Dinoflagellate cyst production on the southern Namaqua shelf of the Benguela upwelling system

GRANT C. PITCHER[1]* AND LINDA B. JOYCE[1,2]

[1]MARINE AND COASTAL MANAGEMENT, PRIVATE BAG X2, ROGGE BAY 8012, CAPE TOWN, SOUTH AFRICA AND [2]DEPARTMENT OF OCEANOGRAPHY, UNIVERSITY OF CAPE TOWN, RONDEBOSCH 7701, CAPE TOWN, SOUTH AFRICA

*CORRESPONDING AUTHOR: gpitcher@deat.gov.za

To study dinoflagellate cyst production in the southern Benguela, a sediment trap was deployed for a period of 3.5 years at a single station located downstream of the Cape Columbine upwelling cell on the southern Namaqua shelf. The cyst assemblage of surface sediments below the trap was also investigated. Twenty-nine different cyst types were recorded of which 25 were from the sediment trap, and 22 from the surface sediments. The flux of cysts followed a clear seasonal trend with an initial peak in spring followed by a major peak in autumn; with a mean flux for the entire period of deployment of 1.4×10^6 cysts m^{-2} day^{-1}. Of the cysts recovered from the trap, those of heterotrophic dinoflagellates were six times more abundant than those of autotrophic dinoflagellates. The study also revealed the presence of cysts of species previously unrecorded in the plankton of the southern Benguela, specifically the toxic dinoflagellate Lingulodinium polyedrum.

INTRODUCTION

Many dinoflagellate species have more or less complex heteromorphic life cycles, and approximately 10% of the 2000 known dinoflagellate species are meroplanktonic in that they include a benthic resting cyst in their life cycle (Head, 1996). This non-motile stage is formed from the sexual fusion of gametes and serves as a resistant dormant stage (Pfiester and Anderson, 1987). Other potential functions of cysts in the overall ecology of dinoflagellates include a role in genetic recombination that may lead to increased variation important for species survival (Anderson, 1984), species dispersal (Anderson et al., 1995), seeding for bloom initialization (Cembella et al., 1988; Ishikawa and Taniguchi, 1996), and survival through unfavourable conditions, including anoxic bottom sediments (Dale, 1983; Nehring, 1993). Cysts therefore contribute significant control in the population dynamics of the planktonic stages of many dinoflagellates.

Cysts are rarely found in the plankton as they are rapidly transported to the seafloor once formed (Anderson et al., 1985; Heiskanen, 1993). For this reason, sediment traps serve as useful tools in the study of cysts as they provide a measure of cyst production in the field and enable linkage to the parent vegetative population and the environmental conditions under which they are formed. However, despite the availability of sediment traps, few in situ measurements of dinoflagellate cyst production and deposition have been made in coastal environments (Heiskanen, 1993; Ishikawa and Taniguchi, 1996; Montresor et al., 1998; Harland and Pudsey, 1999; Kremp and Heiskanen, 1999; Godhe et al., 2001; Wendler et al., 2002; Joyce and Pitcher, 2004; Fujii and Matsuoka, 2006).

The Benguela Current on the west coast of southern Africa is one of four major upwelling systems in the world. In the southern Benguela, three upwelling centres can be distinguished: the Namaqua (30°S), Cape Columbine (33°S) and Cape Peninsula (34°S), where upwelling is most common during spring and summer (Nelson and Hutchings, 1983). The southern

Namaqua shelf, downstream of the Cape Columbine upwelling cell, is clearly characterized by high phytoplankton biomass, as identified from remotely sensed ocean colour (Pitcher and Weeks, 2006). This elevated biomass is a function of the retentive characteristics and consequent increased residence time of the greater St Helena Bay region (Pitcher and Nelson, 2006). Here phytoplankton biomass is highest during the latter half of the upwelling season when conditions become stratified favouring the development of dinoflagellate blooms many of which are considered harmful owing either to their high biomass or toxic properties (Pitcher et al., 1998; Pitcher and Calder, 2000).

Although the role of cysts in the life history of many dinoflagellates, including several harmful dinoflagellates, is clearly recognized, few studies of cysts in the Benguela region have been undertaken. Large-scale studies of relatively low resolution have examined the distribution of cysts in the South Atlantic Ocean (Wall et al., 1977) and more specifically in the Benguela upwelling region (Zonneveld et al., 2001; Bockelmann and Zonneveld, 2007), but only recently have studies focused on the composition, abundance and distribution of dinoflagellate cysts in the neritic environment of the southern Benguela ecosystem (Joyce and Pitcher, 2004, 2006; Joyce et al., 2005). This paper presents the results from a 3.5-year study of dinoflagellate cyst production at a single location on the southern Namaqua shelf. Cyst production was estimated by deployment of a sediment trap and further supported by determination of the composition and abundance of cysts in the surface sediments. Information is thereby provided as to which cyst-forming dinoflagellates species occur locally, the time at which these resting stages are produced (which may dictate the end of the planktonic stage), the number that are produced, and the size of the seed bank population that may serve as innocula for subsequent blooms.

METHOD

Sediment trap

A sediment trap, as described by Knauer et al. (Knauer et al., 1979), was deployed at a station located downstream of the Cape Columbine upwelling centre (32°.05.020 S, 18°.16.010 E), on the southern Namaqua shelf, approximately two nautical miles off Lambert's Bay (Fig. 1). 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
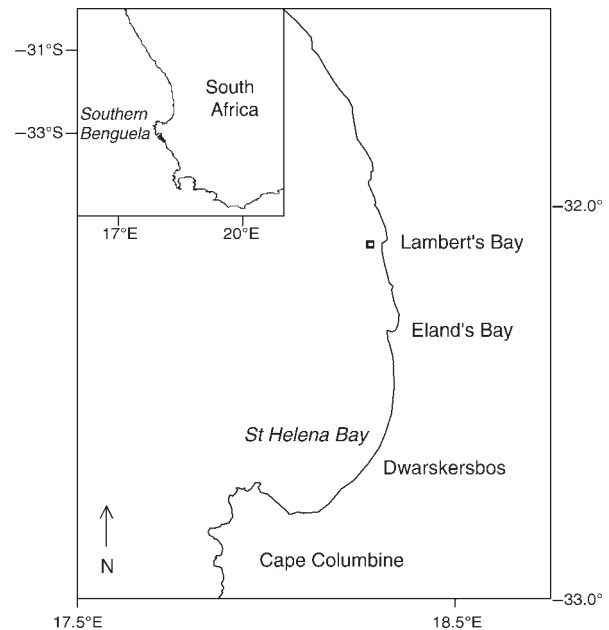

Fig. 1. Map of the study area showing the site of sediment trap deployment and collection of surface sediments.

deployed over a period of 3.5 years, from 9 January 2002 to 21 July 2005. During this period, the trap was in the water for 871 days out of a possible 1288 days. Thirty-four successful deployments of the trap were made and although the intention was to sample the trap monthly, the length of deployments ranged from 2 to 61 days, with a mean length of 26 days. Sub-samples of the sediment trap collections were fixed in 2.5% buffered formalin and stored prior to counting, by means of the Utermöhl method as modified by Hasle (Hasle, 1978), using a Zeiss IM35 inverted microscope.

