THE BENTHIC RESTING CYST: A KEY ACTOR IN HARMFUL DINOFLAGELLATE BLOOMS – A REVIEW

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ABSTRACT. – Resting cysts (RC) constitute a coupling between benthic and pelagic stages and influence the bloom development in a number of bloom forming dinoflagellate species. Encystment capability coupled with high vegetative cell density (> one million cells l⁻¹) contribute to the formation of an accumulation zone: “the cyst bank”, which is directly linked to the success of bloom initiation and its recurrence. The survival time of benthic RCs (few weeks to several years), their viability which could be negatively affected by predation, and their mandatory dormancy period (few days to several months) are variable and influence the seeding potential of the population significantly. Encystment rate, mainly controlled by temperature and oxygen level, and the germinating cells’ viability determine the inoculum size. Many biological processes in RCs have been shown to be controlled by endogenous and environmental factors, and vary between species and within the same species as a function of geographic strains.

**Introduction**

Harmful Algal Blooms (HAB) affect marine organisms negatively, degrade the environment, or cause economic damages (Smayda 1997a & 1997b). HABs only concern 5% of marine phytoplanktonic species (Zingone & Enveoldsen 2000), of which dinoflagellates represent 75% (Smayda 1997b). Among these harmful species, 40% are toxic and cause various syndromes responsible for a large variety of neurological or gastric disorders (Zingone & Enveoldsen 2000). Nearly 10% of dinoflagellates form resting cysts (RC) (Dale 1983), which constitute the coupling between benthic and pelagic stages, and support the bloom development and recurrence (Boero et al. 1996, Yamaguchi et al. 1996, Anderson 1998, Marcus & Boero 1998, Stahl-Delbanc & Hansson 2002). Non-motile benthic stages, surrounded by a dense and resistant external wall (Montresor et al. 1998, Blackburn & Parker 2005) survive in unfavourable environmental conditions, particularly in areas with marked seasonal variations (Montresor et al. 1998, Kremp 2000, Ichimi et al. 2001). The RC accumulation zone, called “cyst bank” or “seed bed” (Persson et al. 2000, Matsuoka et al. 2003, Garcés et al. 2004) represents the seeding source for bloom initiation (Anderson & Morel 1979, McGillicuddy et al. 2003, Anderson et al. 2005). Table I, top summarizes Alexandrium spp. toxic blooms linked to RCs. These resistant cells also allow the geographic dispersion of the population (Hallegraeff 1993). Encystment, mandatory dormancy period (MDP) and encystment influence dinoflagellate bloom dynamics (Kremp & Heiskanen 1999, Kim et al. 2002). Bloom success depends on various factors such as encystment, encystment and the constitution of a sufficient storage of viable RCs (Fig. 1). The aim of this work is to carry out a bibliographic review concerning the central role of RCs in harmful dinoflagellate bloom dynamics on the basis of the whole characteristics of the dinoflagellate group, and the main factors (physical, chemical and biological) implied in their formation, preservation and distribution.

