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

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SEEDING
BIOTURBATION
MATURATION
DISTRIBUTION MODE
DENSITY
SEDIMENT
GERMINATION
RECRUITMENT
SUSPENDED CYST
GEOGRAPHIC STRAIN

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. Excystment rate, mainly controlled by temperature and oxygen level, and the germling 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 & Enevoldsen 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 & Enevoldsen 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-Delbanco & 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 excystment influence dinoflagellate bloom dynamics (Kremp & Heiskanen 1999, Kim *et al.* 2002). Bloom success depends on various factors such as excystment, 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 pseudogonyaulax* (Montresor 1995) to several hours for *Alexandrium (Gonyaulax) tamarense* (Turpin *et al.* 1978). The formed planozygote is a large longitudinal biflagellate cell which accumulates storage compounds like lipidic granules and glucids, 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 &

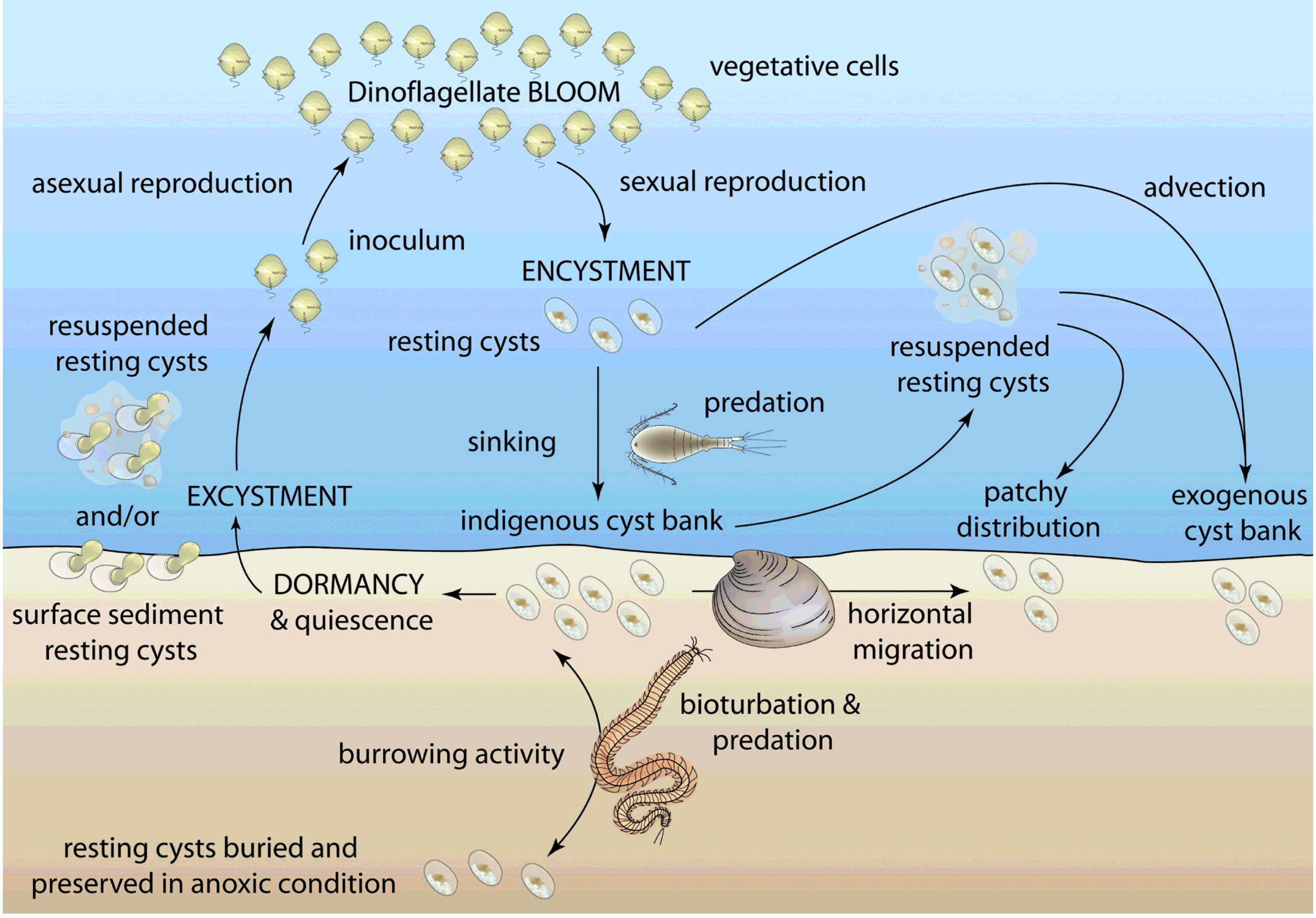

Fig. 1. – Conceptual model showing the key role of resting cysts in dinoflagellate bloom dynamics, the example of *Alexandrium* sp.