Cyst flux (F; cysts m^{-2} day^{-1}) was determined as described by Joyce and Pitcher (Joyce and Pitcher, 2004):

$$F = \frac{(cv/a)}{t},$$

where c is the concentration of cysts in the trap (cysts m^{-3}), v the trap volume (m^3), a the area of the trap aperture (m^2) and t the time for which the trap was deployed (day).

Sediment collection and processing

Surface sediments below the sediment trap were collected in March 2001, 2002, 2003, and August 2004 by means of a small Van Veen grab. For cyst identification and enumeration, the sediment was processed using methods similar to those of Wall and Dale (Wall and Dale, 1968). At no stage were harsh chemicals such as

potassium hydroxide used in the treatment of the sediment. A small amount of the sediment was gently sonicated for 1 min; from this a 2 mL sub-sample was filtered through a 125 μm and a 20 μm mesh sieve. The slurry remaining on the 20 μm mesh was backwashed into a beaker with filtered seawater and the final volume noted. From the final volume, 1 mL was removed by pipette and placed on a Sedgwick-rafter slide for counting under an Olympus BX60 microscope. Cyst concentrations are presented as the number of cysts mL^{-1} wet sediment.

Cyst identification

Cyst identification was carried out under an Olympus BX60 optical microscope. Identification was typically based on cyst morphology, specifically body shape and ornaments, wall structure and colour, and type of archeopyle. Extensive use was made of the many publications listed by Matsuoka and Fukuyo (Matsuoka and Fukuyo, 2003) describing approximately 80 species of modern marine dinoflagellate cysts. Photographic records of cysts were obtained by means of an Olympus DP10 digital camera. In particular cases, cyst identification was confirmed by cyst isolation, incubation and germination, e.g. *Alexandrium catenella* (Joyce and Pitcher, 2006).

RESULTS AND DISCUSSION

The cyst assemblage

Twenty-nine distinctive cyst types were identified of which 25 were recorded from the sediment trap and 22 from the surface sediments (Table I and Fig. 2). Eighteen cyst types were common to both the sediment trap and surface sediment samples. The cyst assemblage of the surface sediments, as sampled in four consecutive years, was consistent, in that 17 or 18 cyst types were identified each year, 15 of which were present in 3 of the 4 years sampled. The Peridiniales were represented by 14 cyst types, including 11 heterotrophic (Organic Peridiniales) and three autotrophic (Calcareous Peridiniales) cysts. The Gonyaulacales were represented by six cyst types, all of which were autotrophic. The cysts of three toxic dinoflagellates, *A. catenella*, *Lingulodinium polyedrum* and *Protoceratium reticulatum*, were included among the Gonyaulacales. The Gymnodiniales were represented by two heterotrophic cysts, *Polykrikos kofoidii* and *Polykrikos schwartzii*, which were identified in accordance with the recommendations of

Table I: The mean flux of dinoflagellate cysts for the period of sediment trap deployment from 9 January 2002 to 21 July 2005, and the concentration of cysts in the surface sediments, at a single station on the southern Namaqua shelf

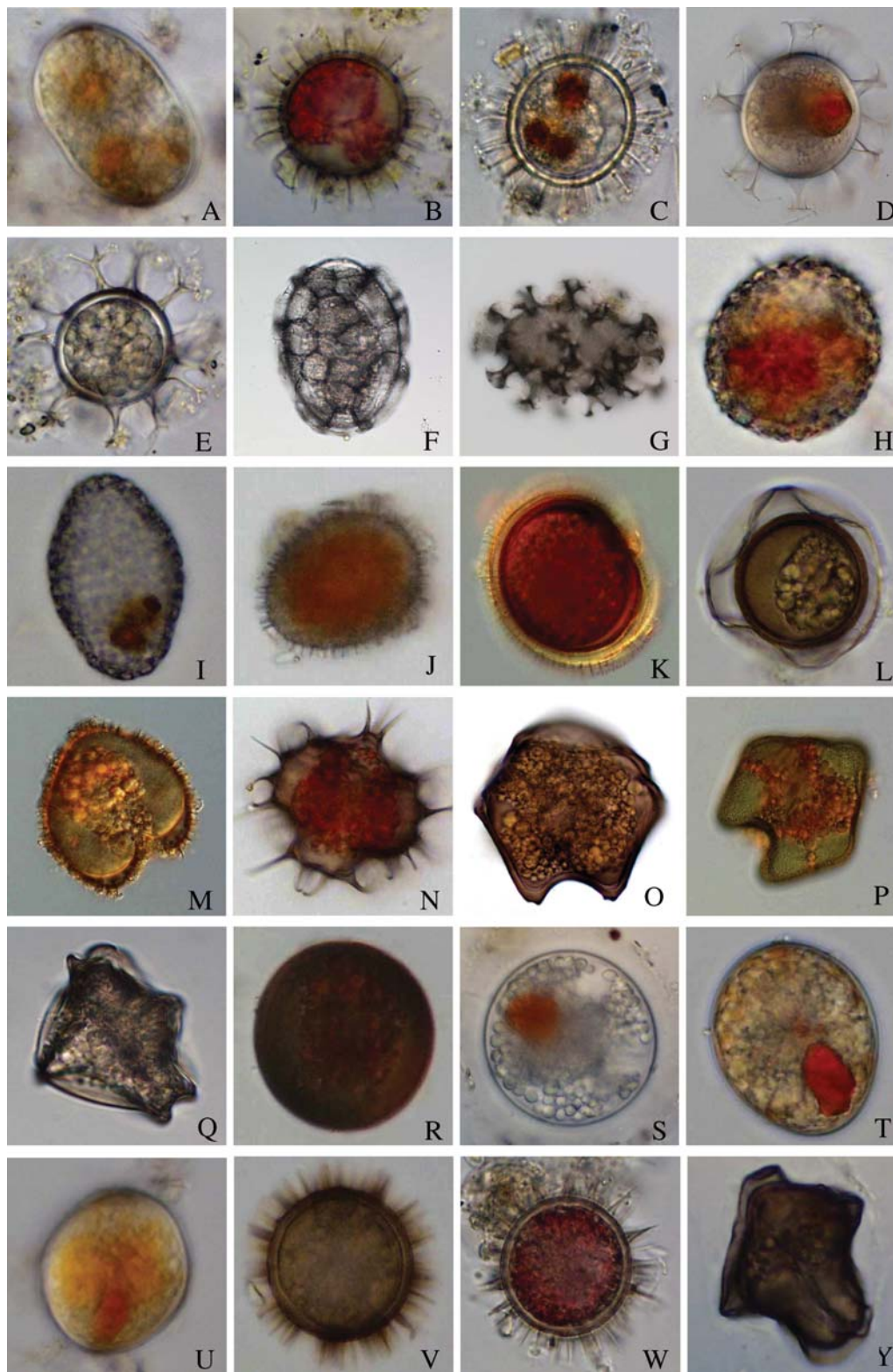| Cyst type	Sediment trap (cysts m^{-2} day^{-1})	Surface sediments (cysts mL^{-1} wet sediments)				
		2001	2002	2003	2004	Mean
Gonyaulacales						
Alexandrium catenella	109 768	138	100	238	88	141
Lingulodinium polyedrum	17 071	–	–	13	13	7
Protoceratium reticulatum	5105	–	–	13	25	10
Spiniferites delicatus	3191	13	13	–	–	7
Spiniferites ramosus	5744	–	25	–	13	10
Spiniferites spp.	–	13	38	13	13	19
Gymnodiniales						
Polykrikos kofoidii	545 648	75	25	50	25	44
Polykrikos schwartzii	100 833	13	50	188	13	66
Calcareous Peridiniales						
Scrippsiella crystallina	638	25	–	–	–	6
Scrippsiella lachrymosa	638	13	–	13	–	7
Scrippsiella trochoidea	26 166	25	25	75	63	47
Organic Peridiniales						
Preperidinium meunieri	351 321	150	163	700	325	335
Protoperidinium americanum	7658	–	13	25	38	19
Protoperidinium claudicans	–	38	25	13	25	25
Protoperidinium conicum	27 442	100	63	88	25	69
Protoperidinium leonis	49 778	50	75	200	225	138
Protoperidinium oblongum	2553	13	13	25	38	22
Protoperidinium pentagonum	–	38	13	–	–	13
Protoperidinium subinerme	–	–	13	25	50	22
Protoperidinium sp 1	4467	13	38	38	–	22
Protoperidinium sp 2	2553	–	–	–	–	–
Round Brown	81 209	75	50	113	400	160
Unidentified						
sp 1	23 613	38	25	50	13	32
sp 2	1915	–	–	–	–	–
sp 3	2553	–	–	–	–	–
sp 4	4467	–	–	–	–	–
sp 5	20 901	–	–	–	–	–
sp 6	638	–	–	–	–	–
sp 7	5105	–	–	–	–	–
Total	1 400 975	825	763	1875	1388	1213

