

Contrasting Bays and Red Tides in the Southern Benguela Upwelling System

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In late summer and autumn of 2007, red tides were present in two prominent bays of the southern Benguela upwelling system, False Bay and St. Helena Bay. In False Bay, the dinoflagellate *Gonyaulax polygramma* attained concentrations of 20×10^6 cells l^{-1} and posed a serious environmental threat through bloom decay and anoxia. In St. Helena Bay, the toxic dinoflagellate *Alexandrium catenella* reached concentrations of 5×10^5 cells l^{-1} and posed a threat to human health by rendering shellfish highly toxic. Multiscale observations obtained from coastal monitoring stations, ship-based transects, and aircraft and satellite remote sensing were used to identify the scale and physical forcing of these blooms, which appear to be localized manifestations within adjacent subsystems of the southern Benguela upwelling region.

INTRODUCTION

In February 2007, large areas of False Bay on the southern African coast (Figure 1) were subjected to extreme discoloration owing to a bloom of the dinoflagellate *Gonyaulax polygramma* (Figure 2). The bloom persisted for two months, and at night the bay was brilliantly luminescent. In late February and early March, the bloom accumulated in Gordons Bay in the northeastern

corner of False Bay, where recorded cell concentrations exceeded 20×10^6 cells l^{-1} . Small mortalities of marine organisms reported in the region of Gordons Bay and the Strand were thought to be a consequence of oxygen depletion resulting from bloom decay.

At this time, some 180 km to the north of False Bay, a bloom of the toxic dinoflagellate *Alexandrium catenella* appeared in a narrow coastal band

in St. Helena Bay (Figure 1). This dinoflagellate is responsible for the production of neurotoxins (saxitoxin [STX] and several derivatives of this molecule) that cause paralytic shellfish poisoning (PSP). Cell concentrations of *A. catenella* in St. Helena Bay reached nearly 5×10^5 cells l^{-1} and levels of toxicity in mussels exceeded $4000 \mu\text{g STX eq } 100 \text{ g}^{-1}$ shellfish, 50 times greater than the regulatory level (of $80 \mu\text{g STX eq } 100 \text{ g}^{-1}$ shellfish) for harvesting shellfish.

Upwelling systems, as with many other marine environments, are increasingly susceptible to the proliferation and negative effects of harmful algae (Kudela et al., 2005). The embayments of upwelling systems in particular create sites favorable for harmful algal bloom (HAB) initiation, development, and retention, and are identified

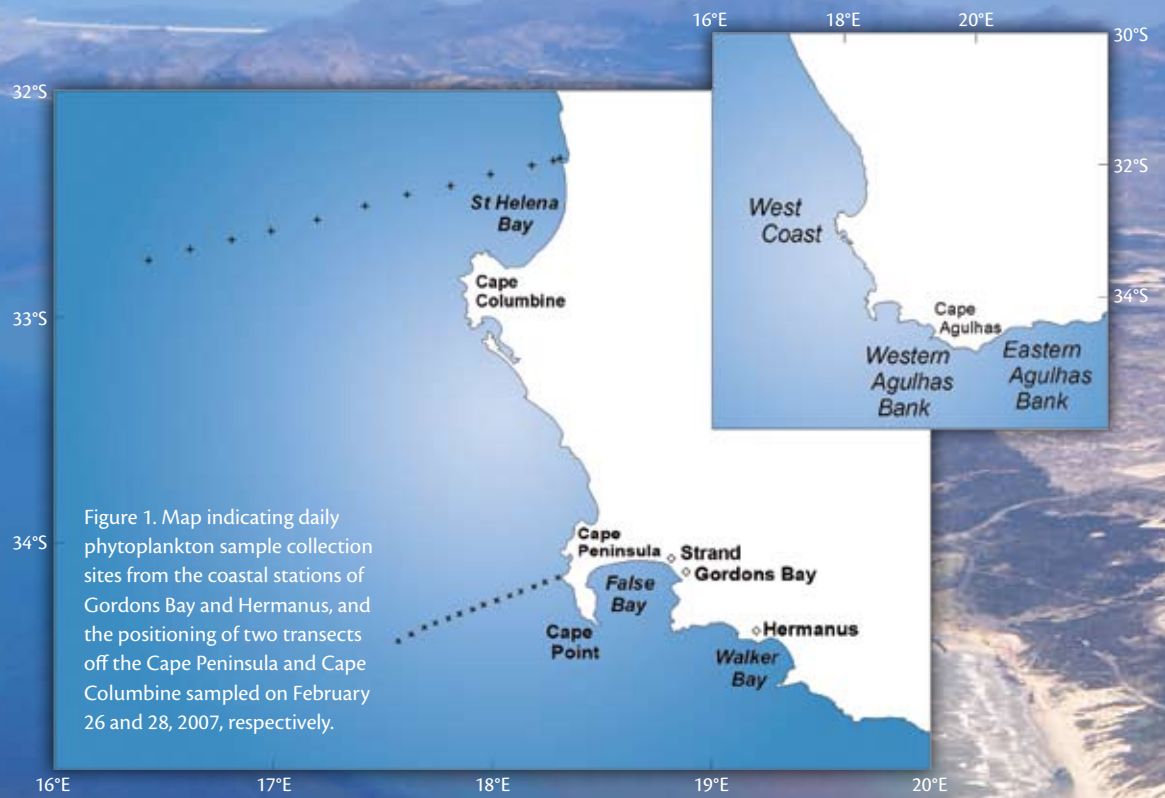


Figure 2. Aerial photograph of the *Gonyaulax polygramma* bloom in False Bay on February 23, 2007. Photo by Anthony Allen

within the international research program GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms) as areas requiring additional research in order to identify the mechanisms underlying HAB population and community dynamics within upwelling systems (GEOHAB, 2005).

