofoid (1911)	<i>Spiniferites bulloideus</i> Deflandre & Cookson (1955) Sarjeant (1970)	Wall & Dale (1968)* Matsuoka (1985a)*
	<i>Spiniferites belerius</i> Reid (1974)	Marret & Zonneveld (2003)
<i>Gonyaulax</i> cf. <i>scrippsae</i> Kofoid (1911)	<i>Spiniferites</i> sp. cf. <i>S. delicatus</i> Reid	Matsuoka (1987)*
<i>Gonyaulax spinifera</i> Claparède & Lachmann (1859) Diesing (1866)	<i>Ataxiodinium choane</i> Reid (1974)	Rochon et al. (2009) Marret & Zonneveld (2003) Price et al. (2017)
	<i>Bitectatodinium tepikiense</i> Wilson (1973)	Rochon et al. (2009) Price et al. (2017)
	<i>Nematosphaeropsis labyrinthus</i> Ostensfeld (1903) Reid (1974)	Wall & Dale (1968)* Rochon et al. (2009) Price et al. (2017)

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Modern taxon	Paleontological taxon	References
	<i>Nematosphaeropsis lemniscata</i> Bujak (1984)	Wall & Dale (1968)* as <i>N.balcombiana</i> Deflandre & Cookson (1955)
	<i>Spiniferites hyperacanthus</i> Deflandre & Cookson (1955) Cookson & Eisenack (1974)	Rochon et al. (2009) Price et al. (2017)
	<i>Spiniferites mirabilis</i> Rossignol (1967) Sarjeant (1970)	Wall & Dale (1968)* Rochon et al. (2009); Price et al. (2017)
	<i>Spiniferites ramosus</i> Ehrenberg (1838) Mantell (1854)	Wall & Dale (1970)* Lewis et al. (1999)* Rochon et al. (2009)
	<i>Spiniferites scabratus</i> Wall (1967) Sarjeant (1970)	Wall & Dale (1968)* as <i>Hystricosphaera scabrata</i> Lewis et al. (1999)*
	<i>Tectatodinium pellitum</i> Wall (1967)	Wall & Dale (1968)* Marret & Zonneveld (2003) Rochon et al. (2009)
<i>Gonyaulax verior</i> Sournia (1973)		Matsuoka et al. (1988)* Zonneveld & Dale (1994)* Ellegaard et al. (1994)*
<i>Lingulodinium polyedrum</i> Stein (1883) Dodge (1989)	<i>Lingulodinium machaerophorum</i> Deflandre & Cookson (1955) Wall (1967)	Kokinos & Anderson (1995)* Lewis & Hallett (1997)* Figueroa & Bravo (2005b)* Mertens <i>et al.</i> (2018)*
<i>Pentaplacodinium saltonense</i> Mertens, Carbonell-Moore, Pospelova & Head (2018)		
<i>Peridiniella catenata</i> Levander (1894) Balech (1977)		Kremp (2000)*
<i>Protoceratium globosum</i> Kofoid & J.R. Michener (1911)		Morquecho et al. (2009)*
<i>Protoceratium reticulatum</i> Claparède & Lachmann (1859) Bütschli (1855)	<i>Operculodinium centrocarpum</i> Deflandre & Cookson (1955) Wall (1967)	Sonneman & Hill (1997)* Rubino et al. (2017)*
	<i>Operculodinium israelianum</i> Rossignol (1962) Wall (1967)	Morquecho et al. (2009)
	<i>Operculodinium psilatatum</i> Wall (1967)	Morquecho et al. (2009)
<i>Pyrodinium bahamense</i> Plate (1906)	<i>Polysphaeridium zoharyi</i> Rossignol (1962) Davey & Williams (1966)	Wall & Dale (1969)* Usup et al. (2012)
<i>Pyrodinium bahamense</i> var. <i>compressum</i> (Böhm) Steidinger, Tester & Taylor	<i>Polysphaeridium zoharyi</i> Rossignol (1962) Davey & Williams (1966)	Matsuoka (1989)* Azanza (1997)* Onda et al. (2014) temporary cysts Steidinger & Davis (1967)* Wall & Dale (1971)*
<i>Pyrophacus horologium</i> Stein (1883)		Wall & Dale (1971)*
<i>Pyrophacus steinii</i> Schiller (1935) Wall & Dale (1971)	<i>Tuberculodinium vancampoeae</i> Rossignol (1962) Wall (1967)	Wall & Dale (1971)*; Matsuoka (1985b)* Faust (1998)*; Pholpuntin et al. (1999)*

