

## Characteristics of the surface boundary layer important to the development of red tide on the southern Namaqua shelf of the Benguela upwelling system

*Grant C. Pitcher*

Marine & Coastal Management, Private Bag X2, Rogge Bay, 8012, Cape Town, South Africa

*Greville Nelson*

Department of Oceanography, University of Cape Town, Rondebosch, 7701, Cape Town, South Africa

### *Abstract*

The southern Namaqua shelf, north of the Cape Columbine upwelling center, is particularly prone to red tide. Two influences of the surface boundary layer on the development of red tide in this area were investigated—the dynamics of the upper mixed layer in determining phytoplankton community composition and the role of mesoscale circulation in bloom concentration and transport. Two survey periods (18 February–11 March 2000 and 13–30 March 2001) are reported during which red tide, dominated by the dinoflagellate *Gyrodinium zeta*, formed in the area. A high degree of concordance between characteristics of stratification and groupings of phytoplankton demonstrated the importance of the upper mixed layer in determining species or life-form selection and development. Ordination of across-shelf phytoplankton samples revealed a consistent banded pattern, created by a wind-induced upwelling plume, tending to isolate a nearshore zone from an offshore domain, thereby creating an area of retention on the coastal side of the plume, favoring development of dinoflagellate blooms. The appearance of red tide was clearly associated with increasingly stratified conditions driven by alongshore flow from the north, following periods of wind relaxation and consequent reversal of surface currents.

The southern Benguela upwelling system forms part of one of four major eastern boundary current regions of the World Ocean. Here, a range of dinoflagellate species is responsible for toxic or otherwise harmful blooms (Pitcher and Calder 2000). These blooms, often referred to as red tides, are common during the latter part of the upwelling season, when the wind moderates and insolation is still strong, causing seasonal stratification to increase. Their accumulation inshore and the formation of red tide is thought to be driven by synoptic weather patterns, which dictate the across-shelf and alongshore movement of blooms (Pitcher et al. 1995; Pitcher and Boyd 1996). Red tide has therefore been closely related to the prevailing winds of the region, which govern most hydrodynamic processes on the continental shelf (Pitcher et al. 1998). These observations are considered to reflect the consequences of two important influences of the surface boundary layer on the development of red tide: the dynamics of the upper mixed layer in determining species selection and development and the role of mesoscale circulation in bloom retention and advection.

In the southern Benguela, three upwelling centers may be distinguished, all of which coincide with a narrowing of the shelf: the Namaqua (30°S), Cape Columbine (33°S), and Cape Peninsula (34°S) upwelling centers (Fig. 1). The region to the north of the Cape Columbine cell is particularly susceptible to red tide formation and its negative impacts, and a historical perspective of faunal

mortalities associated with red tides in this region is given by Cockcroft et al. (2000). Here topographic and bathymetric features alter current patterns and mixing regimes, features considered important in the development of red tide. The shelf broadens to the north of Columbine, favoring stratification and stability of the water column. Airborne radiometer studies within this region have identified upwelling off Cape Columbine and along the coast north of Dwarskersbos (Jury 1985; Taunton-Clark 1985). Under conditions of upwelling, an equatorward coastal jet is formed off the Columbine headland, but wind stress shear promotes clockwise circulation within St. Helena Bay (Jury 1985), thereby favoring retentive, near-surface circulation patterns within the region (Holden 1985; Penven et al. 2000). Alongshore variability of flow, considered to play a dominant role in driving the southward advection of phytoplankton blooms, is thought to be associated with barotropic flow inshore generated by coastally trapped waves over the southern Namaqua shelf with periods of 3 to 6 d (Lamberth and Nelson 1987; Probyn et al. 2000; Weeks et al. 2004).

Although the causes of shifts in phytoplankton community structure favoring flagellate taxa and their blooms have yet to be resolved (Smayda and Reynolds 2001), stratification is often recognized as a precondition for the proliferation of dinoflagellates, which are considered particularly susceptible to turbulence but well adapted to lower-energy, stratified conditions (Cullen and MacIntyre 1998; Estrada and Berdalet 1998). This study specifically investigates the dynamics of the upper mixed layer favoring the development of red tide on the southern Namaqua shelf by relating phytoplankton community composition to the degree of stratification of the surface layer. Those processes driving spatial and temporal changes in the upper mixed

### *Acknowledgements*

We thank all those who participated in the fieldwork and contributed to sample and data collection and analysis—S. Bernard, D. Calder, A. du Randt, S. Etheridge, C. Marangoni, T. Probyn, and C. Roesler.

