

# Encystment of *Zygabikodinium lenticulatum* (Dinophyceae) during a summer bloom of dinoflagellates in the southern Benguela upwelling system

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## Abstract

A sediment trap was placed off Lambert's Bay in the southern Benguela upwelling system for 20 days in March 2001 to investigate the flux of dinoflagellate cysts from the upper mixed layer. A dinoflagellate bloom dominated by the small autotroph *Gyrodinium zeta*, developed in late March in association with intense stratification of the water column. The bloom included several heterotrophic species, in particular *Zygabikodinium lenticulatum*. The mass sedimentation of cysts of *Z. lenticulatum*, indicated by their dominance in the sediment trap, coincided with the maximum abundance of the vegetative stage. Observations of few cysts in the upper mixed layer indicated that cysts were formed over a short period and sank rapidly in the water column. Current patterns revealed predominantly northward flow in surface waters and southward flow in bottom waters, with current shear noticeable between 20 and 30 m depth. The formation of cysts by *Z. lenticulatum* under these patterns of flow serves to retain the population, preventing washout from the coastal environment. Analysis of sediment samples revealed that *Z. lenticulatum* also dominated the cyst assemblage of the sediments. Experimental results indicated a dormancy period of approximately 48 days, however, only a small fraction of cysts (20–28%) germinated under experimental conditions.

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## 1. Introduction

Many dinoflagellate species in coastal temperate waters have been documented to form resting cysts, a resistant, dormant stage that is formed after sexual reproduction in the life cycle of dinoflagellates (Pfeister and Anderson, 1987; Nehring, 1993; Anderson et al., 1995). The formation of cysts has a variety of potential functions in the overall ecology of dinoflagellates, including: a role in genetic recombination that may lead to increased variation which is important for species survival (Anderson, 1984); species dispersal (Anderson et al., 1995); seeding for bloom initialisation (Cembella et al., 1988; Ishikawa and Taniguchi, 1996); and survival

through unfavourable conditions as cysts are able to remain dormant, yet viable, in bottom sediments for many years even in anoxic conditions (Dale, 1983; Nehring, 1993).

In situ measurements of dinoflagellate cyst production and deposition from coastal marine environments are rare. In the field, it is often difficult to link resting cysts to either the parent population or the environmental conditions which induce their formation, as cysts are rarely found in the plankton because they are quickly transported to the seafloor (Anderson et al., 1985; Pitcher, 1986). Episodic encystment events are not usually detected by way of standard water column sampling alone. However, by combining water column and sediment trap studies sufficient information can be provided for the estimation of the flux of cysts to the benthos (Heiskanen, 1993), and on the timing and conditions favouring encystment.

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In order to investigate dinoflagellate cyst production in the southern Benguela upwelling system a sediment trap was deployed off Lambert's Bay on the West Coast of South Africa during March 2001. During the period of deployment a dinoflagellate bloom developed that was dominated by *Gyrodinium zeta*, but included several heterotrophic species, in particular *Zygabikodinium lenticulatum*. The presence of high numbers of *Z. lenticulatum* in the water column and the subsequent encystment of this species provided the opportunity to establish the conditions under which these cysts were formed.

Little information is available on the ecological behaviour of *Zygabikodinium lenticulatum*. It is a heterotrophic dinoflagellate that has been shown to feed on a variety of dinoflagellates and diatoms, and detrital particles (Jacobson and Anderson, 1986). It produces a cyst by means of sexual reproduction (Matsuoka, 1988), and is common worldwide in coastal areas in both vegetative and cyst forms. In this study three forms of *Z. lenticulatum* were observed (Fig. 1): a vegetative stage (Fig. 1a), a pale-pink lenticular cell in which both the epitheca and hypotheca are of similar size and shape, the cingulum is circular, ribbed and has well developed lists; an intermediate stage where the cyst is seen forming within the theca (Fig. 1b and c), the forming cyst is light-brown in colour, with some red pigmentation, is smaller than the vegetative cell and cyst, and it also lacks the hard resistant wall of the mature cyst stage; and, the cyst stage

(Fig. 1d), a dark-brown lenticular cyst with a micro-granulate surface (Matsuoka, 1988). This paper reports on the abundance of these stages of *Z. lenticulatum* in the water column, in sediment trap collections and in surface sediments. The environmental conditions influencing cyst formation were established by monitoring the upper water column and the vertical flux of cysts to the sediments. The dormancy and viability of these cysts were also investigated which, together with observations of current flow patterns, provided insight into the ability of cysts to utilize the advective regime of the upwelling system to seed future populations.

## 2. Materials and methods

### 2.1. Sediment trap

A sediment trap, as described by Knauer et al. (1979), was placed off Lambert's Bay, approximately 2 nautical miles offshore at station S3 (32° .05.020S, 18° .16.010E) (Fig. 2) for a period of 20 days, from 13th March to 1st April 2001. Water depth at the site of deployment was 50 m, and the sediment trap was set below the thermocline at 20 m to collect only newly formed rather than resuspended material. The trap was sampled on 21st and 28th March and 1st April. Sediment trap collections were subsampled to provide material for counting and for germination experiments. Material for