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Modern taxon	Paleontological taxon	References
Order Peridinales Haeckel (1894)		
<i>Archaeperidinium bailongense</i> Liu et al. (2015a)		Liu et al. (2015b)*
<i>Archaeperidinium constrictum</i> Abé (1936) Liu, Mertens, Matsuoka & Gu (2015)		Liu et al. (2015b)*
<i>Archaeperidinium minutum</i> Kofoid (1907) Yamaguchi et al. (2011)		Wall & Dale (1968)*; Ribeiro et al. (2010)* Mertens et al. (2012)*; Liu et al. (2015b)*
<i>Archaeperidinium saanichi</i> Mertens et al. (2012)		Mertens et al. (2012)*
<i>Bysmatrum subsalsum</i> Ostenfeld (1908) Faust & Steidinger (1998)		Gottschling et al. (2012) Anglès et al. (2017)*
<i>Boreadinium breve</i> Abé (1981) Sournia (1984)		Liu et al. (2015a)*
<i>Calciodinellum albatrosianum</i> Kamptner (1963) Janofske & Karwath (2000)	<i>Thoracosphaera albatrosiana</i> Kamptner (1963)	Janofske & Karwath (2000)*
<i>Calciodinellum elongatum</i> Hildebrand-Habel, Willems & Versteegh (1999) Meier, Janofske & Willems (2002)		Meier et al. (2002)*
<i>Calciodinellum levantinum</i> Meier, Janofske & Willems (2002)		Meier et al. (2002)*
<i>Diplopelta globula</i> Abé (1941) Balech (1979)		Liu et al. (2015a)*
<i>Diplopelta symmetrica</i> Pavillard (1913)		Dale et al. (1993)* Zonneveld & Pospelova (2015)
<i>Diplopsalis lenticula</i> Bergh (1881)		Matsuoka (1988)*; Lewis (1990)* Liu et al. (2015a)*
<i>Diplopsalopsis latipeltata</i> Balech & Borgese (1990)		Dale et al. (1993)*
<i>Diplopsalopsis orbicularis</i> (Paulsen) Meunier		Wall & Dale (1968)* Matsuoka (1988)*
<i>Diplopsalopsis ovata</i> Abé (1941) Dodge & Toriumi (1993)		Liu et al. (2015a)*
<i>Ensiculifera carinata</i> Matsuoka et al. (1990)		Matsuoka et al. (1990)*
<i>Ensiculifera imariense</i> Kobayashi & Matsuoka (1995)		Kobayashi & Matsuoka (1995)*
<i>Ensiculifera mexicana</i> Balech (1967)	<i>Pentadinellum oblatum</i> Keupp (1991)	Zonneveld et al. (2005)
<i>Glenodinium foliaceum</i> Stein (1883)		De Sousa & Silva (1962) Head (1996)
<i>Glenodinium hallii</i> Freudenthal & Lee (1963)		Head (1996)
<i>Gotoius abei</i> Matsuoka (1988)		Matsuoka (1988)*
<i>Heterocapsa triquetra</i> Ehrenberg (1840) Stein (1883)		Olli (2004)
<i>Islandinium minutum</i> Harland & Reid (1980) Head, Harland & Matthiessen (2001)	<i>Islandinium minutum</i> Harland & Reid (1980) Head, Harland & Matthiessen (2001)	Potvin et al. (2013)*