Fig. 2. Twenty-four of the 29 dinoflagellate cysts recovered from sediment trap and surface sediment samples: (**A**) *Alexandrium catenella*, (**B**) *Lingulodinium polyedrum*, (**C**) *Protoceratium reticulatum*, (**D**) *Spiniferites delicatus*, (**E**) *Spiniferites ramosus*, (**F**) *Polykrikos kofoidii*, (**G**) *Polykrikos schwartzii*, (**H**) *Scrippsiella crystallina*, (**I**) *Scrippsiella lachrymosa*, (**J**) *Scrippsiella trochoidea*, (**K**) *Preperidinium meunieri*, (L) *Protoperidinium americanum*, (**M**) *Protoperidinium claudicans*, (**N**) *Protoperidinium conicum*, (**O**) *Protoperidinium leonis*, (**P**) *Protoperidinium oblongum*, (**Q**) *Protoperidinium subinerme*, (**R**) round brown cysts, (**S**) sp 1, (**T**) sp 2, (**U**) sp 3, (**V**) sp 4, (**W**) sp 5 and (**Y**) sp 7.

Matsuoka *et al.* (Matsuoka *et al.*, 2009). Seven unidentified species were recorded.

The sedimentary flux of cysts

Cysts were always present in the sediment trap following its retrieval but the flux of cysts per deployment varied considerably (Fig. 3). The lowest flux of 3.2×10^4 cysts m^{-2} day^{-1} was recorded during a 35-day deployment from 12 November to 17 December 2002. Two exceptional peaks in the flux of cysts were observed during the course of trap deployment. A flux of 1.6×10^7 cysts m^{-2} day^{-1}, dominated by *A. catenella* (1.5×10^7 cysts m^{-2} day^{-1}), was observed during a 3-day deployment from 22 to 25 October 2002, and a flux of 2.7×10^7 cysts m^{-2} day^{-1}, dominated by *Polykrikos kofoidii* (2.5×10^7 cysts m^{-2} day^{-1}), was observed during an 8-day trap deployment from 15 to 23 March 2005. The mean flux of cysts for the entire period of trap deployment was 1.4×10^6 cysts m^{-2} day^{-1}.

The mean and maximum fluxes of cysts reported above are high compared with those reported elsewhere. For example, in Onagawa Bay, Japan, Ishikawa and Taniguchi (Ishikawa and Taniguchi, 1996) monitored cyst production for 1.5-years and recorded a maximum yield of 3.2×10^5 cysts m^{-2} day^{-1} in autumn, while deposition rates during the remainder of the year were of the order of 1×10^3 cysts m^{-2} day^{-1}; within the Gulf of Naples on the Mediterranean coast, Montresor *et al.* (Montresor *et al.*, 1998) found the flux of cysts to differ markedly over two annual cycles corresponding to average fluxes of 3.5×10^5 and 1.5×10^5 cysts m^{-2} day^{-1}, with a maximum flux of 1.7×10^6 cysts m^{-2} day^{-1} in autumn; in the Gullmar Fjord, Sweden, Godhe *et al.* (Godhe *et al.*, 2001) established a mean flux of 3.2×10^5 cysts m^{-2} day^{-1} during a 21-day study during which a maximum yield of 2.7×10^6 cysts m^{-2} day^{-1} was recorded; in an upwelling area off northeast Somalia, Wendler *et al.* (Wendler *et al.*, 2002) monitored cyst deposition for a period of 9 months and recorded a mean yield of 4.9×10^5 cysts m^{-2} day^{-1}; and in Omura Bay in West Japan, Fujii and Matsuoka (Fujii and Matsuoka, 2006) recorded an average cyst flux of 7.6×10^5 cysts m^{-2} day^{-1} over a 2-year period, with a minimum and maximum of 7.3×10^3 and 3.7×10^6 cysts m^{-2} day^{-1} respectively. Although not exhaustive, these examples clearly show cyst production in the southern Benguela to be high relative to a variety of other marine systems. This high cyst production is attributable to the high productivity of this and other upwelling systems and to the recognized contribution of dinoflagellates to this high productivity (Mitchell-Innes *et al.*, 2000; Pitcher and Weeks, 2006).