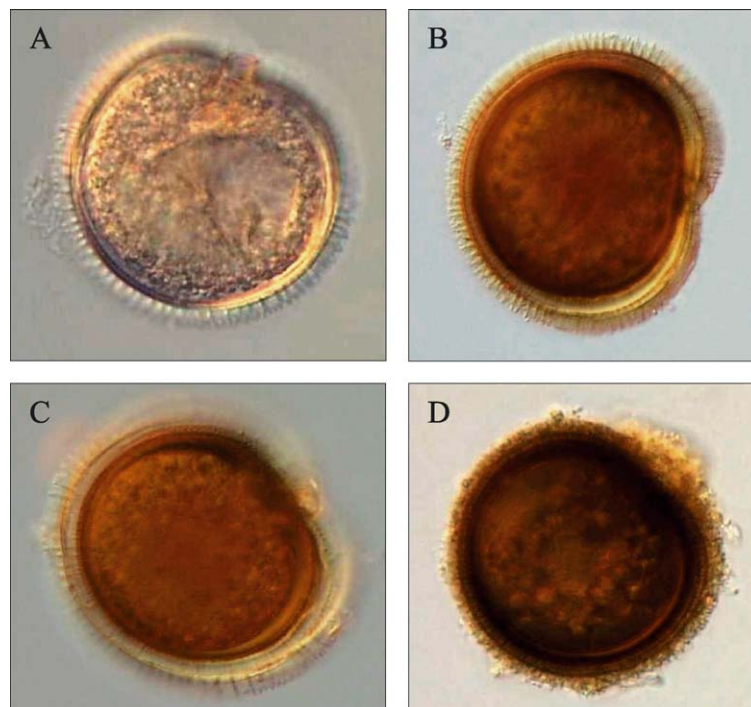


Fig. 1. Observed stages of *Zygabikodinium lenticulatum* off Lambert's Bay. (A) Vegetative cell, (B and C) intermediate stage showing cyst formation within the theca, and (D) cyst.

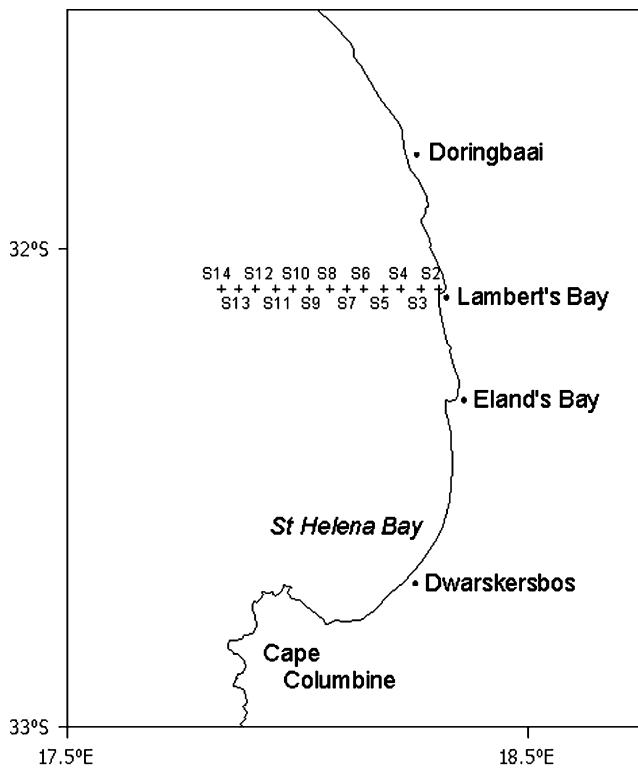


Fig. 2. Map of the study area showing the offshore transect line (S2–S14), and the site of sediment trap deployment, time series measurements and grab sample station (S3).

counting was fixed in 2.5% buffered formalin and material for germination experiments was stored at 4 °C. Cyst flux (cysts  $m^{-2} d^{-1}$ ) was determined by multiplying the concentration of cysts in the trap (cysts  $m^{-3}$ ) by the trap volume ( $m^3$ ), dividing this by the area of the trap aperture ( $m^2$ ), and dividing this by the time for which the trap was deployed (d) (Pitcher, 1986).

## 2.2. Time series

Wind velocity was recorded at a land-based meteorological station for the duration of deployment of the sediment trap, while the water column at the site of deployment (station S3) was intensively monitored. A Seabird CTD and Wetstar fluorometer were used for daily profiles of the water column for temperature and fluorescence. Daily water samples from discrete depths in the water column (0 m, 5 m, 10 m and 20 m) were collected in 1-l NIO water bottles, for nutrient and chlorophyll *a* analyses, and examination of the phytoplankton assemblage. From the 1-l sample, 50 ml was collected for nutrient analysis, 100 ml for chlorophyll analysis, and 200 ml for phytoplankton analysis. Nutrient samples were analysed by means of an auto-analyser as described by Mostert (1983). Chlorophyll *a* samples were analysed by fluorometric analysis as detailed by Parsons et al. (1984) and extracted chlorophyll values were used to

calibrate in situ fluorescence profiles. Phytoplankton samples were preserved with 2.5% buffered formalin and enumerated using an inverted microscope according to the Utermöhl method (Hasle, 1978). Aanderaa current meters were deployed at 10 m and 35 m and current speed and direction were recorded hourly.

## 2.3. Offshore transect

During the course of trap deployment an offshore transect comprising 13 stations (2 nautical miles apart) (Fig. 2) was sampled on 16th March to provide information on the spatial distribution of phytoplankton in relation to the hydrographic regime. A Seabird CTD and Wetstar fluorometer were used to profile the water column for temperature and fluorescence. Water samples from discrete depths in the water column (0 m, 5 m, 10 m and 20 m) were collected for chlorophyll *a* analysis and examination of the phytoplankton assemblage. A 300 kHz Acoustic Doppler Current Profiler (ADCP) was used to measure currents at each station along the transect.

## 2.4. Sediment collection and processing

Surface sediments were collected on 13th March, from station S3 (Fig. 2), by means of a small Van Veen grab (Kingston and Riddle, 1989). A subsample of sediment was removed from the grab and stored in the dark at 4 °C to prevent cyst germination. For cyst identification and enumeration the remaining sediment was further processed according to the method of Wall and Dale (1968). A small amount of the sediment was gently sonicated for 1 min; from this a 2 ml subsample was filtered through a 125  $\mu m$  and a 20  $\mu m$  mesh sieve. The slurry remaining on the 20  $\mu m$  mesh was backwashed into a beaker with FSW and the final volume was noted. From the final volume, 1 ml was removed by pipette and placed on a Sedgwick-Rafter slide and examined under an Olympus microscope. Cyst concentrations were presented as the number of cysts  $ml^{-1}$  wet sediment. Photographs were taken using a digital camera attachment.