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Modern taxon	Paleontological taxon	References
<i>Kryptoperidinium foliaceum</i> Stein (1883) Lindemann (1924)		Figueroa et al. (2009)*
<i>Lebouraia pusilla</i> Balech & Akselman (1988) Dodge & Toriumi (1993)		Liu et al. (2015a)*
<i>Leonella granifera</i> Fütterer (1977) Janofske & Karwath (2000)	<i>Thoracosphaera granifera</i> Fütterer (1977)	Janofske & Karwath (2000)*
<i>Niea acanthocysta</i> Kawami, Iwataki & Matsuoka (2006) Liu et al. (2015a)		Matsuoka (1988)* as <i>Diplopelta parva</i> Kawami et al. (2006)* as <i>Oblea</i> <i>acanthocysta</i> Liu et al. (2015a)*
<i>Niea chinensis</i> Liu et al. (2015a)		Liu et al. (2015a)*
<i>Niea torta</i> Abé (1941) Liu et al. (2015a)		Liu et al. (2015a)*
<i>Oblea rotunda</i> Lebour (1922) Balech ex Sournia (1973)		Lewis (1990)* Liu et al. (2015a)*
<i>Pentapharsodinium dalei</i> Indelicato & Loeblich III (1986)		Lewis (1991)* Zonneveld & Pospelova (2013)
<i>Pentapharsodinium dalei</i> var. <i>aciculiferum</i> Gu (2013)		Gu et al. (2013d)*
<i>Pentapharsodinium jinhaense</i> Li, Han & Shin (2015)		Li et al. (2015c)*
<i>Pentapharsodinium tyrrenicum</i> Balech (1990) Montresor, Zingone & Marino (1993)	<i>Calcicarpinum bivalvum</i> Versteegh (1993)	Montresor et al. (1993)*
<i>Pernambugia tuberosa</i> Kamptner (1963) Janofske & Karwath (2000)	<i>Thoracosphaera tuberosa</i> Kamptner (1963)	Janofske & Karwath (2000)*
<i>Posoniella tricarinelloides</i> Versteegh (1993) Streng, Banasová, Reháková & Willems (2009)		Streng et al. (2009); Gu et al. (2013a)*
<i>Preperidinium meunieri</i> Pavillard (1912) Elbrächter (1993)	<i>Dubridinium caperatum</i> Reid (1977)	Matsuoka (1988)*; Lewis (1990)* Liu et al. (2015a)*
<i>Protoperidinium abei</i> Paulsen (1931) Balech (1974) var. <i>rotunda</i> Abé (1936) Taylor (1967)		Liu et al. (2015b)*
<i>Protoperidinium achromaticum</i> Levander (1902) Balech (1974)		Bolch & Hallegraeff (1990)* as <i>Protoperidinium</i> sp.2 Head (1996)
<i>Protoperidinium americanum</i> Gran & Baarud (1935) Balech (1974)		Lewis & Dodge (1987)*; Zonneveld et al. (2013) Liu et al. (2014)*
<i>Protoperidinium avellana</i> Meunier (1919) Balech (1974)	<i>Brigantidium cariacense</i> Wall (1967) Reid (1977)	Wall & Dale (1968)*; Reid (1977) Matsuoka (1984)*; Liu et al. (2015b)*
<i>Protoperidinium biconicum</i> P. Dangeard (1927) Balech (1974)		Gu et al. (2015a,b)*
<i>Protoperidinium brochii</i> Kofoid & Swezy (1921) Balech (1974)		Blanco (1989b)*
<i>Protoperidinium claudicans</i> Paulsen (1907) Balech (1974)	<i>Votadinium spinosum</i> Reid (1977)	Wall & Dale (1968)*; Matsuoka (1985a)*; Bolch & Hallegraeff (1990)*
<i>Protoperidinium conicoides</i> Paulsen (1905) Balech (1974)	<i>Brigantidium simplex</i> Wall (1965) Reid (1977)	Lewis et al. (1984)*

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Modern taxon	Paleontological taxon	References
<i>Protoperidinium conicum</i> Gran (1900) Balech (1974)	<i>Selenopemphix quanta</i> Bradford (1975) Matsuoka (1985a)	Wall & Dale (1968)*; Marret & Zonneveld (2003); Gu et al. (2015a,b)*
<i>Protoperidinium cf. curvipes</i> Ostenfeld (1906) Balech (1974)		Head (1996)
<i>Protoperidinium denticulatum</i> Gran & Braarud (1953) Balech (1974)	<i>Brigantedinium irregulare</i> Matsuoka (1987)	Matsuoka (1987)*
<i>Protoperidinium divaricatum</i> Meunier (1919) Balech (1974) Gu et al. (2015a,b)*	<i>Xandarodinium xanthum</i> Reid (1977)	Zonneveld et al. (2013)
<i>Protoperidinium cf. divergens</i> Ehrenberg (1841) Balech (1974)	<i>Peridinium ponticum</i> Wall & Dale (1973)	Wall & Dale (1973) Dale (1983)*; Matsuoka & Head (2013)
<i>Protoperidinium excentricum</i> Paulsen (1907) Balech (1974)		Lewis et al. (1984)* Liu et al. (2015b)*
<i>Protoperidinium cf. expansum</i> Abé (1981)		Hallegraeff & Bolch (1992)*
<i>Protoperidinium fukuyoi</i> Mertens, Head, Pospelova & Matsuoka (2013)		Mertens et al. (2013)*
<i>Protoperidinium fuzhouense</i> Liu et al. (2015a)		Liu et al. (2015b)*
<i>Protoperidinium haizhouense</i> Liu, Gu & Mertens (2013)	<i>Islandinium brevispinosum</i> Pospelova & Head (2002)	Liu et al. (2014)*
<i>Protoperidinium humile</i> Schiller (1937) Balech (1974)		Gu et al. (2015a,b)*
<i>Protoperidinium latidorsale</i> Balech (1951) Balech (1974)	<i>Votadinium calvum</i> Reid (1977)	Sarai et al. (2013)*
<i>Protoperidinium latissimum</i> Kofoid (1907) Balech (1974) Gu et al. (2015a,b)*		Wall & Dale (1968)* Wall & Dale (1968)*; Sonneman & Hill (1997)*
<i>Protoperidinium leonis</i> Pavillard (1916) Balech (1974)	<i>Quinquecuspis concretum</i> Reid (1977) Harland (1977)	Lewis et al. (1984)*
<i>Protoperidinium louisianensis</i> Mertens, Gu, Price & Matsuoka (2016)	<i>Trinovantedinium pallidifulum</i> Matsuoka (1987)	Mertens et al. (2016)*
<i>Protoperidinium monospinum</i> Gran & Maarud (1930) Balech (1974)		Zonneveld & Dale (1994)*
<i>Protoperidinium nudum</i> Meunier (1919) Balech (1974)	<i>Selenopemphix quanta</i> Bradford (1975) Matsuoka (1985a,b)	Wall & Dale (1968)*; Matsuoka (1985a,b)*
<i>Protoperidinium obtusum</i> Karsten (1906) Parke & Dodge (1976)		Aydin et al. (2011); Uzar et al. (2010)
<i>Protoperidinium paraoblongum</i> Sarai et al. (2013)	<i>Votadinium pontifossatum</i> Gurdebeke, Mertens, Pospelova, Matsuoka, Li & Louwy	Sarai et al. (2013)*; Gurdebeke et al. (2019)
<i>Protoperidinium parthenopes</i> Zingone & Montesor (1988)		Moscattello et al. (2004); Kawami & Matsuoka (2009)*; Ferraro et al. (2016); Liu et al. (2014)* Rubino et al. (2017)*
<i>Protoperidinium pentagonum</i> Gran (1902) Balech (1974)	<i>Brigantedinium majusculum</i> Reid (1977)	Nehring (1994)* Gu et al. (2015a,b)*