Heterotrophic species dominated the flux of cysts during the period of study (mean 1.2×10^6 cysts m^{-2} day^{-1}); being approximately six times greater than that of autotrophic species (mean 0.2×10^6 cysts m^{-2} day^{-1}; Fig. 3). The flux of heterotrophic cysts was also more
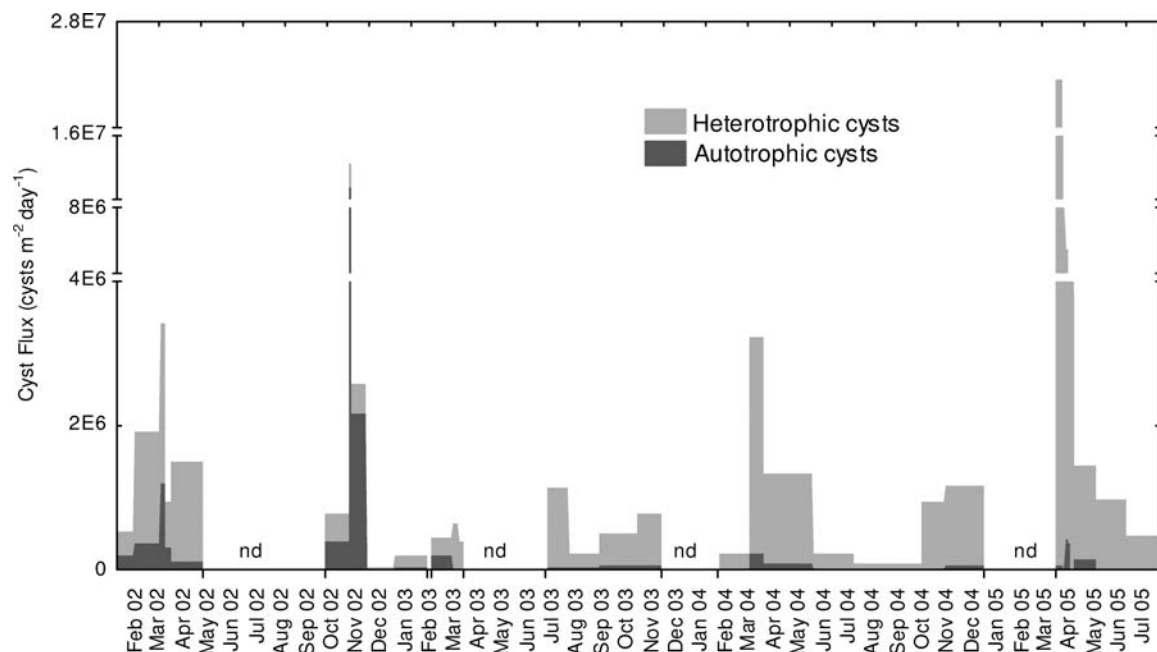
Fig. 3. A time series of the total flux of dinoflagellate cysts, as determined by the deployment of a sediment trap from 9 January 2002–21 July 2005, depicted as autotrophic and heterotrophic cysts.

consistent in that they were present in all 34 trap retrievals, whereas autotrophic cysts were present in only 23 retrievals. The heterotrophic species *Polykrikos kofoidii*, *Polykrikos schwartzii* and *Preperidinium meunieri* contributed 71% of the cysts sinking from the upper mixed layer, whereas the only autotrophic species to contribute significantly to this flux was *A. catenella* (8%). The high number of cysts of heterotrophic species demonstrates the potentially high grazing impact that these dinoflagellates may have in upwelling and other eutrophic systems (Matsuoka, 1999).

Dale (Dale, 1996) and Dale *et al.* (Dale *et al.*, 1999) state that the cyst record at coastal upwelling sites is characterized by relatively low cyst productivity and by cyst assemblages that are dominated by heterotrophic species. They attributed these observations to the dominance of diatoms in upwelling systems. The claim of low cyst productivity in upwelling systems is not supported by our study, which clearly shows cyst production to be high. However, our observations may be a function of the location of deployment of our sediment trap in the greater St Helena Bay region, an area well known for high biomass dinoflagellate blooms and the development of red tides, particularly during the latter part of the upwelling season (Pitcher and Calder, 2000; Pitcher and Weeks, 2006). Our results may therefore not reflect accurately cyst production through the entire Benguela upwelling region. The observations of a high ratio of heterotrophic to autotrophic cysts during our

study are in agreement with those of Dale (Dale, 1996) and Dale *et al.* (Dale *et al.*, 1999). We, however, propose that this ratio of cyst types in the sediment trap and surface sediments of the St Helena Bay region is determined by the dominance of blooms of holoplanktonic dinoflagellates rather than a consequence of the dominance of diatoms within the region. It is now accepted that dinoflagellates and red tides are frequent and fundamental features of upwelling systems; however, non-cyst forming genera, e.g. *Akashiwo*, *Ceratium*, *Dinophysis*, *Gyrodinium*, *Noctiluca* and *Prorocentrum*, appear to dominate the blooms of St Helena Bay (Pitcher and Weeks, 2006), resulting in relatively fewer cysts of autotrophic species.

A seasonal trend in the flux of cysts was not easily distinguished from the 3.5-year time series data owing to the gaps in trap deployment (Fig. 3). However, an annual composite of cyst flux derived from this data revealed a clear seasonal trend with an initial peak in spring followed by a major peak in autumn (Fig. 4). This seasonality in cyst production is not unexpected as seasonality within the southern Benguela is well documented and includes bimodality in alongshore upwelling favourable winds, which extend from September to March with a noticeable lull in mid-summer (Shannon, 1985). Bimodal peaks in the incidence of dinoflagellate-dominated red tides have also been observed, with Horstman (Horstman, 1981) reporting maxima in September and March and Pitcher *et al.* (Pitcher *et al.*, 1995) maxima in October and February. The major peak in dinoflagellate
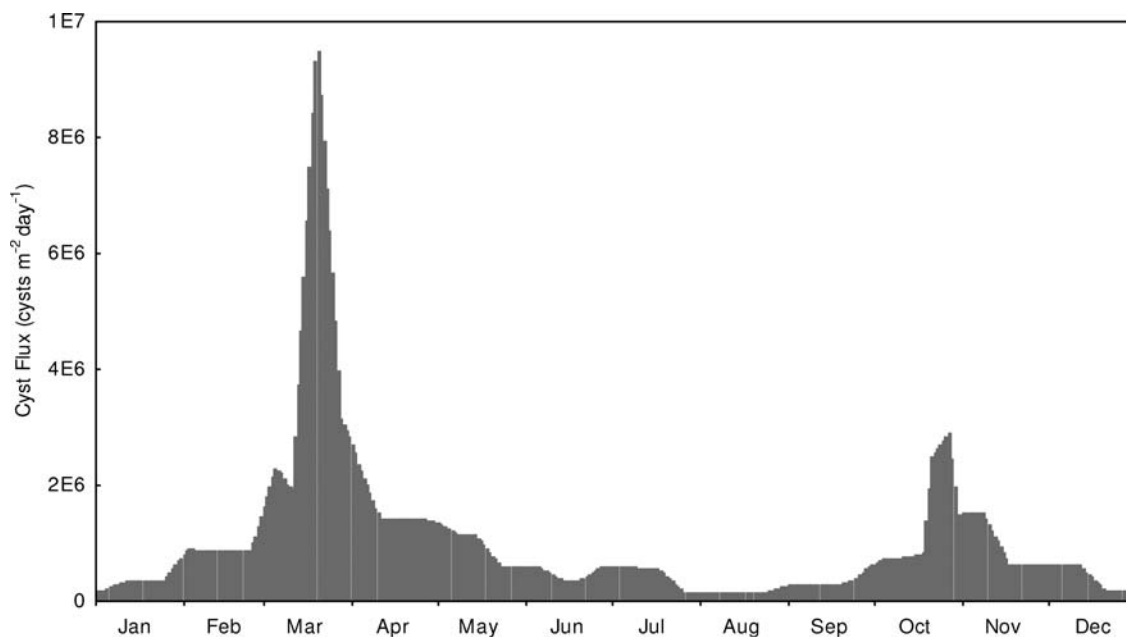