Lively 1985, Kokinos *et al.* 1998, Rochon & Marret 2004). In a majority of dinoflagellates, the wall of RCs is not smooth but spiny which promotes their survival (Sarjeant *et al.* 1987, Belmonte *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.

Alexandrium spp.	origin	site	PSP f.d.	RC density	unit	references
catenella	Chile	strait	1972	78	a	Cordova *et al.*, 2003
catenella	Australia	harbour	1993	> 100	a	Hallegraeff *et al.*, 1998
catenella	France	lagoon	1998	up to 175	b	Lilly *et al.*, 2002; Laabir *et al.*, 2002
catenella or tamarense	Japan	inland sea	1976	up to 869	a	Yamaguchi *et al.*, 1996
catenella or tamarense	Japan	bay	1992	up to 1912	a	Asakawa *et al.*, 1993; Itakura & Yamaguchi, 2001
catenella or tamarense	Japan	bay	1992	up to 3353	b	Mizushima & Matsuoka, 2004
catenella or tamarense	China	estuary	1995	up to 81	d	Wang *et al.*, 2004c; Zhou *et al.*, 2003
catenella or tamarense	China	coast	n.a	up to 398	d	Wang *et al.*, 2004a
tamarense	Argentina	gulf	1995	up to 300	a	Gayoso, 2001
tamarense	Japan	bay	1998	> 100	a	Ichimi *et al.*, 2001
tamarense	Korea	bay	1986	43 to 185	d	Han *et al.*, 1992; Kim *et al.*, 2002
tamarense	Japan	bay	1992	800 to 1300	c	Yamamoto &Tarutani, 1999; Tsujino *et al.*, 2002
tamarense	USA	embayment	n.a	$4.5\ 10^{7}$	e	Anderson *et al.*, 1982
fundyense	USA	gulf	1972	up to 635	a	Shumway *et al.*, 1988; Anderson *et al.*, 2005
fundyense	Canada	bay	1993	45	a	Haya *et al.*, 2003
minutum	France	coast	1985	up to 24000	b	Erard-Le-Denn *et al.*, 1993

resting cyst density in: cysts cm^{-3} (a), cysts g^{-1} dry sediment (b), cysts g^{-1} wet sediment (c), cysts g^{-1} (d), cysts m^{-2} (e). n.a: no available data

dinoflagellate species	origin	rate (%)	measured	induction	references
Alexandrium catenella	Australia	50	l	nutrient limitation	Hallegraeff *et al.*, 1998
Alexandrium tamarense	Japan	30	f	n.a	Ichimi *et al.*, 2001
Alexandrium tamarense	USA	20 to 40	l	nutrient limitation	Anderson *et al.*, 1984
Alexandrium tamarense	USA	20	l	P depletion	Anderson & Lindquist, 1985
Alexandrium tamarense	N-E Pacific	8	l	iron stress	Doucette *et al.*, 1989
Alexandrium minutum	Spain	1	f	n.a	Garcés *et al.*, 2004
Alexandrium pseudogonyaulax	Italy	5 to 11	l	nutrient limitation	Montresor & Marino, 1996
Gonyaulax polyedra	n.a	50 to 90	l	toxic metals	Okamoto *et al.*, 1999
Gyrodinium uncatenum	USA	9 to 13	l	nutrient limitation	Anderson *et al.*, 1985
Scrippsiella hangoei	Finland	40	f	n.a	Kremp & Heiskanen, 1999
Scrippsiella lachrymosa	USA	100	l	none	Olli & Anderson, 2002
Scrippsiella lachrymosa	USA	42	l	N depletion	Kremp & Anderson, 2004
Scrippsiella rotunda	Italy	> 90	l	nutrient limitation	Sgrosso *et al.*, 2001
Scrippsiella trochoidea	USA	10	l	nutrient limitation	Binder & Anderson, 1987
Scrippsiella trochoidea var. aciculifera	Italy	80	l	nutrient limitation	Sgrosso *et al.*, 2001
Pentapharsodinium tyrrhenicum	Italy	25	l	nutrient limitation	Sgrosso *et al.*, 2001
Calciodinellum operosum	Italy	20	l	nutrient limitation	Sgrosso *et al.*, 2001

n.a: no available data

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 (Sgrosso *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 Kirn *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 *Scrippsiella 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