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Modern taxon	Paleontological taxon	References
<i>Protopteridinium punctulatum</i> Paulsen (1907) Balech (1974)	<i>Brigantedinium cariacense</i> Wall (1967) Reid (1977)	Wall & Dale (1968)*
<i>Protopteridinium quadrioblongum</i> Sarai et al. (2013)	<i>Votadinium rhomboideum</i> Gurdebeke, Mertens, Pospelova, Matsuoka, Li & Louwye	Sarai et al. (2013)*; Gurdebeke et al. (2019)
<i>Protopteridinium shanghaiense</i> Gu et al. (2015a)	<i>Trinovantedinium applanatum</i> Bradford (1977) Bujak & Davies (1983)	Zonneveld et al. (2013) Gu et al. (2015a)*
<i>Protopteridinium sinuosum</i> Lemmermann (1905)	<i>Brigantedinium majusculum</i> Reid (1977)	Li et al. (2015b)*
<i>Protopteridinium steidingerae</i> Balech (1979)	<i>Votadinium reidii</i> Gurdebeke, Mertens, Pospelova, Matsuoka, Li & Louwye	Wall & Dale (1968)* Gribble et al. (2009)*; Sarai et al. (2013)* Gurdebeke et al. (2019)
<i>Protopteridinium stellatum</i> Wall (1968) Head (1999)	<i>Stelladinium stellatum</i> Wall (1968) Reid (1977)	Wall & Dale (1968)*; Rochon et al. (1999) Liu et al. (2015b)*
<i>Protopteridinium subinerme</i> Paulsen (1904) Loeblich III (1969)	<i>Selenopemphix nephroides</i> Benedek (1972) Benedek & Sarjeant (1981)	Wall & Dale (1968)* Lewis et al. (1984)*
<i>Protopteridinium thorianum</i> Paulsen (1905) Balech (1974)		Lewis et al. (1984)*
<i>Protopteridinium thulesense</i> Balech (1958) Balech (1973)		Matsuoka et al. (2006)*
<i>Protopteridinium tricingulatum</i> Kawami, van Wezel, Koeman & Matsuoka (2009)		Kawami et al. (2009)* Liu et al. (2014)*
<i>Qia lebouriae</i> Nie (1943) Liu et al. (2015a)		Matsuoka (1988)* as <i>Diplopsalis lebouriae</i> Liu et al. (2015a)*
<i>Scrippsiella acuminata</i> Ehrenb (1836) Kretschmann et al. (2015)		Wall & Dale (1968)*; Montresor et al. (1994)* Janofske (2000)*; Kretschmann et al. (2015)
<i>Scrippsiella bicarinata</i> Zinssmeister, Soehner, Meier & Gottschling (2012)		Zinssmeister et al. (2012)*
<i>Scrippsiella crystallina</i> Lewis (1991)		Lewis (1991)*
<i>Scrippsiella donghaiensis</i> Gu (2008)		Gu et al. (2008)*
<i>Scrippsiella enormis</i> Gu (2013)		Gu et al. (2013c)*
<i>Scrippsiella erinaceus</i> Kamptner (1937) Kretschmann et al. (2014)		Kretschmann et al. (2014) Ferraro et al. (2016)*
<i>Scrippsiella hangoei</i> Schiller (1937) Larsen (1995)		Lewis et al. (1984)* as <i>Protopteridinium hangoei</i> Rintala et al. (2007)* temporary cyst Kremp & Parrow (2006)*
<i>Scrippsiella infula</i> Deflandre (1948) Montresor (2003)	<i>Calcigonellum infula</i> Deflandre (1948)	D'Onofrio et al. (1999)* Montresor et al. (2003)*
<i>Scrippsiella kirschieae</i> Zinssmeister, Soehner, Meier & Gottschling (2012)		Zinssmeister et al. (2012)* Satta et al. (2014); Rubino et al. (2017)*
<i>Scrippsiella lachrymosa</i> Lewis (1991)		Lewis (1991)*