Fig. 4. Seasonal cyst deposition as determined from an annual composite (10-day running mean) of dinoflagellate cyst flux for the 3.5-year period of trap deployment.

abundance towards the end of the upwelling season coincides with intensified stratification owing to decreasing winds and increase solar irradiance (Pitcher and Weeks, 2006). Cyst production appears therefore to either coincide with or immediately follow the maximum abundance of the vegetative stage as reported by several other investigators (Heaney *et al.*, 1983; Heiskanen, 1993; McQuoid and Hobson, 1996; Montresor *et al.*, 1998; Zohary *et al.*, 1998; Kim and Han, 2000).

Superimposed on this general seasonal trend were species-specific patterns in cyst production. Some species sustained high cyst production over several months, whereas others had shorter periods of production. Autotrophic species in particular appeared to have shorter periods of cyst production, e.g. the presence of cysts of *A. catenella* never extended beyond a period of 2 months, and these were particularly abundant in spring (Fig. 5). The heterotrophic species tended to produce cysts over extended periods, e.g. *Preperidinium meunieri* was found in all trap deployments over a 23-month period. The production of cysts of this and other heterotrophic species, e.g. *Polykrikos kofoidii* and *Polykrikos schwartzii*, nevertheless also demonstrated clear seasonal trends, peaking in autumn, coincident with peaks in phytoplankton biomass and dinoflagellate abundance (Fig. 5).

Cysts of the surface sediments

Cyst abundance in the surface sediments varied during the course of the study by more than 2-fold, ranging from 763 cysts mL^{-1} wet sediment in 2002 to 1875 cysts mL^{-1} of wet sediment in 2003 (Table I). The cysts of the surface sediments generally reflected the flux of cysts to the sediments in that the eight cyst types (*A. catenella*, *Polykrikos kofoidii*, *Polykrikos schwartzii*, *Scrippsiella trochoidea*, *Preperidinium meunieri*, *Protoperidinium conicum*, *Protoperidinium leonis*, Round Brown) that dominated the sediment trap also dominated the surface sediments. Variations were nevertheless evident in that the heterotrophic species *Polykrikos kofoidii*, *Polykrikos schwartzii* and *Preperidinium meunieri* appeared underrepresented in the surface sediments, in that their contribution to the sediment trap cyst population of 71% was reduced to 37% in the surface sediments. The contribution of the dominant autotrophic species, *A. catenella* and *S. trochoidea*, increased from 10% of the sediment trap population to 16% of the surface sediment population. These differences may reflect different germination strategies.

Cysts of toxic species

Several toxic dinoflagellates produce resting cysts, and sediment surveys or trap sampling represents an alternative means for their detection. Furthermore, several studies of dinoflagellate cysts recovered from sediment traps and sediment samples have revealed the presence of dinoflagellate species that have not previously been recorded in the plankton (Dale, 1976; Dodge and Harland, 1991; Montresor *et al.*, 1998; Godhe *et al.*, 2001). Cysts of three toxic species were recovered from the sediment trap and surface sediments during the course of our study: *A. catenella*, *Protoceratium reticulatum* and *L. polyedrum*, of which only *A. catenella* was abundant.

The dinoflagellate *A. catenella* is responsible for Paralytic Shellfish Poisoning (PSP), a phenomenon common to the southern Benguela region (Pitcher and Calder, 2000). Having been confirmed within the region in 1948 (Sapeika, 1948), PSP poses a serious threat to seafood safety and is often responsible for the contamination of shellfish on the west coast of South Africa. Cysts of *A. catenella* were observed each year typically during the months of spring and summer, having been recovered from the sediment trap in 7 of the 34 deployments. Only on one occasion, during October 2002, was the flux of cysts abundant. At this time, cysts were present in three consecutive deployments spanning the period 23 September–12 November. A short deployment of 3 days corresponding to the peak of the bloom in the surface waters provided an estimated flux of 1.5×10^7 cysts m^{-2} day^{-1}. Germination studies conducted on these cysts revealed a short dormancy period suggesting that these cysts do not necessarily serve as an over-wintering strategy, but may allow rapid cycling between benthic and planktonic stages (Joyce and Pitcher, 2006). In March 2003, 5 months after this bloom, cysts of *A. catenella* were recorded in the sediments at abundances of 238 cysts mL^{-1} wet sediment, at which time this comprised the second most abundant cyst type after *Preperidinium meunieri*. Although the mean flux of *A. catenella* to the sediments of 1.1×10^5 cysts m^{-2} day^{-1} appeared to be biased by the very high flux of this cyst during the 2002 bloom, the concentrations of this cyst in the surface sediments were consistently high, ranging from 88 to 238 cysts mL^{-1} wet sediment.