**Encystment**

Encystment begins at the peak of exponential growth (Dale 1983). Encystment fluxes remain constant during periods of maintenance and decline of the bloom (Garcés et al. 2004). In many species the RC is a result of sexual reproduction (Turpin et al. 1978, Anderson et al. 1984, Kremp & Heiskanen 1999), but also asexually formed RCs have been reported (Kremp & Parrow 2006). Fusing of gametes started quickly after gametogenesis (Kremp & Heiskanen 1999) and could last 30 minutes for Peridinium gatunense (Pfiester 1977) and Alexandrium pseudo-gonyaulax (Montresor 1995) to several hours for Alexandrium (Gonyaulax) tamarensis (Turpin et al. 1978). The formed planozygote is a large longitudinal biflagellate cell which accumulates storage compounds like lipidic granules and glued, in particular starch, and synthesizes actively carbohydrates (Anderson & Wall 1978, Chapman et al. 1982, Binder & Anderson 1990, Montresor 1995, Olli & Anderson 2002). The planozygote becomes darker with a more condensed nucleus and remains motile for few days before the formation of a RC (Pfiester 1977, Figueroa et al. 2005). Figueroa et al. (2005) suggested that the mechanism by which the theca is pushed out to liberate the RC is ecdysis. The organic RC wall contains a highly resistant biomacromolecular material and its thickness ranges from 0.5 to 1.5 µm (Anderson &
In a majority of dinoflagellates, the wall of RCs is not smooth but spiny which promotes their survival (Sarjeant et al. 1987, Belmote et al. 1997). The size and the morphology of RC are largely variable between species (Cho & Matsuoka 2001, Pospelova et al. 2004, Joyce et al. 2005). The RC is generally surrounded by a mucilaginous layer associated with adherence to sediment particles (Anderson & Lively 1985, Doucette et al. 1989, Bolch et al. 1991, Montresor et al. 1993). This influences the sedimentation process. The RC content shows many storage grains, one or several prominent orange to reddish brown accumulation bodies (4-5 µm in diameter) and the nucleus (Anderson & Wall 1978, Cho & Matsuoka 2001). Its biochemical composition differs significantly from that of the vegetative cell (Binder & Anderson 1990). It is characterized by a reduction of protein and chlorophyll a contents and an increase of the carbohydrate content which constitutes the dominating storage product (Binder & Anderson 1990). These compounds could be significant because of their impact on the length of the dormancy period (Steidinger & Haddad 1981). According to Figueroa et al. (2005), the lapse time between gametogenesis and RC production could vary from 5 to 60 days for A. catenella. The percentage of vegetative cells which form RCs (encystment rate) varies between species and within the same species as a function of geographic strains (Table I, bottom). In the case of massive blooms of Alexandrium minutum, high densities of RCs are uncoupled from high encystment rates (Garcés et al. 2004). Encystment rate, which is related to the switch of a fraction of the motile vegetative population to sexual non-dividing forms such as gamete, planozygote and resting cysts should be considered as a loss factor affecting the vegetative cell population (Olli et al. 2004, Peperzak 2006).

Factors controlling encystment

Laboratory experiments show that nutrient limitation is generally related to encystment in dinoflagellates (Table I, bottom). However, the field study of Godhe et al. (2001) shows that low nutrient concentrations are not correlated with high RCs production. Kremp & Heiskanen (1999) suggest that encystment induction is not a response to environmental stress but results from optimal
Table I. – Top, Resting cyst (RC) densities of *Alexandrium* spp. (Dinophyceae) associated with the paralytic shellfish poisoning (PSP) syndrome. The first detection of PSP (f.d. PSP) in the corresponding area is specified. Bottom, Encystment rate of vegetative cells of some dinoflagellate species measured in laboratory experiments (l) or in field studies (f) and the related induction factor.

<table>
<thead>
<tr>
<th><em>Alexandrium</em> spp.</th>
<th>origin</th>
<th>site</th>
<th>year</th>
<th>RC density</th>
<th>unit</th>
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<td><em>catenella</em></td>
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<td>strait</td>
<td>1972</td>
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<td>b</td>
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<td>1</td>
<td>f</td>
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<td>Sgroso et al., 2001</td>
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RESTING CYSTS DRIVE HARMFUL DINOFLAGELLATE BLOOMS

conditions for vegetative growth. Some laboratory experiments show that encystment could occur in a medium non limited by nutrients and in patches of high cell densities that enhance the success of gamete encounters (Turpin et al. 1978, Uchida 2001, Olli & Anderson 2002). Other factors such as temperature, daylength and salinity have been shown to control encystment (Sgroso et al. 2001, Meier & Willems 2003, Kremp & Parrow 2006) and their interactions determine “species-specific” patterns (Montresor et al. 1998). These illustrate the complexity of encystment phenomenon as a function of species and environmental conditions (Montresor et al. 1998) and may explain that the same species can adopt different encystment strategies in relation to its location.