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<i>Scrippsiella minima</i> Gao & Dodge (1991)		Gao & Dodge (1991)*
<i>Scrippsiella operosa</i> Deflandre (1947) Montresor (2003)		Montresor et al. (1997)* as <i>Calciodinellum operosum</i> Montresor et al. (2003)
<i>Scrippsiella patagonica</i> Akselman & Keupp (1990)	<i>Obliquipithonella irregularis</i> Akselman & Keupp (1990)	Akselman & Keupp (1990)*
<i>Scrippsiella plana</i> Luo, Mertens, Bagheri & Gu (2015)		Luo et al. (2015)*
<i>Scrippsiella precaria</i> Montresor & Zingone (1988)		Montresor & Zingone (1988)*; Montresor et al. (1994)
<i>Scrippsiella ramonii</i> Montresor (1995)		Montresor (1995b)*
<i>Scrippsiella regalis</i> Gaarder (1954) Janofske (2000)		Janofske (2000)*
<i>Scrippsiella rotunda</i> Lewis (1991)		Lewis (1991)*; Gu et al. (2008)*
<i>Scrippsiella spinifera</i> Honsell & Cabrini (1991)		Kobayashi (1995)* Gu et al. (2013c)* Luo et al. (2015)*
<i>Scrippsiella trifida</i> Lewis (1991)		Lewis (1991)*
<i>Vulcanodinium rugosum</i> Nézan & Chomérat (2011)		Zeng et al. (2012)* division cysts
Order Pyrocystales Apstein (1909)		
<i>Dissodinium pseudolunula</i> Swift ex Elbrächter & Drebes (1978)		Gomez & Artigas (2013)*

Note: x* = cyst formation and/or theca/cyst correlation confirmed by encystment/excystment experiments or by observing living cysts within the theca.

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Supplementary Material 3

List of species of planktonic marine Ciliophora producing resting stages.