## 2.5. Germination experiments

Newly formed cysts of *Zygabikodinium lenticulatum* recovered from the sediment trap were used to determine the length of the dormancy period. Material recovered from the sediment trap on 28th March was stored in the laboratory at 4 °C in total darkness. For each batch of germination experiments, 25 cysts were isolated and placed individually into the wells of a culture plate, covered with FSW, and incubated under a 12:12 L:D cycle at 16 or 20 °C; these were then checked daily for any germinations. Three discrete batches of cysts were isolated and incubated 7, 154 and 251 days following their collection in the sediment trap.

### 3. Results

#### 3.1. Wind

Local wind events govern the hydrography and phytoplankton populations of the inshore environment off Lambert's Bay (Pitcher et al., 1998). The period of sediment trap deployment was initially dominated by southerly winds favouring upwelling, while the latter half of deployment was marked by an extended period of wind reversal favouring downwelling (Fig. 3).

#### 3.2. Hydrographic observations and dinoflagellate bloom development

As a consequence of the observed wind patterns, sea surface temperatures were initially low, but were followed by a period of warming and intense stratification (Fig. 4a). Chlorophyll *a* concentrations increased dramatically with increased stratification, and in some instances exceeded  $100 \text{ mg m}^{-3}$  (Fig. 4b). Community analyses indicated a shift from a community dominated by diatoms, notably a *Thalassiosira* species, to one dominated by dinoflagellates, in particular *Gyrodinium zeta* (Fig. 5).

Nutrient distributions reflected the thermal structure, in that nitrate concentrations were negatively correlated to temperature. Nitrate levels in surface waters initially ranged between 4 and  $8 \mu\text{g l}^{-1}$ , but declined to around  $2 \mu\text{g l}^{-1}$  in association with the development of the dinoflagellate bloom in stratified waters (Fig. 4c). Having initially been observed in low numbers, the vegetative

population of *Zygabikodinium lenticulatum* showed a gradual increase from 22nd until 25th March when a maximum number of  $48,981 \text{ cells l}^{-1}$  was recorded at the surface (Fig. 4d). This increase in the vegetative population of *Z. lenticulatum* coincided with the increase in chlorophyll *a* concentration. No cysts of *Z. lenticulatum* were found in the surface waters. Intermediate stages were observed, primarily in deeper water between 26th and 30th March following a marked decline in the number of vegetative stages in the surface waters (Fig. 4e). Current data at 10 m depth indicated a higher incidence of northward flow compared to that at 35 m (Fig. 6).

#### 3.3. Offshore transect

The 24 nautical mile transect comprising 13 stations off Lambert's Bay was sampled on 16th March 2001 following persistent upwelling winds. Consequently a progression from relatively well mixed water close inshore to a strongly stratified water column further offshore was observed (Fig. 7a). Here a thermocline at approximately 25 m depth separated warm surface water of approximately  $14 \text{ }^\circ\text{C}$  from cold bottom water of approximately  $11 \text{ }^\circ\text{C}$  (Fig. 7a). Chlorophyll *a* values were highest in the frontal boundary region where stratified and mixed waters met, between stations 4 and 6. The chlorophyll *a* maximum offshore of the frontal region was subsurface (Fig. 7b). *Zygabikodinium lenticulatum* concentrations at the offshore stations were extremely low and cells were observed only in surface waters. Inshore they were at a maximum,  $48,764 \text{ cells l}^{-1}$ , in surface waters at station 5 which corresponded

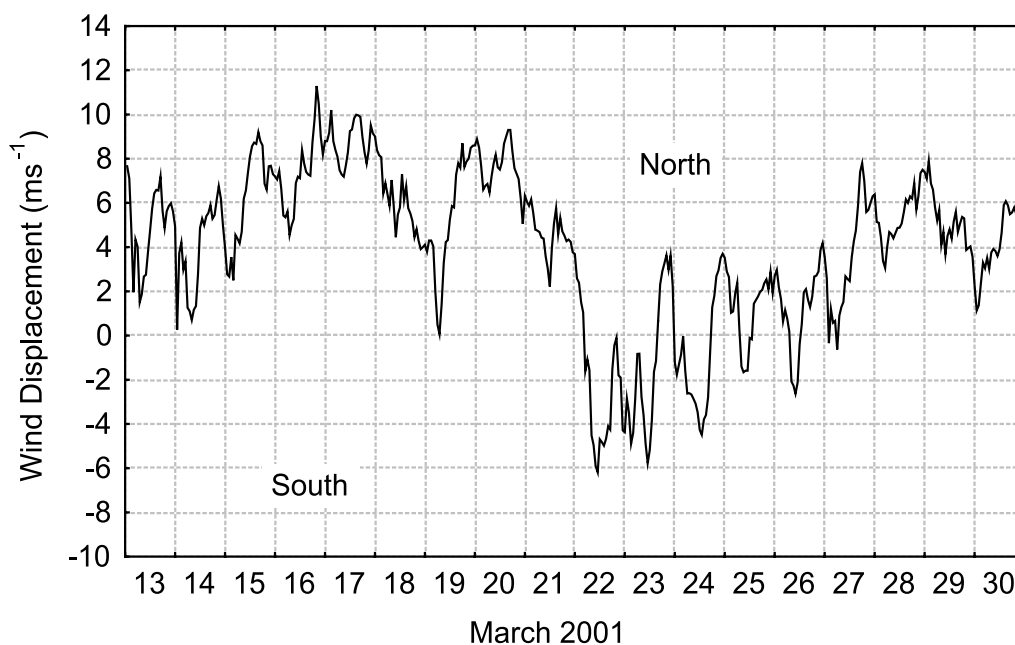


Fig. 3. Time series of wind displacement for the period 13–30 March 2001.