False Bay and St. Helena Bay comprise the largest and most productive bays of the southern Benguela upwelling system. This article uses data from coastal monitoring stations and two ship-based transects, supported by remote observations from aircraft and satellite, to report on blooms within these bays during the late summer and early autumn of 2007. It also places the incidence and potential threat posed by these blooms in historic context, and identifies the different physical forcing underlying these blooms by demarcating adjacent subsystems of the southern Benguela upwelling system.

GONYAULAX POLYGRAMMA BLOOM IN FALSE BAY

Grindley and Taylor (1964) provide the only other account of a bloom of *G. polygramma* in False Bay. Occurring in March and April 1962, this bloom shared many similarities with the bloom reported here. The 1962 bloom was estimated to have reached concentrations of approximately 10×10^6 cells l^{-1} , and under

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conditions of northwesterly winds, the bloom accumulated in the Gordons Bay area; the sea became slimy with rotting plankton and the water produced an unbearable stench. At this time, dead and dying fish and invertebrates, estimated at over 100 tons, were washed up on the beaches between Gordons Bay and the Strand, apparently due to the depletion of oxygen by decaying plankton.

Although marine mortalities attributed to anoxia are common off the southern African coast, these occurrences are typically reported on the West Coast (Pitcher and Calder, 2000). Therefore, the 1962 bloom of *G. polygramma* in and subsequent mortality were unexpected, as nothing similar had occurred in False Bay within living memory (Grindley and Taylor, 1964). Following the 1962 bloom, several other harmful blooms have been reported in

False Bay, the most notable of which were blooms of a toxic *Gymnodinium* species (Horstman et al., 1991), later described as *Karenia cristata* (Botes et al., 2003). This species, first observed in the late 1980s, was responsible for extensive mortalities, including 40 tons of abalone, and the production of an aerosol toxin responsible for eye, nose, throat, and skin irritations in humans. However, to date, *G. polygramma* remains the only bloom-forming species to have been linked to anoxia in False Bay.

G. polygramma is considered to be a cosmopolitan species in cold temperate to tropical waters, with worldwide distribution. A tapered epitheca with a moderate apical horn and two antapical spines on a rounded hypotheca identify *G. polygramma*, and mature cells are further characterized by thecal reticulae and striae (Figure 3). Although

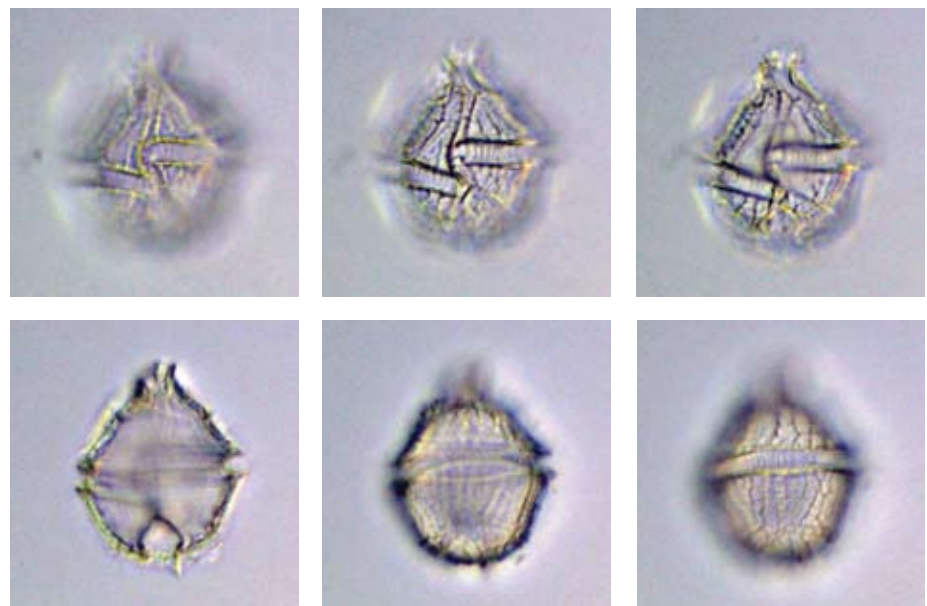


Figure 3. Series of light micrographs from high to low focus of a single cell of *Gonyaulax polygramma*, showing the tapered epitheca with a short apical horn, and rounded hypotheca with two antapical spines. The thecal reticulae and striae are a characteristic of this species.

G. polygramma has been previously considered exclusively autotrophic, it was recently shown to be mixotrophic, feeding on prey cells by engulfing them through the apical horn and sulcus (Jeong et al., 2005). This finding alters our previous perception of the bloom dynamics of *G. polygramma* and of the factors important in the development, persistence, and decline of blooms.