**Sinking of the resting cyst**

Figueroa et al. (2005) showed that, the nonmotile planozygote of *A. catenella* settles at the bottom before producing a RC. In contrast Kim et al. (2005) suggested that the RC of *Alexandrium* spp. is formed in the water column and settles at the bottom like a negatively buoyant particle (Dale 1983). The RC settling velocity in *Gyrodinium uncatenum*, *A. tamarense* and *Scapassula trochoidea* approaches 0.010 cm s⁻¹, but could vary with cell size, morphology, cell orientation during sinking and the seawater viscosity (Anderson & Lively 1985). The self aggregation of RCs or their aggregation with other particles through the mucus secretion probably increases their fall (Smetacek 1985) and limits their exposition to predation. This biological control can be exerted on the RCs in the water column in particular by copepods and heterotrophic dinoflagellates (Persson 2000, Montresor et al. 2003). The RC sinking characteristics control their distribution tightly in the water column and in the bottom sediment, and the constitution of an indigenous “cyst bank” (Smetacek 1985, Amorin et al. 2001).

**Resting periods**

The RC enters in a mandatory dormancy period (MDP) during which excystment can not occur. When the

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MDP is achieved, the RC enters a quiescence period or excysts depending on environmental conditions (Montresor & Marino 1996, Kremp 2000, Sombrero et al. 2004, Blackburn & Parker 2005). During these resting periods the metabolic activity is drastically reduced, the photosynthetic activity is inhibited and the respiration rate decreases to 10% (MDP) or 1.5% (quiescence period) of the vegetative rate (Binder & Anderson 1990). The reduced metabolic activity is necessary to maintain the cell integrity in an anoxic environment through anaerobic respiration which requires suitable storage substrate (Marcus & Boero 1998). Important morphological changes result from this residual metabolic activity depending on temperature level and the MDP duration time (Anderson 1980, Binder & Anderson 1990). A thickening of the cell wall, a reduction of their photosynthetic pigmentation and a clearing of the cell content linked to the consumption of storage products were observed (Turpin et al. 1978, Anderson 1980, Chapman et al. 1982, Amorin et al. 2001, Kirn et al. 2005). This strategy maximizes fitness of a species to environmental fluctuations exceeding the tolerance range of vegetative cells (Montresor & Marino 1996). The MDP varies from a few days to several months between species and strains influencing the population dynamic and bloom development (Table II). A long MDP (> 1 month) induces blooms seasonality and the long term survival of the population (Kim et al. 2002). Whereas a short MDP (< 1 month) is more related to a “fast switch” between the benthic and pelagic stages and promotes the occurrence and the maintenance of blooms through a continuous encystment/excystment process (Pfister 1977, Montresor et al. 1998, Giacobbe & Yang 1999, Figueroa et al. 2005).

Factors controlling the MDP

Vernalisation is an important factor associated with MDP (Anderson 1980). Without a thermic triggering like an exposure to low temperatures, the excystment success could decrease, RCs could degenerate or enter a longer MDP (Anderson & Wall 1978, Montresor & Marino 1996). The existence of an endogenous annual clock driving MDP has been reported (Anderson & Morel 1979, Anderson & Keafer 1987, Castell-Perez et al. 1998, Matrai et al. 2005). This type of control would represent an advantage in deep waters where stable environmental conditions do not trigger the termination of MDP (Anderson 1998). In contrast, in a shallow environment, the MDP control by an endogenous clock may be unfavourable compared to a more opportunistic strategy implying a direct linkage to environmental fluctuations as temperature variations (Anderson & Keafer 1987, Matrai et al. 2005).