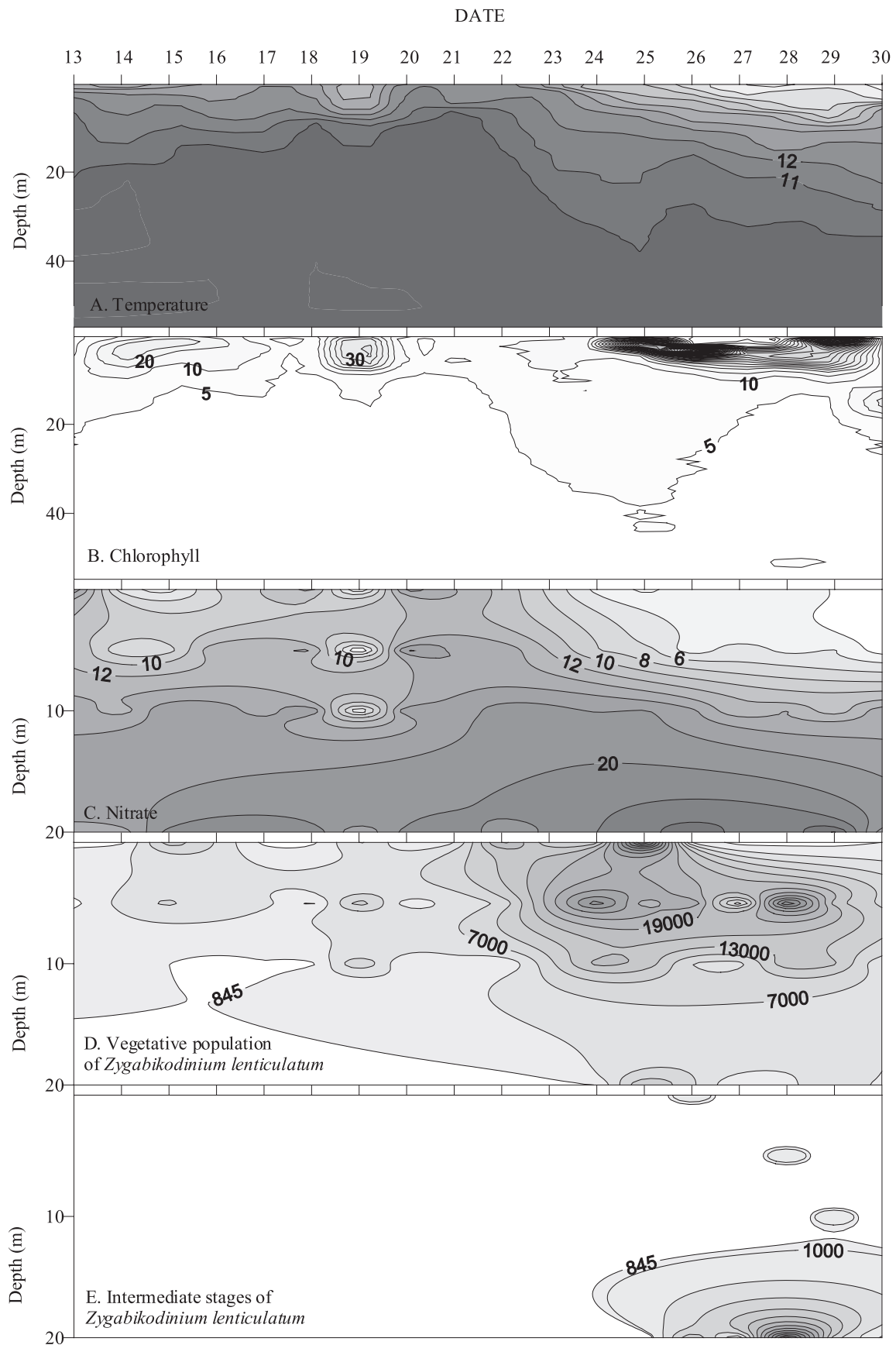


Fig. 4. Time series of (A) temperature ( $^{\circ}\text{C}$ ), (B) chlorophyll ( $\text{mg m}^{-3}$ ) (depth scale 0–50 m), (C) nitrate ( $\mu\text{g l}^{-1}$ ), (D) vegetative population (cells  $\text{l}^{-1}$ ), and (E) intermediate stages (cells  $\text{l}^{-1}$ ) of *Zygaibokodinium lenticulatum* (depth scale 0–20 m) off Lambert's Bay (station S3) from 13 to 30 March 2001.