Taxon	Cyst name	References
<i>Acanthostomella norvegica</i> (Daday, 1887) Jörgensen (1927)		Yu et al. (2012)
<i>Acanthostomella</i> sp.		Kamiyama (2013)
<i>Amphorides amphora</i> (Claparede & Lachmann, 1858) Strand (1928)		Yu et al. (2012)
<i>Chaetospira mulleri</i> Lachmann (1856)		Reid & John (1983)
<i>Codonella aspera</i> Kofoid & Campbell (1929)		Rubino et al. (2013)
<i>Codonella orthoceras</i> (Haeckel) Jørgensen (1924)		Rubino et al. (2013)
<i>Codonellopsis monacensis</i> (Rampi) Balech (1950)		Rubino et al. (2013)
<i>Codonellopsis schabii</i> (Brandt) Kofoid & Campbell (1929)		Rubino et al. (2013)
<i>Coxiella helix</i> (Claparede & Lachmann, 1858)		Yu et al. (2012)
<i>Cyrtostrombidium boreale</i> Kim, Suzuki & Taniguchi (2002)		Kim, Suzuki & Taniguchi (2002)
<i>Cyttarocylis cassis</i> (Haeckel, 1837)		Yu et al. (2012)
<i>Diophrys oligothrix</i> Borror (1965)		Gong et al. (2018)
<i>Diophrys scutum</i> (Dujardin, 1841) Kahl (1932)		Reid & John (1983)
<i>Epipliocylis undella</i> (Ostenfeld & Schmidt) Jörgensen (1924)		Rubino et al. (2013)
<i>Eutintinnus apertus</i> Kofoid & Campbell (1929)		Yu et al. (2012)
<i>Eutintinnus fraknoi</i> (Daday, 1887) Kofoid & Campbell (1929)		Yu et al. (2012)
<i>Eutintinnus ludus-undae</i> (Entz, 1885)		Yu et al. (2012)
<i>Eutintinnus tubulosus</i> (Ostenfeld, 1899) Kofoid & Campbell (1939)		Kamiyama (2013)
<i>Fabrea salina</i> Henneguy (1890)		Moscatello et al. (2004)
<i>Favella ehrenbergii</i> (Claparede & Lachmann, 1858) Jörgensen (1924)		Yu et al. (2012)
<i>Gastrostyla steinii</i> Engelmann (1862)		Reid & John (1983)
<i>Halteria grandinella</i> (Muller, 1773) Dujardin (1840)		Kamiyama (2013)
<i>Helicostomella longa</i> (Brandt, 1906)		Kamiyama (2013)
<i>Helicostomella subulata</i> (Ehrenberg, 1833) Jörgensen (1924)		Reid & John (1983)
<i>Helicostomella</i> sp.		Ichinomiya et al. (2004)
<i>Laboea strobila</i> Lohmann (1908)		Rubino et al. (2009)
<i>Laurentiella strenua</i> (Dingfelder, 1962) Berger & Foissner (1989)		Kamiyama (2013)
<i>Leprotintinnus bottnicus</i> Jörgensen (1900)		Yu et al. (2012)
<i>Leprotintinnus pellucidus</i> (Cleve, 1899)		Yu et al. (2012)
<i>Leprotintinnus</i> sp.		Kamiyama (2013)
<i>Limnostrombidium viride</i> (Stein, 1867) Krainer (1995)	<i>Sphaeropsis</i> sp.	Agatha et al. (2005)
<i>Meseres corlissi</i> Petz & Foissner (1992)	<i>Sphaeropsis</i> type	Foissner et al. (2005)
<i>Metacylis</i> sp.		Kamiyama (2013)
<i>Nyctotherus ovalis</i> Leidy (1850)	<i>Nyctotherus</i> type	Reid & John (1983); Rubino et al. (2009)
<i>Oxytricha bifaria</i> Stokes (1887)		Verni & Rosati (2011)
<i>Oxytricha fallax</i> Stein (1859)		Reid & John (1983)
<i>Oxytricha granulifera</i> Foissner & Adam (1983)		Kamiyama (2013)
<i>Parafavella denticulata</i> (Ehrenberg, 1840)		Yu et al. (2012)
<i>Parafavella edentata</i> (Brandt, 1896)		Yu et al. (2012)
<i>Parafavella gigantea</i> Brandt (1896)		Yu et al. (2012)
<i>Parundella caudata</i> (Ostenfeld, 1899) Jörgensen (1924)		Yu et al. (2012)
<i>Parundella</i> sp.		Kamiyama (2013)
<i>Pelagostrombidium fallax</i> (Zacharias, 1896) Krainer (1991)	<i>Sphaeropsis</i> sp.	Kamiyama (2013)
<i>Pleurotricha lanceolata</i> (Ehrenberg, 1835) Stein (1859)		Reid & John (1983)

(Continued)