Survival time and viability of resting cysts in the sediment

A large fraction of RCs are not able to excyst (Kremp 2000). It concerns the RCs which have not achieved their MDP, those which are dead, and those which have been degraded by predation processes. In the last two cases, the RCs are considered as nonviable. The RC survival time probably has a genetic basis and depends on the parental origin of the gametes (Figueroa et al. 2005). Lewis et al. (1999) showed that the RCs’ survival time in the sediment is limited and varies from 12 (A. tamarense) to 66 months (Gonyaulax spinifera). Mizushima & Matusoka (2004) suggested a longer survival time of 8 years in the natural environment for A. catenella/tamarense. Anderson (1980) observed in laboratory experiments a shorter survival time (< 3 weeks) for the same species. In the sediment, viability related to excystment capability could be affected by ingestion and therefore digestion process or gut passage in the benthic macroorganisms (Persson & Rosenberg 2003). The majority of Alexandrium sp. RCs ingested by the mollusc Theola fragilis are partially or totally digested (Tsujino & Uchida 2004). For the non digested cysts the excystment success seems not to be affected by the gut passage in the polychaetes T. fragilis, Perinereis nuntia and Paraprionospio sp. (Tsujino et al. 2002, Tsuji & Uchida 2004). In the same way, the excystment success of Scrippsiella lachrymosa does not seem to be affected by gut passage in other polychaete species as Capitella sp., Streblosos benedicti and Polydora cornata (Kremp et al. 2003). In contrast, the excystment success of Scrippsiella ramonii was reduced after Nereis laevigata gut transit (Giangrande et al. 2002). The viability of RCs has a high impact on population dynamics. Any decrease in viability has to be compensated by a regular renewal of the cyst bank which depends on excystment success of previous blooms. In contrast, an increase in viability has a cumulative effect, which, in turn, enhances RC density in the sediment.

Excystment

The excystment is the process of RC germination (hatching), resulting in a motile planktonic cell (Anderson & Wall 1978, Blackburn & Parker 2005). This pro-
cess is preceded by an increase in the respiratory rate of up to 50% of the vegetative rate and followed by an increase in other metabolic activities using endogenous reserves for energy production (Binder & Anderson 1990). Most of the RC studied under laboratory conditions showed an excystment success between 70% and 100% (Table III). However a field study suggested a lower percentage of the cyst pool of Scrippsia hangoei that excysts (Kremp 2000). Excystment can be synchronous for S. lachrymosa (Olli & Anderson 2002) or asynchronous for A. tamarense (Anderson 1980). It suggests that the synchronization of excystment provides a massive inoculum over a very short time and may increase the success of bloom initiation when RC density is low. However this strategy may be unsuccessful in the case of an adverse environmental condition like an intensive mixing of the water column. This can result in a reduction or a complete failure of the inoculum development. In contrast, asynchronous excystments combined with high RC density would support a continuous seeding and limit consequences of unfavourable events on the newly formed cells.

Factors controlling the excystment

Temperature seems to be the main factor controlling excystment (Rengefors & Anderson 1998, Itakura & Yamaguchi 2001, Kim et al. 2002). In fact, the excystment induction was mainly linked with a temperature variation (warming or cooling) around an optimal range (Anderson & Morel 1979, Anderson 1980). Indeed, dinoflagellate RCs excystment can occur in a large temperature range and varies as a result of geographic strains (Table III). Anderson & Wall (1978) showed that low temperatures inhibit excystment, whereas other works (Binder & Anderson 1987, Anderson et al. 2005) showed that low temperatures only seem to slow down excystment. The possible inhibition of excystment in anoxic conditions (Anderson et al. 1987, Rengefors & Anderson 1998) explains that buried RCs in the anoxic sediment cannot excyst (Kirm et al. 2005). In the same way, in a semi-enclosed shallow embayment, when algal matts continuously cover the sediment, a limitation in oxygen can affect excystment success (Kremp 2000). Light can also affect excystment success, but its effect depends on the studied species: excystment of S. hangoei increases significantly, whereas Peridiniella catenata excysts successfully in both light and dark conditions (Kremp 2001). Darkness inhibits Scrippsia rotunda and S. trochoidea excystments (Nuzzo & Montresor 1999) but not that of Alexandrium sp. (Castell-Perez et al. 1998, Anderson et al. 2005, Kirn et al. 2005). Anderson et al. (1987) suggested that darkness does not inhibit but only slows down the germination process, and a short light exposure could be sufficient to trigger excystment. Nutrient concentration and salinity have been shown to be unconnected to
excystment success (Anderson & Wall 1978, Kim et al. 2002, Figueroa et al. 2005). However, Binder & Anderson (1987) demonstrated that excystment of S. trochoidea slows down significantly in a nutrient-depleted medium. The seasonal excystment pattern of A. tamarine in Masan Bay (Korea) shows similar seasonalities with salinity and dissolved oxygen (Kim et al. 2002). In conclusion, unfavourable conditions seem only to slow down excystment which results in a bloom initiation lengthening.