Both *Protoceratium reticulatum* and *L. polyedrum* produce yessotoxins (YTX) (Satake *et al.*, 1997; Paz *et al.*, 2004). The mean flux of *Protoceratium reticulatum* (5.1×10^3 cysts m^{-2} day^{-1}) and *L. polyedrum* (1.7×10^4 cysts m^{-2} day^{-1}) from the surface waters was generally low and their respective concentrations in the sediments of 10 and 7 cysts mL^{-1} wet sediment were correspondingly low. Cysts of *Protoceratium reticulatum* were recovered from 4 of the 34 trap deployments and their presence was limited to spring and summer. The
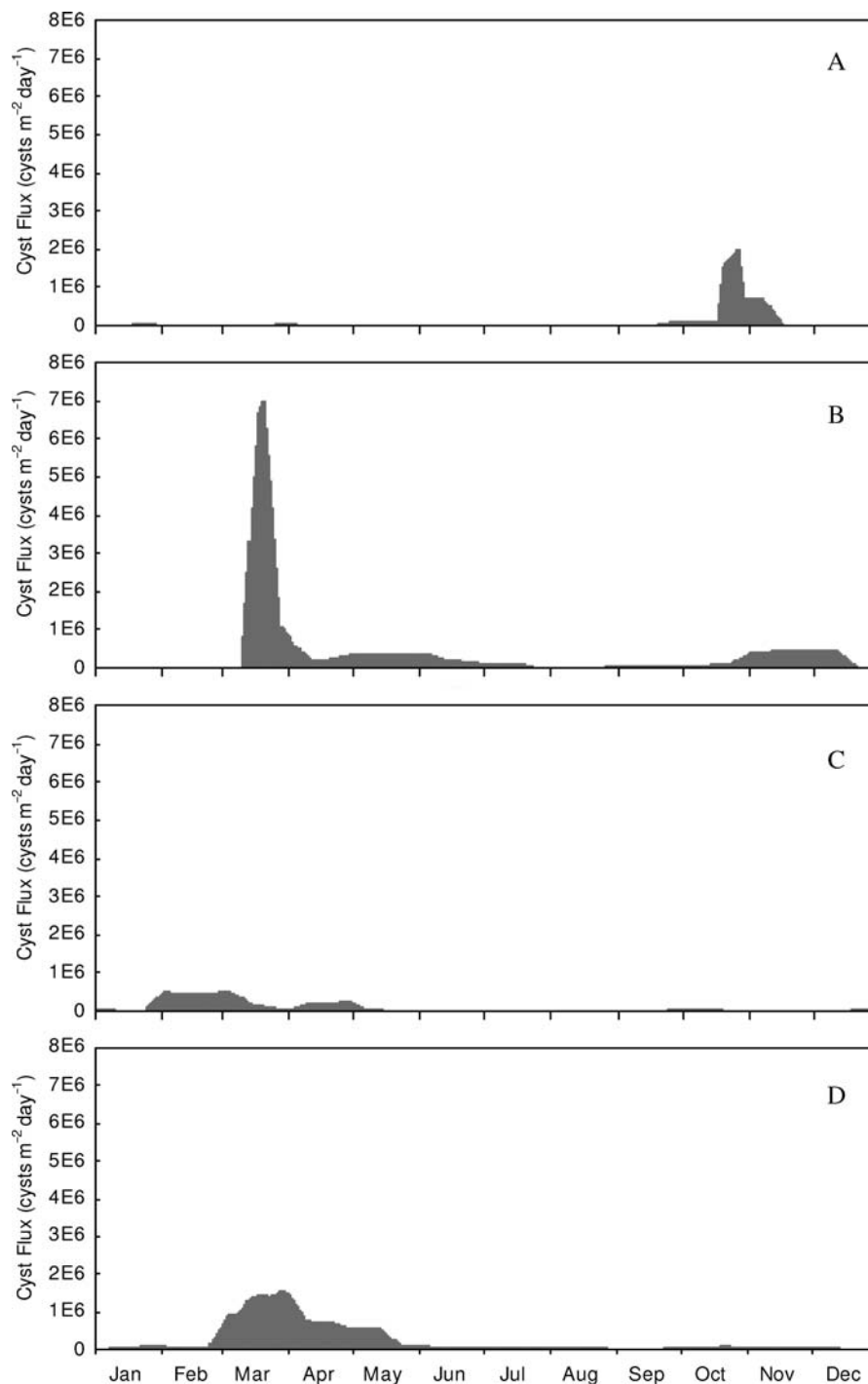
Fig. 5. Seasonal deposition of cysts of (**A**) *Alexandrium catenella*, (**B**) *Polykrikos kofoidii*, (**C**) *Polykrikos schwartzii* and (**D**) *Preperidinium meunieri*, as determined from an annual composite (10-day running mean) of dinoflagellate cyst flux for the 3.5-year period of trap deployment.

production in the southern Benguela of YTX by this species was only recently confirmed (Fawcett *et al.*, 2007; Krock *et al.*, 2008). It is, however, noteworthy that *Protoceratium reticulatum* has in the past been associated with large mortalities of both white (*Donax serra*) and black

(*Choromytilus meridionalis*) mussels on the west coast of South Africa (Grindley and Nel, 1968, 1970; Horstman, 1981).

Cysts of *L. polyedrum* were recovered from 2 of the 34 trap deployments, both of which were deployed in late summer to early autumn. Motile stages of *L. polyedrum*

have yet to be detected in the plankton of the southern Benguela. As a result, *L. polyedrum* has not been listed as a harmful species within the region (Pitcher and Calder, 2000). The recovery of cysts of *L. polyedrum* during this study from the sediment trap points to the recent presence of motile cells in the plankton, suggesting a potential risk for outbreaks of toxicity. The absence of prior records of motile planktonic stages of *L. polyedrum* in the Benguela is particularly surprising in view of the observations of Lewis (Lewis, 1988) that *L. polyedrum* produces relatively few cysts (ca. 4:1000 cyst:theca ratio).

Meroplanktonic dinoflagellates within an upwelling regime

The most abundant and seasonally recurrent dinoflagellates in upwelling systems are holoplanktonic in that they do not have a cyst-based life history (Smayda and Trainer, in press). The high number of bloom-forming dinoflagellate species without a cyst stage demonstrates the availability of multiple life cycle options to survive, seed, sustain and otherwise support their population dynamics. The success of holoplanktonic dinoflagellates in upwelling systems confounds the enigmatic role of resting cysts as propagules seeding dinoflagellate blooms in these systems. Thus, the presence of a cyst stage does not necessarily indicate a capability to attain higher concentrations, nor the timely seasonal occurrence of a particular species in the plankton. Although some meroplanktonic dinoflagellates (e.g. *A. catenella*) are important bloom species in upwelling systems, their bloom behaviour, when compared with that of holoplanktonic dinoflagellates, does not appear to be favoured by their capacity to form cysts (Smayda and Trainer, in press).

Cyst stages do nevertheless contribute significant control in the population dynamics of meroplanktonic dinoflagellates and this is achieved by the control of transitions between different life stages, particularly between motile planktonic and non-motile benthic stages. Our data provide useful information as to which cyst-forming dinoflagellates are common to the southern Namaqua shelf, to the magnitude and timing of the transition from planozygote to hypnozygote (non-motile cyst), and to the size and composition of the seed bank population that may serve as innocula for future blooms. Quantitative data of this nature provide essential information for incorporation into species-specific models of population dynamics in order to improve predictive capabilities. The development of species-specific models of toxic or otherwise harmful species (e.g. *A. catenella*) is particularly beneficial in managing the impacts of the blooms of these species.