MDP is achieved, the RC enters a quiescence period or excysts depending on environmental conditions (Montresor & Marino 1996, Kremp 2000, Sombrito *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 determinism (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 (Pfiester 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).

Table II. – Mandatory dormancy period (MDP) of resting cysts of several dinoflagellate species.

dinoflagellate species	origin	MDP (days)	references
Alexandrium catenella	Spain	< 5	Figueroa *et al*., 2005
Alexandrium catenella	Australia	28 to 55	Hallegraeff *et al*., 1998
Alexandrium tamarense	USA	60 to 180	Anderson & Keafer, 1987
Alexandrium tamarense	Korea	150	Kim *et al*., 2002
Alexandrium taylori	Italy	< 15	Giacobbe & Yang, 1999
Pirodinium gatunense	n.a	0,5	Pfiester, 1977
Scrippsiella hangoei	Baltic Sea	120	Kremp & Parrow, 2006
Scrippsiella lachrymosa	USA	60	Olli & Anderson, 2002
Scrippsiella trochoidea	USA	30	Binder & Anderson, 1987

n.a: no available data

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, Tsujino & 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., *Streblospio benedicti* and *Polydora cornuta* (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 encystment 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-

Table III. – Excystment rate of dinoflagellate species resting cysts (RC) isolated from natural sediment samples (a) or producted in laboratory experiment culture (b). Timing (d) represents the duration (days) of excystment corresponding to the rate observed.

dinoflagellate species	origin	excystment				references
		rate (%)	timing (d)	T° (C)	RC	
Alexandrium catenella	Spain	up to 90	< 20	24	b	Figueroa *et al.*, 2005
Alexandrium catenella	Australia	up to 100	98	17	b	Hallegraeff *et al.*, 1998
Alexandrium fundyense	USA	> 90	60 to 90	2 to 15	a	Anderson *et al.*, 2005
Alexandrium tamarense	USA	80-100	n.a	16	a	Anderson & Wall, 1978
Alexandrium tamarense	USA	> 90	< 20	7 to 19	a	Anderson & Morel, 1979
Alexandrium tamarense	USA	up to 67	20	15	a	Anderson *et al.*, 1987
Alexandrium tamarense	Canada	up to 99	n.a	4 to 15	a	Castell-Perez *et al.*, 1998
Alexandrium tamarense	Japan	up to 74	10	10 to 15	a	Itakura & Yamaguchi, 2001
Alexandrium tamarense	Korea	up to 70	10	14	a	Kim *et al.*, 2002
Alexandrium tamarense	Japan	65	14	12	a	Tsujino *et al.*, 2002
Alexandrium pseudogonyaulax	Italy	up to 83	n.a	20	b	Montresor & Marino, 1996
Gonyaulax verior	USA	up to 96	20	15	a	Anderson *et al.*, 1987
Gonyaulax rugosum	USA	up to76	20	20	a	Anderson *et al.*, 1987
Gymnodinium catenatum	Portugal	up to 100	n.a	18	a	Amorin *et al.*, 2001
Gymnodinium nolleri	Danemark/Sweden	90	60	20	b	Figueroa *et al.*, 2006
Gyrodinium uncatenatum	USA	up to 84	20	15	a	Anderson *et al.*, 1987
Lingulodinium polyedrum	Scotland	up to 97	n.a	20	a	Lewis *et al.*, 1999
Scrippsiella lachrymosa	USA	70	6	15	b	Olli & Anderson, 2002
Scrippsiella ramonii	Italy	96-100	n.a	20	b	Montresor *et al.*, 2003
Scrippsiella trochoidea	Italy	65-100	n.a	20	b	Montresor *et al.*, 2003
Scrippsiella trochoidea	USA	60-100	n.a	15	b	Binder & Anderson, 1987
Scrippsiella trochoidea	USA	70	5	18	b	Binder & Anderson, 1990
Zygabikodinium lenticulatum	South Africa	20-28	< 3	16 & 20	a	Joyce & Pitcher, 2004