Although *G. polygramma* has never been associated with the production of toxins, it has been the cause of red tides in the coastal waters of many other countries, including Algeria, Belize, China, Hong Kong, Japan, Korea, Mexico, and the United States. In several cases, these blooms have caused mortalities of finfish and shellfish, usually attributed to anoxia (Jeong et al., 2005). For example, blooms of *G. polygramma* appeared for the first time in Tolo Harbor, a bay on the north-eastern coast of Hong Kong, in February 1988 (Lam and Yip, 1990). Eutrophic conditions within the bay were thought to favor the bloom, which persisted for three and a half months, reaching concentrations of 23×10^6 cells l^{-1} . Three fish-kill events and two shellfish-mortality incidents were attributed to anoxic conditions associated with this bloom, the most serious of which resulted in the loss of 35 tons of fish.

Coastal Monitoring Time Series

The 2007 bloom of *G. polygramma* in False Bay represents only the second time this species has posed an environmental threat to the South African coast. In 1992, the government agency Marine and Coastal Management initiated a harmful algal bloom monitoring program in False Bay, incorporating daily phytoplankton sampling from the harbor wall in

Gordons Bay. The resulting 16-year time series of *G. polygramma* concentrations (Figure 4), plotted as weekly means, indicates the occurrence of three *G. polygramma* blooms: during the spring of 2000, during the spring and late summer of 2004–2005, and during the summer and early autumn of 2007. Higher cell densities indicate the greater magnitude of the 2007 bloom in comparison to the 2000 and 2004–2005 blooms. Although only three blooms were detected during

this monitoring period, *G. polygramma* has been a consistent component of the plankton at low concentrations. It is present in the plankton most often (one in every three years) in the eleventh (early autumn) and forty-third (spring) weeks of the year (Figure 5). A bimodal trend in red tide occurrence in the southern Benguela is well established and coincides with bimodality in upwelling-favorable winds (Pitcher et al., 1995). Taking into account the regular appearance

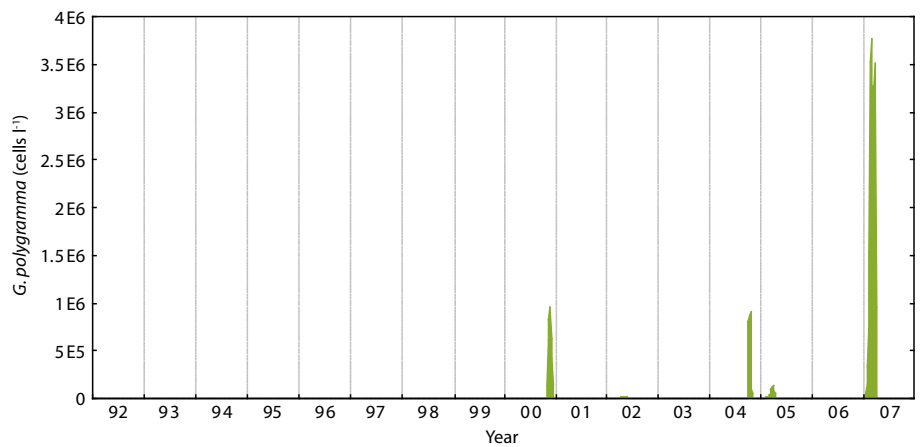


Figure 4. Sixteen-year time series of *Gonyaulax polygramma* derived from the collection of daily phytoplankton samples at Gordons Bay. Data are plotted as weekly means.

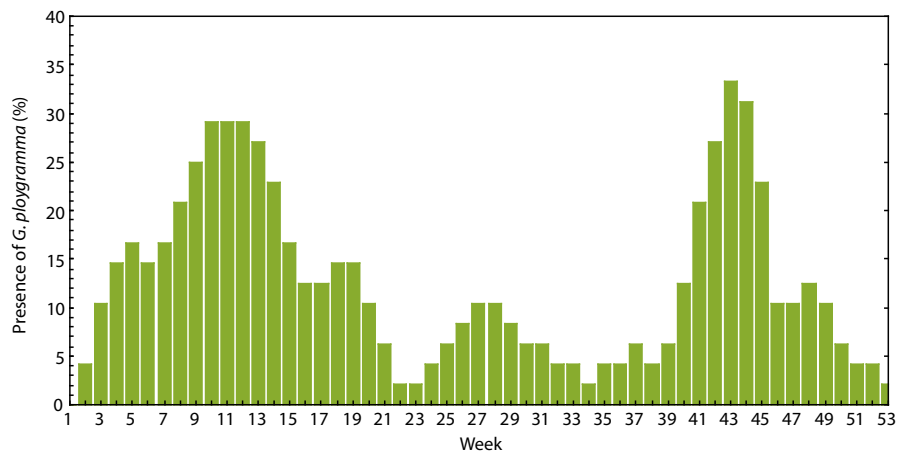


Figure 5. The presence of *G. polygramma* during each week of the year (expressed as a mean percentage) as established from the 16-year time series (1992–2007).

of *G. polygramma* in the plankton, it is surprising that blooms of this species are not more common.

A six-month time series (December 2006–May 2007), derived from daily monitoring of the phytoplankton at Gordons Bay and Hermanus, showed similar trends in the densities of *G. polygramma* at both sites, suggesting that these blooms are local manifestations, in False Bay and Walker Bay, respectively, of a general increase in the abundance of this dinoflagellate on the Western Agulhas Bank (Figure 6). The presence of *G. polygramma* in the plankton was first observed at Hermanus during December 2006. Increases in cell densities ($> 10^5$ cells l^{-1}) at both Hermanus and Gordons Bay were evident during January 2007, and a red tide ($> 10^6$ cells l^{-1}) was observed at

both localities in early February. Cell concentrations at both sites demonstrated extreme variability owing to the highly patchy nature of the blooms, and their advection within the bays, typically driven by the predominant winds (Figure 6). The blooms persisted within these bays for approximately two months and disappeared rather abruptly from both monitoring sites toward the end of March.