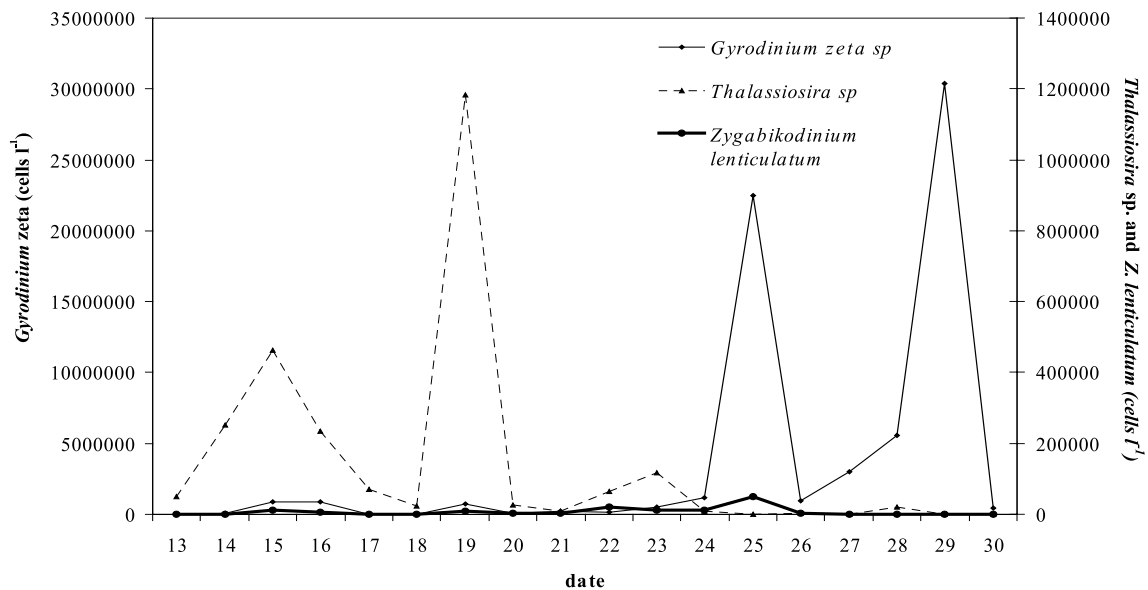


Fig. 5. Time series: surface (0 m) cell concentrations of *Zygaibokodinium lenticulatum* in relation to the dominant species of phytoplankton between 13 and 30 March 2001.

with the chlorophyll *a* maximum associated with the upwelling front (Fig. 7c). Current data along the transect (Fig. 7d) indicated that surface flow was predominantly northward as expected under conditions of upwelling. Northward flow was centred at stations 9 and 10, with an offshore component evident to the flow at the inner stations. Strong current shear was observed between 20 and 30 m depth with southward flow dominating the colder bottom waters.

### 3.4. Sediment trap collections

Few cysts were present following the first retrieval of the sediment trap, on 21st March, seven days after deployment, except for a small number of cysts of *Zygaibokodinium lenticulatum* and unidentified Round Brown cysts (Table 1). The second retrieval, seven days later, on 28th March, revealed a high number of intermediate stages and cysts of *Z. lenticulatum*. Although intermediate stages and cysts of *Z. lenticulatum* again dominated the final trap retrieval four days later, on 1st April, cysts of *Protoperidinium conicum*, *Protoperidinium leonis*, *Polykrikos schwartzii* and unidentified Round Brown cysts were also present (Table 1). The flux of *Z. lenticulatum* was greatest during the final period of deployment, from 28th March to 1st April, when 169,337 cysts  $m^{-2} d^{-1}$  were lost from the surface waters (Table 1).

### 3.5. Sediment assemblage

Sixteen distinctive cyst types were identified in the surface sediments off Lambert's Bay (Table 1). Total cyst abundance was 805 cysts  $ml^{-1}$  sediment consisting

primarily of cysts formed from heterotrophic dinoflagellates belonging to the Protoperidiniaceae. Cysts of autotrophic dinoflagellates were rare, with the exception of cysts of *Alexandrium catenella*. *Zygaibokodinium lenticulatum*, *A. catenella* and *Protoperidinium conicum* dominated the assemblage (Table 1). *Zygaibokodinium lenticulatum* thus appeared to be an important component of the cyst-forming dinoflagellates in the Southern Benguela upwelling system.

### 3.6. Germination experiments

Cysts incubated at 16 and 20 °C on 4th April, seven days after collection demonstrated similar mandatory dormancy periods of 49 and 48 days, respectively (Fig. 8a). The number of cysts germinating at both temperatures was low, 20%. In additional experiments, 154 and 251 days after collection, the number of cysts germinating was again low, ranging between 20 and 28%. The additional experiments also revealed that having been through the mandatory dormancy period, cysts of *Zygaibokodinium lenticulatum* were able to germinate within two or three days of isolation and incubation (Fig. 8b and c).

## 4. Discussion

The bloom off Lambert's Bay at the end of March 2001 consisted primarily of dinoflagellate species dominated by *Gyrodinium zeta* which attained cell concentrations in excess of  $20 \times 10^6$  cells  $l^{-1}$ . The heterotrophic dinoflagellate *Zygaibokodinium lenticulatum* attained a maximum concentration of 48,981 cells  $l^{-1}$  on 25th