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Taxon	Cyst name	References
<i>Rhabdonella spiralis</i> (Fol 1881)		Rubino et al. (2013)
<i>Salpingella acuminata</i> (Claparede & Lachmann, 1858) Jörgensen (1924)		Yu et al. (2012)
<i>Schmidingerella serrata</i> (Mobius, 1987) Agatha & Struder-Kypke (2012)		Reid & John (1983)
<i>Schmidingerella taraiakensis</i> Hada (1932) (Agatha & Strüder-Kypke, 2012)		Kamiyama (2013)
<i>Steinia sphagnicola</i> Foissner (1989)		Kamiyama (2013)
<i>Stenosemella oliva</i> (Meunier, 1910)		Yu et al. (2012)
<i>Stenosemella ventricosa</i> (Claparède & Lachmann, 1858) Jörgensen (1924)		Rubino et al. (2013)
<i>Stentor</i> sp.	<i>Stentor</i> type	Moscattello et al. (2004)
<i>Strombidium acutum</i> Claparède & Lachmann (1859)	<i>Sphaeropsis</i> sp., elongate	Rubino et al. (2009)
<i>Strombidium biarmatum</i> Agatha, Struder-Kypke, Beran & Lynn (2005)	<i>Sphaeropsis</i> sp.	Agatha et al. (2005)
<i>Strombidium capitatum</i> (Leegaard, 1915) Kahl (1932)	<i>Sphaeropsis</i> sp.	Ichinomiya et al. (2004)
<i>Strombidium conicum</i> (Lohmann, 1908) Wulff (1919)	<i>Sphaeropsis</i> sp.	Kim & Taniguchi (1995)
<i>Strombidium crassulum</i> (Leegaard, 1915) Kahl (1932)	<i>Sphaeropsis</i> sp.	Reid (1987)
<i>Strombidium rassoulzadegani</i> MacManus, Xu, Costas & Katz (2010)	<i>Sphaeropsis</i> sp.	McManus et al. (2010)
<i>Strombidium stylifer</i> Levander (1894)	<i>Sphaeropsis</i> sp.	Katz et al. (2005)
<i>Strombidium tintinnodes</i> Entz (1884)	<i>Sphaeropsis</i> sp.	Jonsson (1994)
<i>Strombidinopsis</i> sp.	<i>Sphaeropsis</i> sp.	Ichinomiya et al. (2004)
<i>Stylonethes sterkii</i> Garnjobst (1937)		Reid & John (1983)
<i>Tintinnidium mucicula</i> (Claparède & Lachmann, 1858) Daday (1997)		Yu et al. (2012)
<i>Tintinnopsis baltica</i> Brandt (1896)		Yu et al. (2012)
<i>Tintinnopsis beroidea</i> Stein (1867)		Rubino et al. (2013)
<i>Tintinnopsis buetschlii</i> Daday (1887)		Rubino et al. (2013)
<i>Tintinnopsis campanula</i> Ehrenberg (1840)		Yu et al. (2012)
<i>Tintinnopsis corniger</i> Hada (1964)		Kamiyama (2013)
<i>Tintinnopsis cylindrica</i> Daday (1887)		Yu et al. (2012)
<i>Tintinnopsis directa</i> Hada (1932)		Kamiyama (2013)
<i>Tintinnopsis fracta</i>		Yu et al. (2012)
<i>Tintinnopsis karajacensis</i> Brandt (1896)		Yu et al. (2012)
<i>Tintinnopsis kofoidi</i> Hada (1932)		Yu et al. (2012)
<i>Tintinnopsis lohmanni</i> Laackmann (1906)		Yu et al. (2012)
<i>Tintinnopsis meunieri</i> Kofoid & Campbell (1929)		Yu et al. (2012)
<i>Tintinnopsis nucula</i> (Fol, 1884)		Yu et al. (2012)
<i>Tintinnopsis radix</i> (Imhof, 1886)		Yu et al. (2012)
<i>Tintinnopsis rapa</i> Meunier (1910)		Yu et al. (2012)
<i>Tintinnopsis subacuta</i> Jörgensen (1899)		Yu et al. (2012)
<i>Tintinnopsis tocaninensis</i> Kofoid & Campbell (1929)		Yu et al. (2012)
<i>Tintinnopsis tubulosa</i> Levander (1900)		Yu et al. (2012)
<i>Tintinnopsis urnula</i> Meunier (1910)		Yu et al. (2012)
<i>Tintinnopsis</i> sp.		Kamiyama (2013)
<i>Undella claparedei</i> (Entz) Daday (1887)		Rubino et al. (2013)
<i>Urocryptum tortum</i> (Maupas, 1883)		Perez-Uz & Guinea (2001)
<i>Uronema marinum</i> Dujardin (1841)		Fenchel (1990)

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Supplementary Material 4

List of species of planktonic marine Metazoa producing resting stages.

Taxon	References
Rotifera	
<i>Asplanchna pryodonta</i> Gosse (1850)	Viitasalo & Katajisto (1994)
<i>Brachionus</i> sp.	Marcus et al. (1994)
<i>Hexarthra fennica</i> Levander (1892)	Moscatello & Belmonte (2004)
<i>Keratella</i> sp.	Viitasalo & Katajisto (1994)
<i>Ptygura</i> sp.	Moscatello & Belmonte (2004)
<i>Synchaeta</i> sp.	Viitasalo & Katajisto (1994)
Cladocera	
<i>Bosmina maritima</i> P.E. Muller (1868)	Purasjoki (1958)
<i>Daphnia cucullata</i> G.O. Sars (1862)	Viitasalo & Katajisto (1994)
<i>Evadne nordmanni</i> Lovén (1836)	Onbé (1985)
<i>Evadne tergestina</i> Claus (1864)	Onbé (1973)
<i>Moina</i> sp.	Moscatello & Belmonte (2004)
<i>Penilia avirostris</i> Dana (1849)	Onbé (1972)
<i>Podon intermedius</i> Lilljeborg (1853)	Onbé (1991)
<i>Podon leuckarti</i> Sars G.O. (1862)	Onbé (1985)
<i>Podon polyphemoides</i> Leuckart (1859)	Onbé et al. (1977)
Copepoda Calanoida	
<i>Acartia adriatica</i> Steuer (1910)	Belmonte (1997)
<i>Acartia bifilosa</i> Giesbrecht (1881)	Castro-Longoria and Williams (1999)
<i>Acartia bilobata</i> Abraham (1970)	Beyrend-Dur et al. (2014)
<i>Acartia californiensis</i> Trinast (1976)	Johnson (1980)
<i>Acartia clausi</i> Giesbrecht (1889)	Kasahara et al. (1974)
<i>Acartia erythraea</i> Giesbrecht (1889)	Kasahara et al. (1974)
<i>Acartia discadudata</i> Giesbrecht (1882)	Lindeque et al. (2013)
<i>Acartia hudsonica</i> Pinhey (1926)	Sullivan & McManus (1986)
<i>Acartia italica</i> Steuer (1910)	Belmonte (1997)
<i>Acartia lilljeborgi</i> Giesbrecht (1889)	Ara (2001)
<i>Acartia longiremis</i> Lilljeborg (1853)	Marcus (1990)
<i>Acartia pacifica</i> Steuer (1915)	Uye (1985)
<i>Acartia omori</i> Bradford (1976)	Itoh and Aoki (2010)
<i>Acartia sinjiensis</i> Mori (1940)	Uye (1985)
<i>Acartia spinicauda</i> Giesbrecht (1889)	Marcus (1996)
<i>Acartia steueri</i> Smirnov (1936)	Uye (1980)
<i>Acartia teclae</i> Bradford (1976)	Naess (1996)
<i>Acartia tonsa</i> Dana (1849)	Zillioux & Gonzalez (1972)
<i>Acartia tsuensis</i> Ito (1956)	Uye (1985)
<i>Anomalocera ornata</i> Sutcliffe (1949)	Marcus (1996)
<i>Anomalocera patersoni</i> Templeton (1837)	Ianora & Santella (1991)
<i>Boeckella hamata</i> Brehm (1928)	Hall & Burns (2001)
<i>Boeckella poppei</i> Mrazec (1901)	Jiang et al. (2012)
<i>Calanopia americana</i> Dahl F. (1894)	Marcus (1996)
<i>Calanopia thompsoni</i> Scott A. (1909)	Kasahara et al. (1974)