The recruitment

Only benthic RCs present in the first millimeters of oxic sediment and/or pelagic RCs resuspended in the water column participate in the recruitment of a population. In the sediment, favourable conditions for excystment decrease quickly with depth. The photic and the oxic zone are limited to the first millimeters of mud (Fenchel & Straarup 1971, Revsbech et al. 1980, Elbaz-Poulichet et al. 2005). The bioturbation, implied mixing process due to macrofauna activity, ensures a continuous “turn over” of the sediment surface (Marcus 1984, Mugnai et al. 2003). This has an important role in recruitment through the transport of RCs from depth to the sediment surface, where they are exposed to favourable conditions for excystment (Stahl-Delbano & Hansson 2002, Anderson et al. 2005). In the case of deep water environment, the resuspension of RCs toward the photic zone represents an advantage in species for which excystment is a light-dependant process. In addition, for the majority of species, excystment occurs only under oxic conditions. Resuspension can be also an advantage for the subsequent vegetative growth. However, the hydrodynamism, implied in resuspension, affects dinoflagellate RCs species differently depending on their size and morphology (Kremp 2001). For example, resuspended Alexandrium spp. RCs in the Gulf of Maine and the Bay of Fundy (USA), resulting from an intense mixing of the water column, have been shown to contribute significantly to the bloom initiation (Kirn et al. 2005).

Germling cell viability

The total restoration of the metabolic activity before excystment allows the germling cell to survive and to divide (Binder & Anderson 1990). However, Kremp (2001) suggested “that the resources of P. catenata cysts are sufficient to ensure not only the survival of the germling but also the first cell divisions”. Parrow & Burkhoder (2003) showed that gametes emerge from excystment of Pfiesteria shumwayae. However, for Gonyaulax excavata and A. catenella, meiosis occurs after excystment. In this case the germling cell (planomeiocyte) is a diploide cell (Anderson & Wall 1978, Figueroa et al. 2005). For A. catenella and Gymnodinium nolleri, the post-meiotic viability can vary from 50 to 90% (Figueroa et al. 2005, 2006). Haploid vegetative cells divide by binary fission (Montresor 1995). The success of viability of the produced vegetative cell can be increased with nutrient concentration for S. lachrymosa (Olli & Anderson 2002), and with chelators and light for A. tamarensis (Anderson & Wall 1978). Increase in light also promotes the germling survival of S. hangoei, whereas a low light level still has a positive effect on the germling survival of P. catenata (Kremp 2001). These results imply different recruitment strategies as a seeding-resuspension dependent mechanism for light-adapted species such as S. hangoei (Kremp 2001). However, in laboratory experiments the viability success of Gymnodinium catenatum remains low because it leads rarely to a viable culture (Amorin et al. 2001). These results suggest that a proportion of the initial seeding population dies and is not involved in bloom initiation and development.

Bloom initiation

Bloom initiation

Bloom is initiated in very different areas which could be closed or more open (Table 1). Their success is closely linked to the size of the inoculum produced by the “seeding population” which depends on RC density, the excystment success and the viability of germling cells (Anderson 1998, Kremp 2000). For example, Joyce et al. (2005) suggested that the low density (13 cysts cm⁻³ of sediment) of A. catenella RCs in Sal danh ba bay (South Africa) should not allow a bloom initiation, whereas RC densities in Lambert’s Bay (113-175 cysts cm⁻³ of sediment) allow bloom development in this area. In contrast, the high density (4.5 10⁷ cysts m⁻² of sediment) of A. tamarensis RCs in Perch Pond (USA) should provide a large inoculum in this shallow (1.5 m depth)embayment (Anderson et al. 1982). In some cases, the seeding capacity is not enough to explain the seasonal proliferation of vegetative cells in a defined area. An inoculum coming from an exogenous cyst bank and being transported through advection can contribute to the bloom initiation at a given site. For example, in the Gulf of Maine (USA), downwelling conditions expose the coast to cell populations of Alexandrium fundyense that originated from offshore waters (McGillcuddy et al. 2003). The existence of a residual over-wintering survival population of vegetative cells could also contribute to the bloom initiation (Anderson & Morel 1979, Kirn et al. 2005).