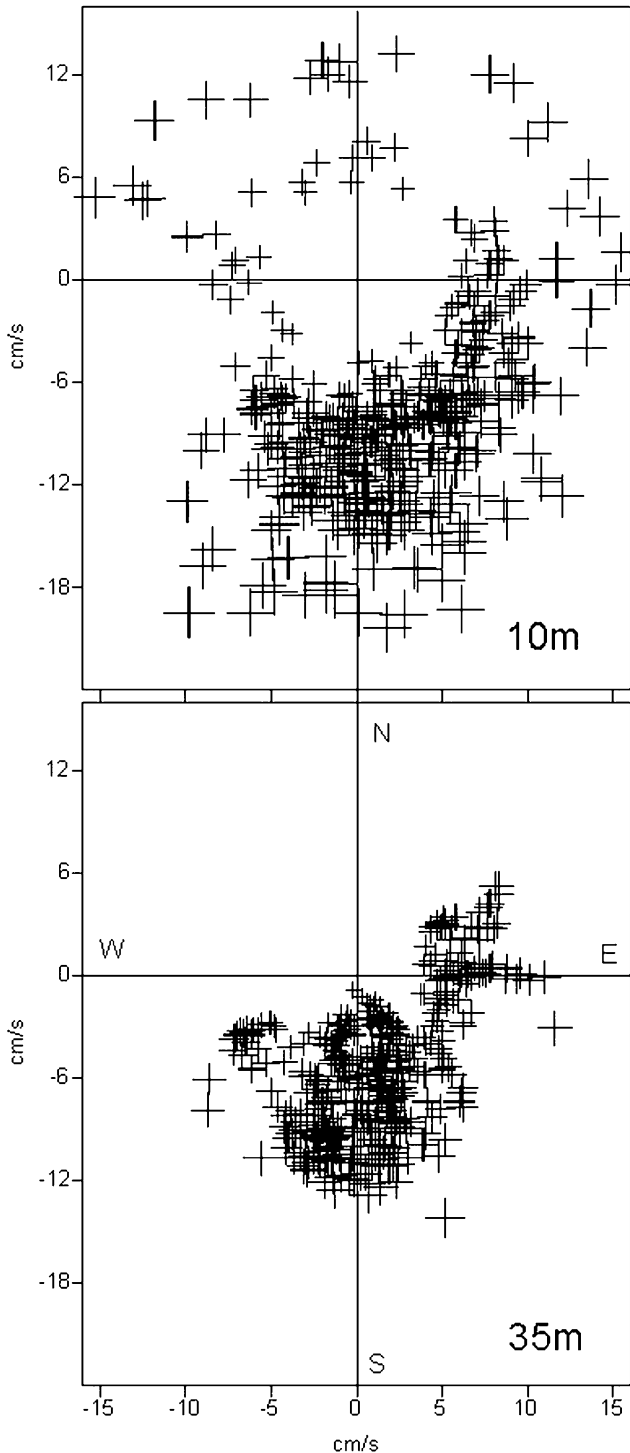


Fig. 6. Current components at 10 and 35 m depth at the monitoring station (S3) off Lambert's Bay, 13–30 March 2001.

March and was the most abundant cyst-forming species encountered during the study. Although few resting stages were seen in the surface waters the sediment trap was dominated by intermediate stages and cysts of this species, indicating that *Z. lenticulatum* contributed significantly to the phytoplankton settling from the

upper mixed layer. Few other cyst-forming dinoflagellate species were sufficiently abundant in the water column to produce large depositions of cysts.

Little is known about what stimulates cysts to form in the natural environment. Under laboratory conditions nutritional factors, especially nitrogen starvation (Pfeister, 1975; Anderson et al., 1984; Pfeister and Anderson, 1987; Blanco, 1995; Nehring, 1996), are argued to be the most important factors leading to cyst formation, and to a lesser extent, temperature and light intensity (Anderson et al., 1983; Sgroso et al., 2001) also influence cyst formation. These findings have been reported for both heterotrophic and autotrophic species, although the majority of studies on cyst production have been conducted on autotrophic species (Anderson et al., 1984; Coats et al., 1984; Binder and Anderson, 1987; Blackburn et al., 1989; Blanco, 1995; Ichimi et al., 2001; Sgroso et al., 2001). Consequently cysts are generally considered to form in response to adverse conditions. Past studies of cyst formation in the field have largely been inconclusive regarding the stimulus for cyst induction. Wall and Dale (1968) monitored cyst abundance of three dinoflagellate species during the latter stages of three different blooms, and Anderson and Morel (1979) studied the formation of cysts during a bloom of *Gonyaulax tamarensis* yet no one was able to explain the timing of encystment as no obvious nutritional deficiencies or environmental cues were identified. Anderson (1998), Kremp and Heiskanen (1999) and Godhe et al. (2001) concluded that there was no evidence of nutrient limitation inducing encystment in the field. Encystment of *Zygabikodinium lenticulatum* during this study corresponded to nutrient deficient conditions typifying warm stratified coastal waters following downwelling. The influence of the inorganic nutrient environment on the physiological status of a heterotrophic dinoflagellate such as *Z. lenticulatum* is, however, uncertain and any possible link between the observed low nutrient conditions and encystment is expected to be indirect.

It was apparent from this study that the major production of cysts of *Zygabikodinium lenticulatum* followed shortly after the maximum observed concentration of vegetative cells in the surface waters. Dinoflagellate cysts are produced through sexual reproduction which has previously been found to coincide with or immediately follow the maximum abundance of the vegetative stage (Heaney et al., 1983; Heiskanen, 1993; McQuoid and Hobson, 1996; Montresor et al., 1998; Zohary et al., 1998; Kim and Han, 2000). Off Lambert's Bay the initial flux of cysts was low, 1016 cysts  $m^{-2} d^{-1}$ , but increased until a flux of 169,337 cysts  $m^{-2} d^{-1}$  was recorded three to seven days after detecting the maximum vegetative cell concentration. Intermediate stages in the water column were first observed, albeit in very low numbers, on 26th March.