(Continued)

Taxon	References
<i>Centropages abdominalis</i> Sato (1913)	Kasahara et al. (1974)
<i>Centropages furcatus</i> Dana (1849)	Marcus (1989)
<i>Centropages hamatus</i> Lilljeborg (1853)	Mauchline (1998)
<i>Centropages ponticus</i> Karavaev (1895)	Sazhina (1968)
<i>Centropages typicus</i> Krøyer (1849)	Lindley (1990)
<i>Centropages velificatus</i> Oliveira (1947)	Chen & Marcus (1997)
<i>Centropages yamadai</i> Mori (1934)	Kasahara et al. (1974); Marcus (1996)
<i>Epilabidocera amphitrites</i> Mc Murrich (1916)	Marcus (1990); Johnson (1980)
<i>Eurytemora affinis</i> Poppe (1880)	Johnson (1980)
<i>Eurytemora americana</i> Williams (1906)	Marcus (1984)
<i>Eurytemora pacifica</i> Sato (1913)	Uye (1985)
<i>Eurytemora velox</i> Lilljeborg (1853)	Gaudy & Pagano (1987)
<i>Gippslandia estuarina</i> Bayly & Arnott (1969)	Newton & Mitchell (1999)
<i>Gladioferens pectinatus</i> Brady (1899)	Hall and Burns (2001)
<i>Labidocera aestiva</i> Wheeler (1900)	Grice and Lawson (1976)
<i>Labidocera bipinnata</i> Tanaka (1936)	Uye et al. (1979)
<i>Labidocera mirabilis</i> Fleminger (1957)	Chen & Marcus (1997)
<i>Labidocera rotunda</i> Mori (1929)	Itoh and Aoki (2010)
<i>Labidocera scotti</i> Giesbrecht (1897)	Marcus (1989)
<i>Labidocera trispinosa</i> Esterly (1905)	Uye (1985)
<i>Labidocera wollastoni</i> Lubbock (1857)	Grice & Gibson (1982)
<i>Paracartia grani</i> Sars G.O. (1904)	Guerrero & Rodrigues (1998)
<i>Paracartia latisetosa</i> Kriczaguin (1893)	Belmonte (1992)
<i>Pontella meadi</i> Wheeler (1900)	Grice & Gibson (1977)
<i>Pontella mediterranea</i> Claus (1863)	Sazhina (1968)
<i>Pteriacartia josephinae</i> Crisafi (1974)	Belmonte & Puce (1994)
<i>Sinocalanus tenellus</i> Kikuchi K. (1928)	Hada et al. (1986)
<i>Sulcanus confictus</i> Nicholls (1945)	Newton & Mitchell (1999)
<i>Temora longicornis</i> Müller O.F. (1785)	Marcus (1996)
<i>Tortanus derjugini</i> Smirnov (1935)	Chen & Li (1991)
<i>Tortanus dextrilobatus</i> Chen & Zhang (1965)	Chen & Li (1991)
<i>Tortanus discaudatus</i> Thompson I.C. & Scott A. (1903)	Marcus (1990)
<i>Tortanus forcipatus</i> Giesbrecht (1889)	Kasahara et al. (1974)

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