Satellite Remote Sensing

Several MERIS (Medium Resolution Imaging Spectrometer) chlorophyll *a* images clearly depict the bloom of *G. polygramma* in False Bay and Walker Bay (Figure 7). An image obtained on February 25, 2007, shows the bloom to be concentrated on the eastern side of the bay as indicated in aerial photographs of

the bloom off the Steenbras River mouth taken on the same day (Figure 8). On March 13, 2007, the bloom was concentrated on the western side of the bay with evidence of advection of the bloom from the Western Agulhas Bank onto the shelf of the West Coast (Figure 8).

Ship-Based Transect

A ship-based transect off Cape Peninsula was compared with satellite-based observations. The 42-nm transect conducted on February 26, 2007, comprised 14 stations positioned 3-nm apart (Figure 1). Vertical temperature and fluorescence profiles were made using a CTD-rosette sampler, and samples for the enumeration of phytoplankton were collected from the surface at each station. The vertical temperature section distinguished cool water inshore of a strong

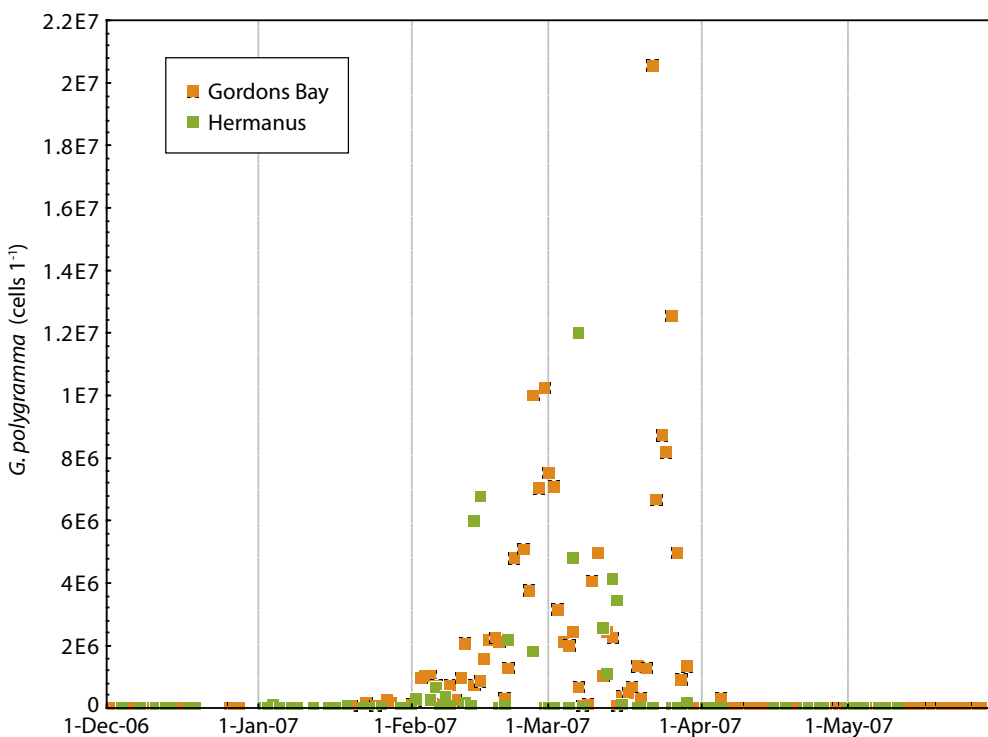


Figure 6. Time series of *Gonyaulax polygramma* obtained from the daily collection of phytoplankton samples at Gordons Bay and Hermanus from December 1, 2006, to May 31, 2007. Simultaneous increases in the densities of *G. polygramma* at both monitoring sites in early February suggest that these blooms are local manifestations of a general increase in abundance of this dinoflagellate on the Western Agulhas Bank.