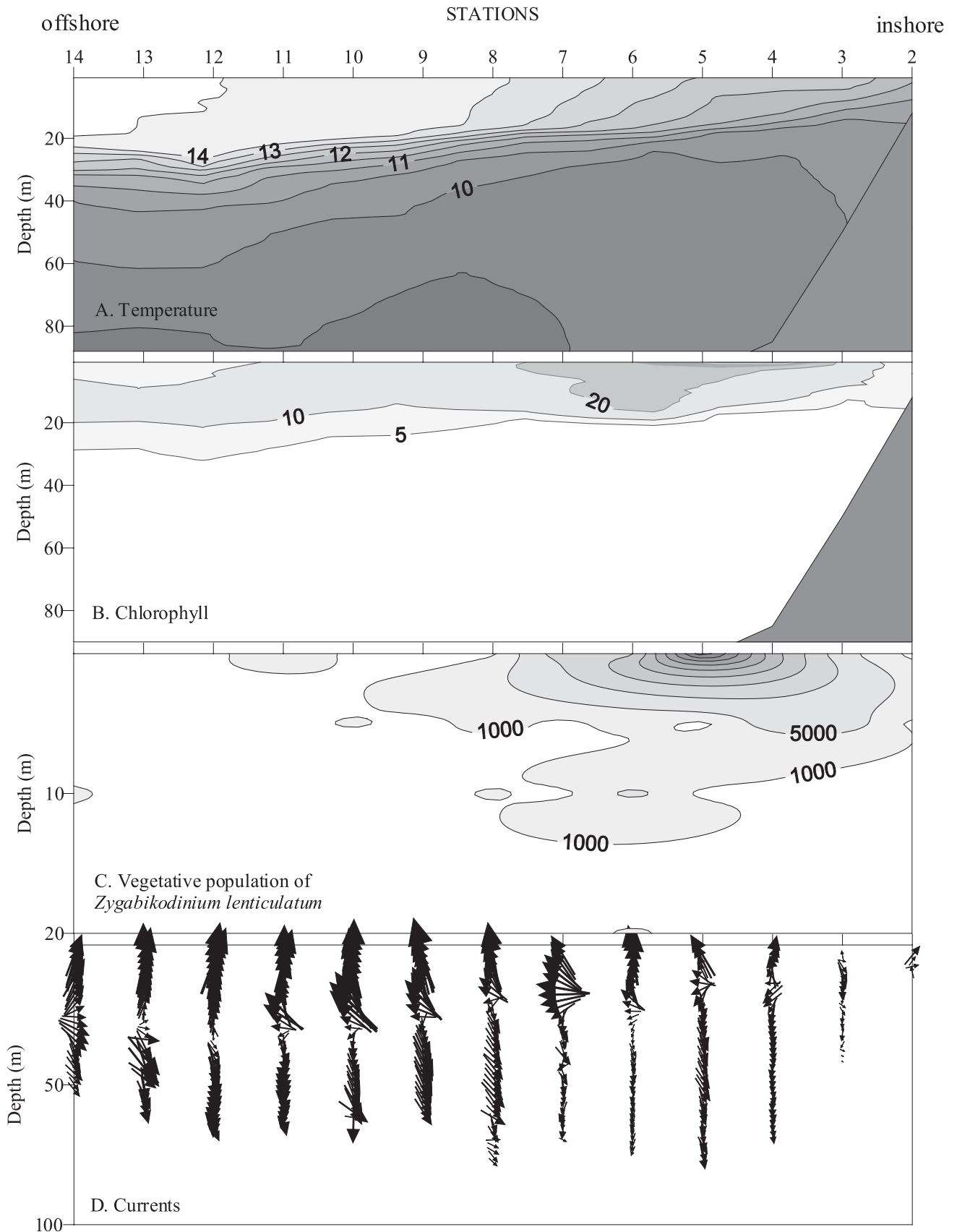


Fig. 7. A 24 nautical mile transect off Lambert's Bay conducted on 16th March 2001 of (A) temperature ( $^{\circ}\text{C}$ ), (B) chlorophyll ( $\text{mg m}^{-3}$ ) (depth scale 0–80 m), (C) vegetative population ( $\text{cells l}^{-1}$ ) of *Zygaibikodinium lenticulatum* (depth scale 0–20 m), and (D) current vectors (depth scale 0–100 m).

Table 1

The flux of dinoflagellate cysts from the upper mixed layer, from 13th March to 1st April 2001, as determined from sediment trap deployments, and the concentration of cysts in the sediments off Lambert's Bay

Species list	Sediment trap						Sediments	
	Sampling date and cyst flux ( $\text{m}^{-2} \text{d}^{-1}$ )						Concentration	
	21/3/01	%	28/3/01	%	1/4/01	%	( $\text{ml}^{-1}$ sediment)	%
<i>Scrippsiella crystallina</i>							25	3.1
<i>S. lachrymosa</i>							13	1.6
<i>S. trochoidea</i>							13	1.6
<i>Protoperidinium claudicans</i>							38	4.7
<i>P. conicum</i>					1039	0.6	100	12.4
<i>P. leonis</i>					1039	0.6	50	6.2
<i>P. oblongum</i>							13	1.6
<i>P. pentagonum</i>							38	4.7
<i>Protoperidinium</i> spp.							13	1.6
<i>Polykrikos schwartzii</i>					2078	1.2	75	9.3
<i>Polykrikos kofoidii</i>							13	1.6
<i>Zygabikodinium lenticulatum</i>	1016	67	109,027	100	169,337	96	150	18.6
Round Brown	508	33			2078	1.2	75	9.3
<i>Alexandrium catenella</i>							138	17.1
<i>Spiniferites</i> sp. 1							13	1.6
sp. 1							38	4.7
Total	1524	100	109,027	100	175,571	100	805	100

The temporal inconsistency between the water column maximum of vegetative cells, on 25th March, and the major deposition of intermediate stages, on 28th March, indicates the possibility of a motile planozygote stage preceding the hypnozygote stage (Heiskanen, 1993), as has been observed elsewhere. Motile planozygotes, produced after fusion of gametes, can remain viable in the water column for 3–20 days (Dale, 1983), before losing their motility and changing into hypnozygotes (Pfeister and Anderson, 1987). The fact that resting cysts were not observed in the water column, that the maximum number of intermediate stages was observed at 20 m, and that the sediment trap collections were entirely dominated by cysts, indicates that cysts were formed over a short period and sank rapidly from the surface layer.

For dinoflagellates with a distinctive cyst stage, studies of vegetative and cyst cycles, coupled with studies of their physical environment, may reveal strategies of introduction and maintenance of local populations. The ability of dinoflagellate cysts to sink rapidly (Anderson et al., 1985), and to maintain their viability in bottom sediments under adverse conditions over long periods provides many dinoflagellate species with a means of sustaining local populations. Within the upwelling system off Lambert's Bay, cyst formation appears to equip dinoflagellates with a survival strategy preventing washout from the coastal environment. Here the dinoflagellate populations appear as surface blooms associated with equatorward flow in the region of the upwelling front, which is displaced from the coast during the active phase of upwelling (Pitcher et al., 1998). During these conditions cyst formation and their

flux into the predominantly poleward undercurrent will serve to maintain populations within their area of origin. Alternately blooms accumulate inshore following a decline in wind stress causing cross-shelf currents to be directed onshore. Under these conditions the onshore movement of the upwelling front and associated bloom is often accompanied by barotropic poleward flow (Pitcher et al., 1998), thereby retaining both vegetative and cyst populations within their area of origin.