Resting cysts abundance and vertical distribution

Dinoflagellate RCs represent generally less than 1% of the total sedimentary organic matter (Persson & Rosenberg 2003). The RC density varies between species, history of the bloom and geographic areas. For example, Scrippsiella spp. RC density varied from 10⁴ to 10⁷ cysts cm⁻³ (Kremp 2000), whereas Alexandrium spp. RC densi-
Joyce activities, strongly affects RCs distribution and recruitment (Marcus & Schmidt-Gengenbach 1986, Tsujino et al. 2002). For example, *N. laevisagata* mixed the sediment surface in 30 days resulting in an upward transport of “older” RCs and burying of newly formed RCs (Giangrande et al. 2002). This process induces a continuous genetic mixing of the different RC cohorts of the cyst bank. Horizontal migrations seem to have a limited impact on RCs distribution (Meier & Willems 2003). This mixing process changes with the season and the composition of macrobenthic community (Keaf et al. 1992, Yokoyama 1998, François et al. 1999, Mugnai et al. 2003, Persson & Rosenberg 2003). High sedimentation rates also affect the burying of RCs and decreases their abundance through dilution by organic and mineral supplies (Keaf et al. 1992, Erard-Le-Denn et al. 1993, Meier & Willems 2003, Pospelova et al. 2004, Wang et al. 2004c). In the Thau lagoon (French Mediterranean coast) the sedimentation rate varied in a range of 0.16 to 0.33 cm year$^{-1}$ (Elbaz-Pouliquen et al. 2005), in Manila Bay (Philippines) it could reach 2.0 cm year$^{-1}$ (Sombrito et al. 2004). The RCs distribution is affected strongly by resuspension. RCs are considered like inert particles which can be removed with the fine sediment fraction (Anderson & Lively 1985, Erard-Le-Denn et al. 1993, Godhe & McQuoid 2003). For example, in the Gulf of Maine, resuspended RCs density can reach 8000 cysts m$^{-3}$ in the water column (Kirn et al. 2005). This process is also reported by Gayoso (2001) who observed resuspended RCs up to 140 m from the bottom probably due to a high mixing. Generally, in a shallow environment ($<7$ m) the reported wind velocity which allows resuspension is about 4 m s$^{-1}$ (Demers et al. 1987). In the case of a lagoon system, the first top centimeter of sediment was resuspended when the current velocity ranged between 10-30 cm s$^{-1}$. This process is due in particular to shell fragments which increase the erosion process (Denis et al. 1996). After their resuspension, pelagic RCs can be transported through advection and constitute new exogenous cyst banks. These are able to form new “hot spots” for bloom initiation if suitable conditions for vegetative growth are met (Anderson & Lively 1985, Kremp 2000, Kirn et al. 2005). In addition, pelagic RCs of *Alexandrium* spp. probably contribute to shellfish poisoning in the South China Sea (Wang et al. 2004b). Indeed the RC toxic profile is close to that of vegetative cells (Oshima et al. 1982).

**Importance of resting cysts in bloom dynamics**

Wyatt & Jenkinson (1997) suggested that bloom dynamics of cyst-forming dinoflagellates and more generally their persistence in a site are closely linked to all the factors which can affect the seed population. They also offered to take into account the frequency of periods in which the life cycle is successfully complete in order to determine the renewal of the cyst bank. The germinating cell survival, the population density, the probability of two gametes fusing to form a planozygote and the proportion of the planozygotes able to achieve encystment process determine the proportion of the newly produced RCs which modulate the renewal of cyst bank. The capacity of a dinoflagellate population to complete its life cycle depends on genetic characteristics (Figueroa et al. 2005). As suggested by Wyatt and Jenkinson (1997), the appropriate genetic basis is related to the accumulation of RCs in the sediment over the years. The beginning of a MDP


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