The region downstream of the Cape Columbine upwelling cell is characterized by stratified conditions favourable for dinoflagellate growth; and retentive circulation patterns facilitate the build-up of dense dinoflagellate blooms during the latter months of the upwelling season and result in a high incidence of red tides (Pitcher and Nelson, 2006). For this reason, the high flux of cysts measured on the southern Namaqua shelf, and their deposition in the sediments beneath the trap is to be expected. Within the coastal upwelling system, it is possible that cyst-forming dinoflagellate species utilize circulation patterns to control movement between the planktonic phase and the seed bank thereby ensuring spatial coherence or closure between these stages, and preventing washout from the coastal environment (Joyce and Pitcher, 2004). During active upwelling, the flux of cysts from equatorward flowing surface water into a predominantly poleward undercurrent serves to maintain populations within their area of origin. Alternately, following a decline in upwelling wind stress, alongshore surface currents reverse and barotropic poleward flow serves to retain both vegetative and cyst populations within their area of origin.

ACKNOWLEDGEMENTS

REFERENCES

Anderson, D. M. (1984) Shellfish toxicity and dormant cysts in toxic dinoflagellate blooms. In Ragelis, E. (ed.), *Seafood Toxins*. ACS Symposium Series, No. 262. Washington, D.C, pp. 125–138.

Anderson, D. M., Lively, J. J., Reardon, E. M. *et al.* (1985) Sinking characteristics of dinoflagellate cysts. *Limnol. Oceanogr.*, **30**, 1000–1009.

Anderson, D. M., Fukuyo, Y. and Matsuoka, K. (1995) Cyst methodologies. In Hallegraeff, G. M., Anderson, D. M. and Cembella, A. D. (eds), *Manual on Harmful Marine Microalgae*. IOC Manuals and Guides, No. 33. UNESCO, Paris, pp. 229–249.

Bockelmann, F.-D. and Zonneveld, K. A. F. (2007) Assessing environmental control on dinoflagellate cyst distribution in surface sediments of the Benguela upwelling region (eastern South Atlantic). *Limnol. Oceanogr.*, **52**, 2582–2594.

Cembella, A. D., Turgeon, J., Therriault, J. C. *et al.* (1988) Spatial distribution of *Protogonyaulax tamarensis* resting cysts in nearshore sediments along the north coast of the Lower St Lawrence Estuary. *J. Shellfish Res.*, **7**, 597–609.

Dale, B. (1976) Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in recent sediments from Trondheimsfjord, Norway. *Rev. Palaeobot. Palynol.*, **22**, 39–60.

Dale, B. (1983) Dinoflagellate resting cysts: "benthic plankton". In Fryxell, G. A. (ed.), *Survival Strategies of the Algae*. Cambridge University Press, Cambridge, pp. 69–136.

Dale, B. (1996) Dinoflagellate cyst ecology: modeling and geological applications. In Jansonius, J. and McGregor, D. C. (eds), *Palynology: Principles and Applications*. The American Association of Stratigraphic Palynologists Foundation, Publishers Press, Salt Lake City, pp. 1249–1276.

Dale, B., Thorsen, T. A. and Fjellså, A. (1999) Dinoflagellate cysts as indicators of cultural eutrophication in the Oslofjord, Norway. *Estuarine Coastal Shelf Sci.*, **48**, 371–382.

Dodge, J. D. and Harland, R. (1991) The distribution of planktonic dinoflagellates and their cysts in the eastern and northeastern Atlantic Ocean. *New Phytol.*, **118**, 593–603.

Fawcett, A., Pitcher, G. C., Bernard, S. *et al*. (2007) Contrasting wind patterns and toxigenic phytoplankton in the southern Benguela upwelling system. *Mar. Ecol. Prog. Ser.*, **348**, 19–31.

Fujii, R. and Matsuoka, K. (2006) Seasonal change of dinoflagellates cyst flux collected in a sediment trap in Omura Bay, West Japan. *J. Plankton Res.*, **28**, 131–147.

Godhe, A., Norén, F., Kuylenstierna, M. *et al*. (2001) Relationship between planktonic dinoflagellate abundance, cysts recovered in sediment traps and environmental factors in the Gullmar Fjord, Sweden. *J. Plankton Res.*, **23**, 923–938.

Grindley, J. R. and Nel, E. (1968) Mussel poisoning and shellfish mortality on the West Coast of Africa. *S. Afr. J. Sci.*, **64**, 420–422.

Grindley, J. R. and Nel, E. A. (1970) Red water and mussel poisoning at Elands Bay, December 1966. *Fish. Bull. S. Afr.*, **6**, 36–55.

Harland, R. and Pudsey, C. J. (1999) Dinoflagellate cysts from sediment traps deployed in the Bellingshausen, Weddell and Scotia seas, Antarctica. *Mar. Micropaleontol.*, **37**, 77–99.

Hasle, G. R. (1978) The inverted-microscope method. In Sournia, A. (ed.), *Phytoplankton Manual*. UNESCO, Paris, pp. 88–96.

Head, M. J. (1996) Modern dinoflagellate cysts and their biological affinities. In Jansonius, J. and McGregor, D. C. (eds), *Palynology: Principles and Applications*. The American Association of Stratigraphic Palynologists Foundation, Publishers Press, Salt Lake City, pp. 1197–1248.

Heaney, S., Chapman, D. and Morison, H. (1983) The role of the cyst stage of the dinoflagellate *Ceratium hirundella* within a small productive lake. *Br. Phycol. J.*, **18**, 47–49.

Heiskanen, S. (1993) Mass encystment and sinking of dinoflagellates during a spring bloom. *Mar. Biol.*, **116**, 161–167.

Horstman, D. A. (1981) Reported red-water outbreaks and their effects on fauna of the west and south coasts of South Africa, 1959–1980. *Fish. Bull. S. Afr.*, **15**, 71–88.

Ishikawa, A. and Taniguchi, A. (1996) Contribution of benthic cysts to the population dynamics of *Scrippsiella* spp. (Dinophyceae) in Onagawa Bay, northeast Japan. *Mar. Ecol. Prog. Ser.*, **140**, 169–178.

Joyce, L. B. and Pitcher, G. C. (2004) Encystment of *Zygabikodinium lenticulatum* (Dinophyceae) during a summer bloom of dinoflagellates in the southern Benguela upwelling system. *Estuarine Coastal Shelf Sci.*, **59**, 1–11.

Joyce, L. B. and Pitcher, G. C. (2006) Cysts of *Alexandrium catenella* on the west coast of South Africa: distribution and characteristics of germination. In Pitcher, G. C., Probyn, T. A. and Verheye, H. M. (eds), *Harmful Algae 2004. Afr. J. Mar. Sci.*, **28**, 295–298.

Joyce, L. B., Pitcher, G. C., du Randt, A. *et al*. (2005) Dinoflagellate cysts from the surface sediments of Saldanha Bay, South Africa: an indication of the potential risk of harmful algal blooms. *Harmful Algae*, **4**, 309–318.

Kim, Y.-O. and Han, S. (2000) Seasonal relationships between cyst germination and vegetative population of *Scrippsiella trochoidea* (Dinophyceae). *Mar. Ecol. Prog. Ser.*, **204**, 111–118.