Many dinoflagellate cysts have an endogenously controlled mandatory dormancy period lasting from weeks to months, during which germination is not possible (Anderson et al., 1985; Ishikawa and Taniguchi, 1996). Results obtained in this study, indicate that the dormancy period for *Zygabikodinium lenticulatum* is of the order of six to seven weeks, but the number of germinating cysts is low, between 20 and 28%. A small number of germinating cysts has also been observed in other species of heterotrophic dinoflagellates, e.g. *Protoperidinium claudicans* and *Protoperidinium conicum* (Ishikawa and Taniguchi, 1997). Following the dormancy period, the germination of cysts is likely to depend on a range of external factors (Nehring, 1993) and the number of germinating cysts may be considerably higher in their natural environment. Within an upwelling system there are also several physical mechanisms that may potentially resuspend cysts, thereby introducing them into the photic zone and so contributing to the development of future vegetative populations.

Dale et al. (1999) argue that strong coastal upwelling usually favours diatoms and other phytoplankton groups rather than dinoflagellates, and that this is

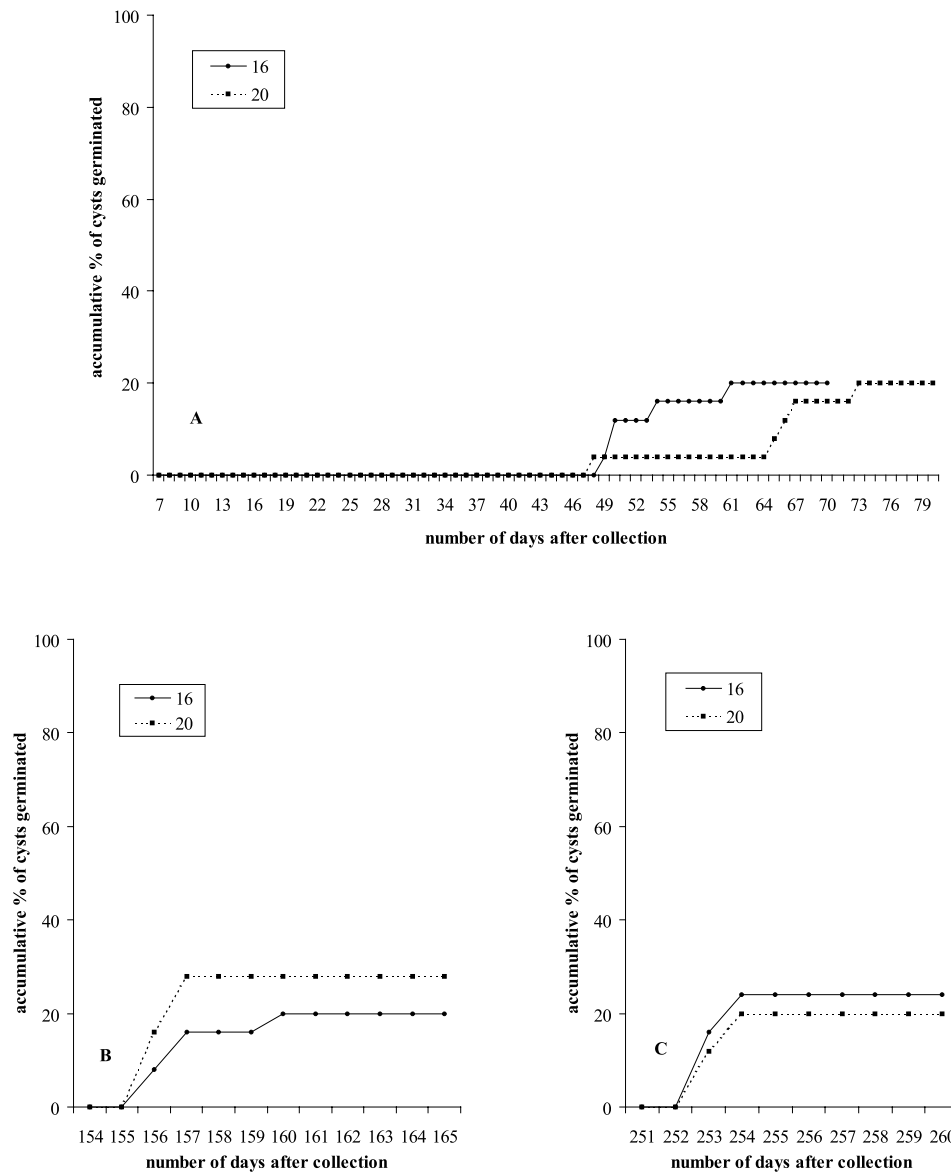


Fig. 8. *Zygabikodinium lenticulatum* germination experiments (25 cysts in each batch) (A) seven days, (B) 154 days and (C) 251 days after the collection of cysts.

reflected in the cyst record by relatively low cyst abundance and by cyst assemblages that are dominated by heterotrophic species. Observations off Lambert's Bay tend to support those of Dale et al. (1999) in that cyst abundance is low (805 cysts ml<sup>-1</sup> sediment) and cysts of heterotrophic dinoflagellates dominate the assemblage, the most abundant cyst being *Zygabikodinium lenticulatum* (150 cysts ml<sup>-1</sup> sediment). However, the Lambert's Bay region is well known for its many red tides attributed to high biomass dinoflagellate blooms (Pitcher and Calder, 2000), and cysts of the toxic dinoflagellate *Alexandrium catenella*, a species known to form blooms in the region, were the second most abundant cyst species in the sediments (138 cysts ml<sup>-1</sup>). Most of the dinoflagellates that form blooms in this area are from non-cyst forming genera, e.g. *Ceratium*,

*Prorocentrum*, *Dinophysis*, *Gymnodinium* (Pitcher and Calder, 2000), therefore leading to relatively fewer cysts from autotrophic species. It is therefore proposed that the dominance of heterotrophic cyst types in the sediments off Lambert's Bay is attributed to the dominance of autotrophic dinoflagellates with no known cyst stage rather than a consequence of the dominance of diatoms and other groups of phytoplankton.

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