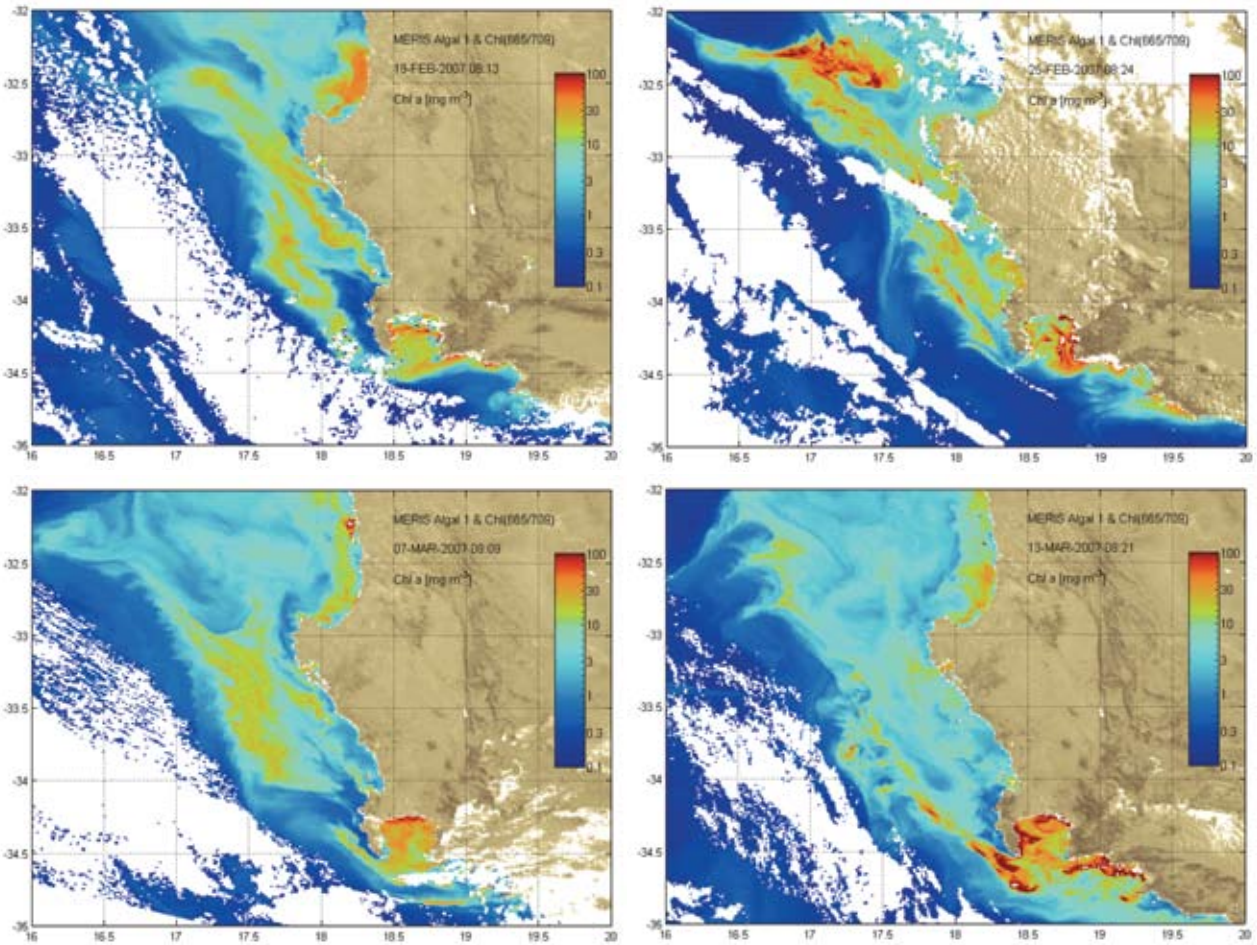


Figure 7. Satellite-derived images of 1-km resolution from the Medium Resolution Imaging Spectrometer (MERIS) sensor, detailing the development of the *Gonyaulax polygramma* bloom in the False Bay area in February–March 2007 and its transport along the shelf edge of the West Coast. The simultaneous development of a bloom dominated by the toxic *Alexandrium catenella* in the St. Helena Bay region is also evident. Chlorophyll *a* (Chl) products were calculated using merged data from the standard MERIS Algal 1 algorithm for Chl < 25 mg m⁻³ and a locally derived red-band empirical algorithm for Chl > 25 mg m⁻³. No flags were applied to the data so as to allow bloom transport to be observed in images where absolute Chl is relatively less important (except where high sun glint caused the failure of the Algal 1 product).

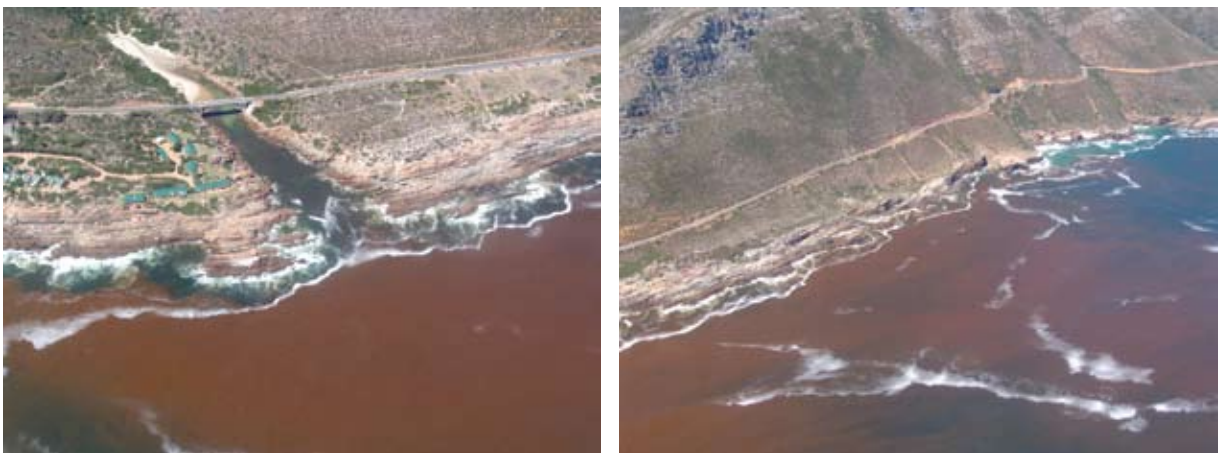


Figure 8. Aerial photographs of the *Gonyaulax polygramma* bloom taken off the Steenbras River mouth on the eastern side of False Bay on February 25, 2007. Photo by Brent Johnson