n.a: no available data

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 *Scrippsiella hangoei* that excysts (Kremp 2000). Excystment can be synchrone for *S. lachrymosa* (Olli & Anderson 2002) or asynchrone 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, asynchrone 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 (Kirn *et al.* 2005). In the same way, in a semi-enclosed shallow embayment, when algal mattes 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 *Scrippsiella 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. tamarense* 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-Delbanco & 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 & Burkholder (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 (planomeiocyst) is a diploïde 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. tamarense* (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

Blooms are initiated in very different areas which could be closed or more open (Table I). 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 Saldanha 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 10^{7} cysts m^{-2} of sediment) *of A. tamarense* 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 (McGillicuddy *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 10^{4} to 10^{6} cysts cm^{-3} (Kremp 2000), whereas *Alexandrium* spp. RC density was generally about 10^2 cysts cm^{-3} and rarely exceeded 10^3 cysts cm^{-3} (Table I). In tropical areas the RC density is clearly lower than in temperate areas (Godhe *et al.* 2000). Moreover, preferential areas for the deposition and the accumulation of RCs are very different but seem to be related to enclosed areas such as lagoons or embayments, or more open areas like upwelling zones (Table I). For example in shallow lagoons (Southern New England) and a bay (Tokyo, Japan) the RC density reaches 10^2 to 10^3 cysts cm^{-3} (Matsuoka *et al.* 2003, Pospelova *et al.* 2004), and in coastal upwelling sites (South Africa) RC density could reach up to 10^2 cysts cm^{-3} (Joyce *et al.* 2005).

Distribution mode

The RCs distribution is generally heterogeneous resulting in accumulation patches (Cho & Matsuoka 2001, Matsuoka *et al.* 2003, Garcés *et al.* 2004, Pospelova *et al.* 2004). RCs are mainly distributed in the first 3 cm of sediment. Their density decreased considerably with depth but they could be detected down to 27 cm in the sediment (Anderson *et al.* 1982, Erard-Le-Denn *et al.* 1993, Irwin *et al.* 2003). Buried RCs in anoxic sediment seem to conserve their viability, depending on species (Keafer *et al.* 1992). For example, RCs of the genus *Alexandrium* buried down to 13 cm sediment depth are viable and could participate to the seeding once they are transported to the sediment surface (Mizushima & Matsuoka 2004).

Factors controlling resting cyst distribution

The composition and the density of the cyst bank are directly linked to the composition, the density and the encystment capability of each species in the overlying water column. It has been shown that the higher RCs densities are found in areas of maximum vegetative cell density (Garcés *et al.* 2004, Joyce *et al.* 2005). The RC density also increased in fine sediment with high organic matter content, which resulted in a preferential accumulation of RCs in mud rather than a sandy substrate (Yamaguchi *et al.* 1996, Kremp 2000, Gayoso 2001, Godhe & McQuoid 2003, Matsuoka *et al.* 2003, Wang *et al.* 2004c, Joyce *et al.* 2005). Bioturbation, responsible for vertical and horizontal migrations due to polychaete and mollusc activities, strongly affects RCs distribution and recruitment (Marcus & Schmidt-Gengenbach 1986, Tsujino *et al.* 2002). For example, *N. laevigata* 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 (Keafer *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 (Keafer *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-Poulichet *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 germling 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

(Table II) and the survival time of RCs (Anderson 1980, Lewis *et al.* 1999) define a "species-specific" dynamic pattern in a determined area. The proportion of RCs within the cyst bank which is able to excyst and to survive determines the inoculum size (Anderson 1998, Kremp 2000). Hydrodynamical processes affect the distribution of RCs which can be transported into areas where excystments occur in environment unsuitable for vegetative growth and for bloom initiation. Seasonal variations of the cyst bank density can be related to a temporary unbalance between supplies (encystment) and losses (excystment). The possibility that gradual losses combined with less supplies could result in a decrease in the intensity and the frequency of the bloom can not be excluded (Kremp 2000, Kim *et al.* 2002, Anderson *et al.* 2005).

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