Knauer, G. A., Martin, J. H. and Bruland, K. W. (1979) Fluxes of particulate carbon, nitrogen, and phosphorous in the upper water column of the northeast Pacific. *Deep-Sea Res.*, **26**, 97–108.

Kremp, A. and Heiskanen, S. (1999) Sexuality and cyst formation of the spring-bloom dinoflagellate *Scrippsiella hangoei* in the coastal northern Baltic Sea. *Mar. Biol.*, **134**, 771–777.

Krock, B., Alpermann, T., Tillmann, U. *et al*. (2008) Yessotoxin profiles of the marine dinoflagellates *Protoceratium reticulatum* and *Gonyaulax spinifera*. In Moestrup, O. *et al*. (eds), *Proceedings of the 12th International Conference on Harmful Algae*. International Society for the Study of Harmful Algae and Intergovernmental Oceanographic Commission of UNESCO, Copenhagen.

Lewis, J. (1988) Cysts and sediments: *Gonyaulax polyedra* (*Lingulodinium machaerophorum*) in Loch Creran. *J. Mar. Biol. Assoc. UK*, **68**, 701–714.

Matsuoka, K. (1999) Eutrophication process recorded in dinoflagellate cyst assemblages—a case of Yokohama Port, Tokyo Bay, Japan. *Sci. Total Environ.*, **231**, 17–35.

Matsuoka, K. and Fukuyo, Y. (2003) Taxonomy of cysts. In Hallegraeff, G. M., Anderson, D. M. and Cembella, A. D. (eds), *Manual on Harmful Marine Algae*. UNESCO Monographs on Oceanographic Methodology 11, Paris, pp. 563–592.

Matsuoka, K., Kawami, H., Nagai, S. *et al*. (2009) Re-examination of cyst-motile relationships of *Polykrikos kofoidii* Chatton and *Polykrikos schwartzii* Bütschli (Gymnodiniales, Dinophyceae). *Rev. Palaeobot. Palynol.*, **154**, 79–90.

McQuoid, M. R. and Hobson, L. A. (1996) Diatom resting stages. *J. Phycol.*, **32**, 889–902.

Mitchell-Innes, B. A., Pitcher, G. C. and Probyn, T. A. (2000) Productivity of dinoflagellate blooms on the west coast of South Africa, as measured by natural fluorescence. *S. Afr. J. Mar. Sci.*, **22**, 273–284.

Montresor, M., Zingone, A. and Sarno, D. (1998) Dinoflagellate cyst production at a coastal Mediterranean site. *J. Plankton Res.*, **20**, 2291–2312.

Nehring, S. (1993) Mechanisms for recurrent nuisance algal blooms in coastal zones: resting cyst formation as life-strategy of dinoflagellates. In Sterr, H., Hofstede, J. and Plag, H. P. (eds), *Proceedings of the International Coastal Congress, ICC-Kiel, 1992*. Peter Lang, Frankfurt, pp. 454–467.

Nelson, G. and Hutchings, L. (1983) The Benguela upwelling area. *Prog. Oceanogr.*, **12**, 333–356.

Paz, B., Riobo, P., Fernandez, M. L. *et al*. (2004) Production and release of yessotoxins by the dinoflagellates *Protoceratium reticulatum* and *Lingulodinium polyedrum* in culture. *Toxicon*, **44**, 251–258.

Pfiester, L. A. and Anderson, D. M. (1987) Dinoflagellate reproduction. In Taylor, F. J. R. (ed.), *The Biology of Dinoflagellates*. Blackwell Scientific Publications, Oxford, pp. 611–648.

Pitcher, G. C. and Calder, D. (2000) Harmful algal blooms of the southern Benguela current: a review and appraisal of monitoring from 1989 to 1997. *S. Afr. J. Mar. Sci.*, **22**, 255–271.

Pitcher, G. C. and Nelson, G. (2006) Characteristics of the surface boundary layer important to the development of red tide on the southern Namaqua shelf of the Benguela upwelling system. *Limnol. Oceanogr.*, **51**, 2660–2674.

Pitcher, G. C. and Weeks, S. J. (2006) The variability and potential for prediction of harmful algal blooms in the southern Benguela ecosystem. In Shannon, V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C., Woods, J. *et al.* (eds), *Benguela: Predicting a Large Marine Ecosystem. Large Marine Ecosystems*. Vol. 14. Elsevier B.V., The Netherlands, pp. 125–146.

Pitcher, G., Agenbag, J., Calder, D. *et al.* (1995) Red tides in relation to the meteorology of the southern Benguela upwelling system. In Lassus, P., Arzul, G., Erard, E., Gentien, P., Marcaillou, C. *et al.* (eds), *Harmful Marine Algal Blooms*. Technique et Documentation, Intercept Ltd, Lavoisier, pp. 657–662.

Pitcher, G. C., Boyd, A. J., Horstman, D. A. *et al.* (1998) Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the Southern Benguela upwelling system. *Mar. Ecol. Prog. Ser.*, **172**, 253–264.

Sapeika, N. (1948) Mussel poisoning. *S. Afr. Med. J.*, **22**, 337–338.

Satake, M., MacKenzie, L. and Yasumoto, T. (1997) Identification of *Protoceratium reticulatum* as the biogenetic origin of yessotoxin. *Nat. Toxins*, **5**, 164–167.

Smayda, T. J. and Trainer, V. Dinoflagellate blooms in upwelling systems: seeding, variability, and contrasts with diatom bloom behaviour. *Prog. Oceanogr.* (in preparation).

Shannon, L. V. (1985) The Benguela Ecosystem Part I. Evolution of the Benguela, physical features and processes. *Oceanogr. Mar. Biol. Ann. Rev.*, **23**, 105–182.

Wall, D. and Dale, B. (1968) Modern dinoflagellate cysts and evolution of the Peridiniales. *Micropalaeontology*, **14**, 265–304.

Wall, D., Dale, B., Lohmann, G. P. *et al.* (1977) The environmental and climatic distribution of dinoflagellate cysts in modern marine sediments from regions in the North and South Atlantic Oceans and adjacent seas. *Mar. Micropaleontol.*, **2**, 121–200.

Wendler, I., Zonneveld, K. A. F. and Willems, H. (2002) Production of calcareous dinoflagellate cysts in response to monsoon forcing off Somalia: a sediment trap study. *Mar. Micropaleontol.*, **46**, 1–11.

Zohary, T., Pollingher, U., Hadas, O. *et al.* (1998) Bloom dynamics and sedimentation of *Peridinium gatunense* in Lake Kinneret. *Limnol. Oceanogr.*, **43**, 175–186.

Zonneveld, K. A. F., Hoek, R. P., Brinkhuis, H. *et al.* (2001) Geographical distributions of organic-walled dinoflagellate cysts in surficial sediments of the Benguela upwelling region and their relationship to upper ocean conditions. *Prog. Oceanogr.*, **48**, 25–72.