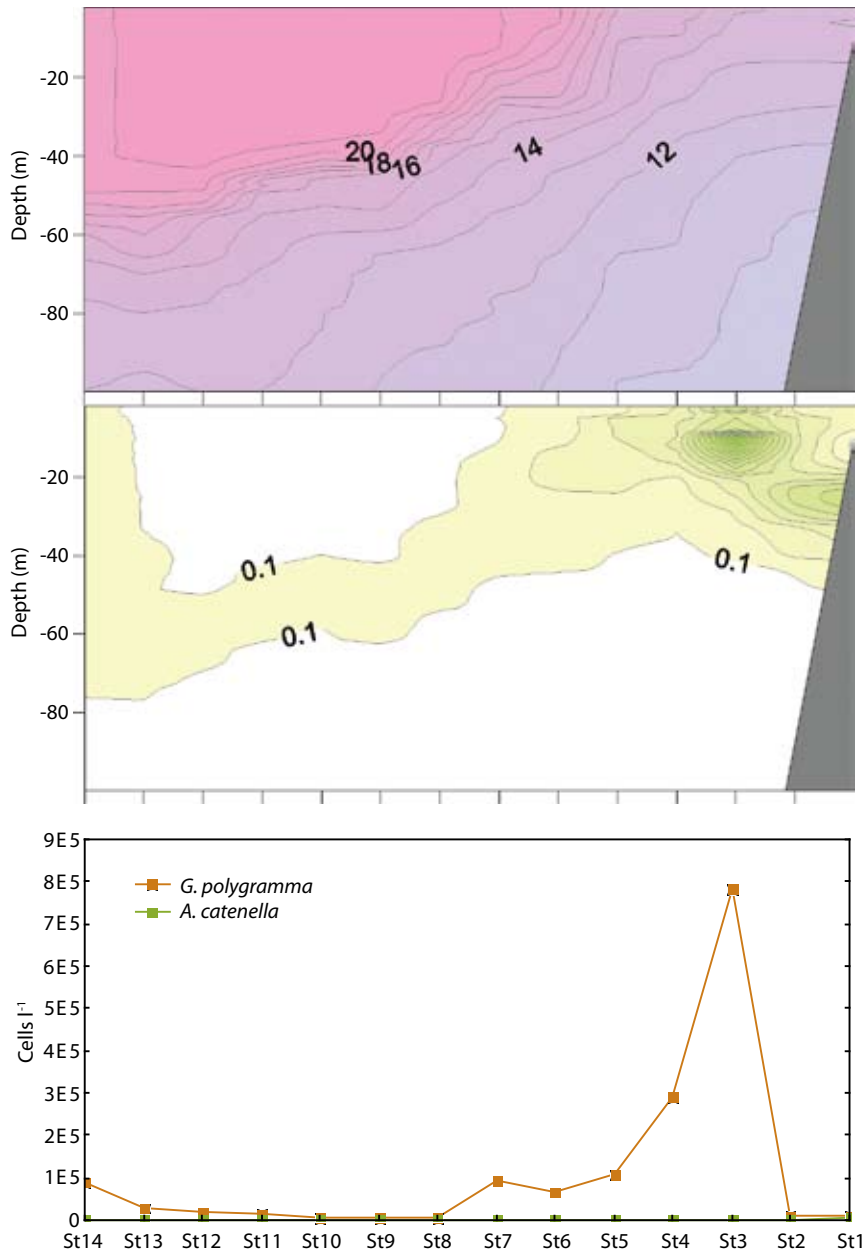


Figure 9. Transect off the Cape Peninsula on February 26, 2007, depicting temperature (°C), fluorescence (arbitrary units), and concentrations of *Gonyaulax polygramma* and *Alexandrium catenella* determined from samples collected at the surface.

frontal system centered at Stations 5 and 6 (Figure 9). High concentrations of *G. polygramma* were found both within and inshore of the front, between Stations 3 and 7. Cell concentrations of *G. polygramma* were highest at Station 3, which also corresponded to a peak in fluorescence. Cells of *G. polygramma* were absent from the inner two stations. A strong northward flowing baroclinic jet current associated with the frontal system (Shannon and Nelson, 1996) is a likely vector for the transport and loss of the *G. polygramma* bloom from False Bay and the Western Agulhas Bank.

ALEXANDRIUM CATENELLA BLOOM IN ST. HELENA BAY

PSP has been known off the west coast of South Africa for many years and is typically attributed to the dinoflagellate *Alexandrium catenella*, which is a regular component of the West Coast plankton (Pitcher and Calder, 2000). Blooms of this dinoflagellate are most common to the north of Cape Columbine, as is the incidence of PSP. Although *A. catenella* blooms may be advected southward during late summer and autumn, they do not appear to extend beyond Cape Point, which consequently corresponds to the southernmost PSP records (Pitcher and Calder, 2000; Pitcher et al., 2001).

St. Helena Bay is characterized by consistently high phytoplankton biomass, owing to persistent stratification and retentive circulation patterns, which also make it prone to red tide, particularly toward the end of the upwelling season (Pitcher and Nelson, 2006). The detection of PSP toxins in shellfish in the greater St. Helena Bay region, as in February–March 2007, is therefore considered a fairly common occurrence.

Satellite Remote Sensing

In addition to the *G. polygramma* bloom in False Bay and Walker Bay, and its advective loss from the western Agulhas Bank in the jet current off the Cape Peninsula, satellite imagery also provided clear evidence of high biomass blooms in St. Helena Bay (Figure 7, for example, on February 19, 2007). The identity of this bloom was confirmed by means of ship-based sampling.

Ship-Based Transect

A 97-nm transect sampled on February 28, 2007, out of St. Helena Bay comprised 12 stations (Figure 1). Again, vertical temperature and fluorescence profiles were taken using a CTD-rosette sampler, and samples for the enumeration of phytoplankton were collected from the surface and the fluorescence maximum at each station. The vertical temperature section out of St. Helena Bay was more complex than that off the Cape Peninsula as it transected St. Helena Bay, the Cape Columbine upwelling cell, and the frontal jet (Figure 10).

The inner two stations confirmed the presence of a bloom of *A. catenella* in St. Helena Bay, confined to a narrow inshore band and reaching concentrations of approximately 5×10^5 cells l^{-1} . Of particular interest was the identity of the bloom offshore of Cape Columbine. Here, high concentrations of *G. polygramma* were once again clearly associated with the frontal system and jet current. Concentrations of *G. polygramma* at Station 7 exceeded 3×10^6 cells l^{-1} at both the surface and subsurface fluorescence maximum. These high concentrations of *G. polygramma* in offshore West Coast waters, some 200 km from the initial site of bloom detection,

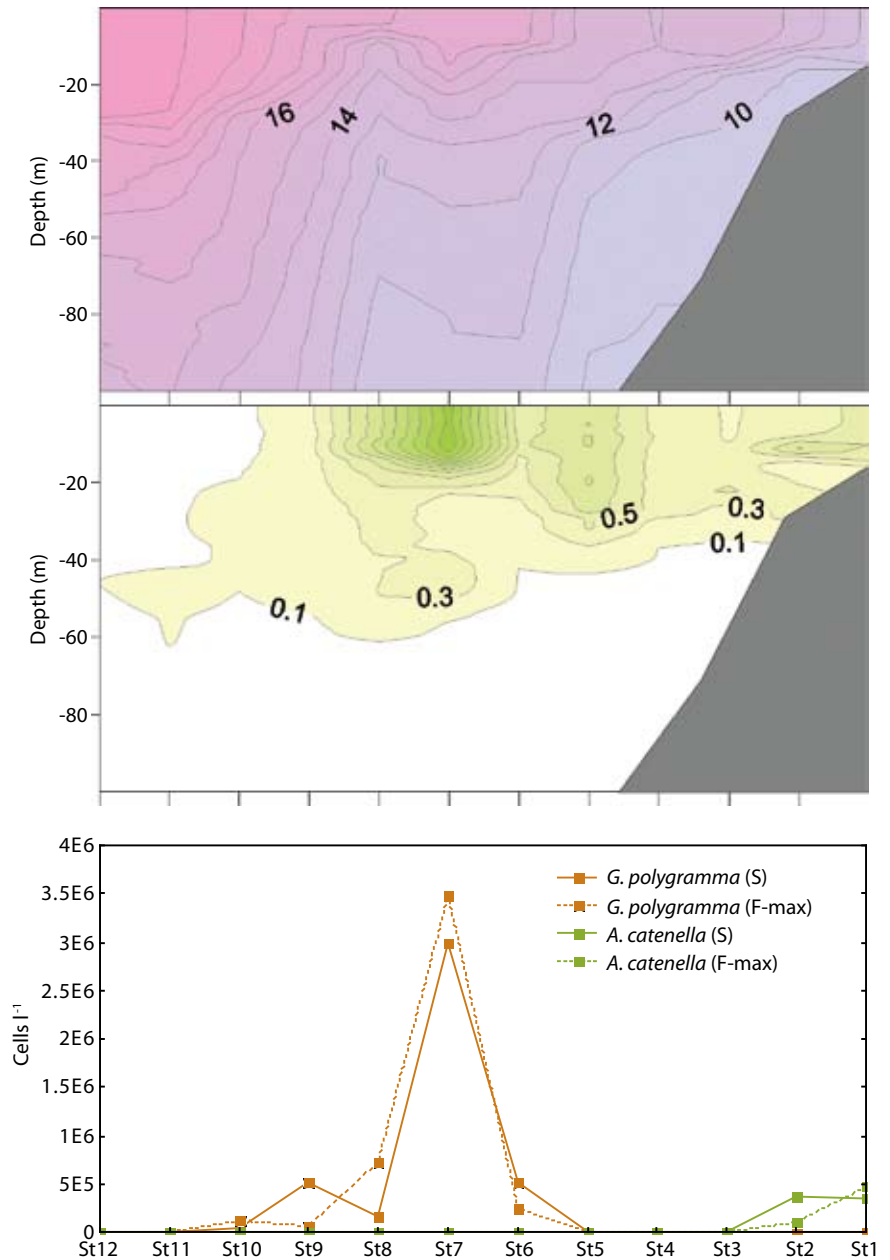


Figure 10. Transect out of St. Helena Bay on February 28, 2007, depicting temperature ($^{\circ}C$), fluorescence (arbitrary units), and concentrations of *Gonyaulax polygramma* and *Alexandrium catenella* established from samples collected at the surface and the fluorescence maximum.

demonstrated the magnitude and vast coverage of the bloom. The transect also served to clearly distinguish two dinoflagellate blooms of distinctly different origin, demarcating adjacent subsystems.

PHYSICAL FORCING OF BLOOMS

The Benguela current system is bounded in the south by the warm Indian Ocean western boundary Agulhas Current (Shannon and Nelson, 1996). The system is topographically steered, and surface currents are predominantly equatorward, with vigorous coastal upwelling cells, strong and narrow equatorward shelf edge jets, and a poleward undercurrent (Shillington et al., 2006). Cape Agulhas, the southern point of the continent, is typically considered the appropriate southern boundary of the upwelling system (Nelson and Hutchings, 1983), although upwelling between Cape Point and Cape Agulhas is generally reduced owing to changes in the orientation of the coastline and wind field at Cape Point (Andrews and Hutchings, 1980). The southern Benguela is thus effectively divided into two subsystems: the West Coast and the Western Agulhas Bank systems.

Embedded on the West Coast are three cells of enhanced upwelling—the Namaqua, Columbine, and Cape Peninsula cells. A well-developed along-shore thermal system of fronts demarcates the seaward extent of upwelled water, with the Coastal Transition Zone Front effectively forming the outer boundary of the productive West Coast waters. A poleward current may occur inshore, particularly during winter when barotropic reversals in alongshore flow

take place (Shannon and Nelson, 1996). The permanent northward flowing baroclinic jet off the Cape Peninsula and the periodic presence of southward flow shoreward of the jet result in a distinct retroflexion zone off the Cape Peninsula (Nelson and Hutchings, 1983). On the Western Agulhas Bank, a convergent northwest-oriented current system funnels into the West Coast jet current off the Cape Peninsula. Thus, on the western side of the Agulhas Bank, the sluggish Benguela drift carries water equatorward, thereby contributing Agulhas water to the West Coast shelf region (Nelson and Hutchings, 1983).

Our observations of red tide as reported here appear to reflect the mesoscale physics described above, resulting in the distinction of two red tides clearly ascribed to two subsystems of the southern Benguela. Harmful blooms on the South African coast, most of which are ascribed to dinoflagellate species, are generally confined to the area west of Cape Agulhas, and are therefore clearly associated with the upwelling system (Pitcher and Calder, 2000). However, in examining the species responsible for these blooms, Cape Point appears to be the natural divide for those bloom species that dominate the West Coast from those that dominate the Western Agulhas Bank (Pitcher and Boyd, 1996; Pitcher et al., 1998). Many West Coast dinoflagellate blooms appear to initiate downstream of Cape Columbine within the greater St. Helena Bay region. Here, the broad shelf, favoring stratification, and the retentive properties of the bay result in the development of high biomass and sometimes toxic dinoflagellate blooms. Poleward surface flow associated

with an inshore counter current, attributed to barotropic flow generated by coastal trapped waves, is responsible for the southward propagation of red tide on the West Coast. However, the retroflexion of poleward flow off the Cape Peninsula maintains the distinction between blooms of the West Coast and the Western Agulhas Bank.


Less is known of the dynamics of dinoflagellate blooms on the Western Agulhas Bank. Concurrent observations of *G. polygramma* blooms, in False Bay and Walker Bay, suggest that these blooms are in all likelihood local expressions of a widespread bloom and that the Bays serve only as sites of accumulation. Previous research points to a general cyclonic circulation in False Bay, with water entering the bay along the western side and leaving along the eastern side, particularly during upwelling-favorable winds (Atkins, 1970). These conditions are likely to favor the introduction of blooms of the Western Agulhas Bank into False Bay, and the strongly stratified conditions characteristic of late summer are expected to further advance bloom development. Under these conditions, the blooms tend to develop in a clockwise manner as previously observed by Horstman et al. (1991). The presence of a semi-enclosed circulation cell off Gordons Bay, somewhat independent of that of the rest of the bay (Atkins, 1970), tends to trap blooms in the northeastern corner of False Bay. For this reason, blooms often concentrate off Gordons Bay, making this particular region of False Bay more vulnerable to the negative impact of harmful blooms.

Reversals of upwelling-favorable wind, prevalent toward the end of the

upwelling season, also tend to force the reversal of surface currents in False Bay. These anticyclonic circulation patterns allow the leakage of blooms from the bay and their entrainment into the Benguela jet current off the Cape Peninsula. This northward-flowing current, therefore, serves as a mechanism of export of the *G. polygramma* bloom from False Bay along the shelf edge of the West Coast.

The Agulhas Bank is tremendously important to the pelagic fishery of the southern Benguela upwelling system as it is a major spawning ground for several pelagic species. The Benguela frontal jet current in turn plays a crucial role in the life histories of these fish species because it allows eggs and larvae spawned on the Western Agulhas Bank to be transported to the productive West Coast nursery areas (Hutchings and Boyd, 1992). Starvation is a major source of recruitment variation, as eggs and larvae are transported from the spawning grounds. The export of the *G. polygramma* bloom from False Bay and its transport in the frontal jet current therefore provides a mechanism to ensure an adequate food supply for first-feeding larval fish transported to the West Coast by the same means. In this way, *G. polygramma* blooms may contribute positively to recruitment success within the pelagic fishery.

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