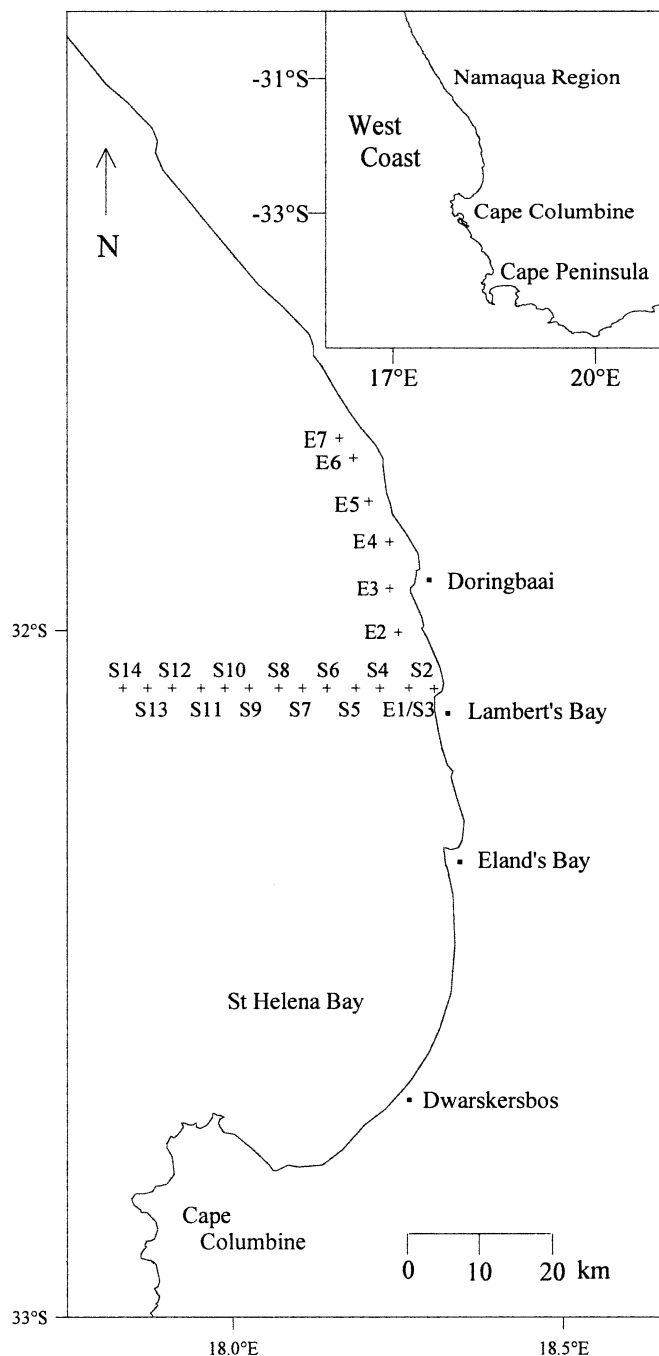


Fig. 1. Map depicting positions of across-shelf (S2–S14) and alongshore (E1–E7) stations off Lambert's Bay on the southern Namaqua shelf.

layer characteristics, responsible for changes in the community composition, are also assessed.

Blooms of dinoflagellates are observed to appear in coastal environments of the Benguela far more rapidly and to reach concentrations far higher than can be explained by local growth. It is therefore important to examine these blooms from a quantitative population dynamics perspective that includes not only the population in the region of potential impact but also the dynamics of the broader populations from which they may originate. In some cases

it is therefore appropriate to consider the local population in the region of interest as an integral part of a much larger population, while in other cases it is useful to consider the population as being of limited spatial extent and to examine the advection of that population in a Lagrangian manner. However, the lack of coincident data on water movements and phytoplankton populations has prevented investigators from establishing the role of physical transport in the local development and composition of red tides. This study thus further undertook the simultaneous measurement of currents with observations of bloom formation, thereby identifying and quantifying the across-shelf and alongshore currents associated with the formation of blooms.

## Methods

The fieldwork was conducted off Lambert's Bay, north of the Cape Columbine upwelling center (Fig. 1). Two survey periods are reported, 18 February–11 March 2000 and 13–30 March 2001. During these surveys, the inshore stations (S2, S3, and S4) of an across-shelf transect were sampled daily. The entire across-shelf transect comprising 14 stations (52 km) and an alongshore transect comprising seven stations (44 km) were sampled occasionally.

Wind velocity was recorded from a meteorological station situated in the Cape Columbine region. A 300-kHz Acoustic Doppler Current Profiler was used to measure earth-referenced currents at each station. During the 2001 survey, two Andraa current meters were moored at station S3, at 10- and 35-m depth. A Sea Bird CTD and Wetstar fluorometer were used to profile the water column for temperature and fluorescence. Samples for nitrate, chlorophyll *a* (Chl *a*), and phytoplankton analysis were collected from discrete depths. Nitrate samples were frozen and later analyzed according to the methods of Mostert (1983). Chl *a* samples were analyzed by fluorometric analysis as detailed by Parsons et al. (1984), and extracted chlorophyll values were used to calibrate in situ fluorescence profiles. Samples for phytoplankton analysis were fixed in buffered formalin and enumerated by the Utermöhl method (Hasle 1978).

The vertical stability of the water column was described in terms of a stratification index (*SI*), which was calculated as follows:

$$SI = \frac{dt}{dz} D / T_s$$

The temperature gradient  $dt/dz$  at the base of the upper mixed layer was chosen as a surrogate for stability. With dimensions of  $^{\circ}\text{C m}^{-1}$ , it was multiplied by the depth of the mixed layer (*D*, measured as the transition point in the second derivative ( $\frac{d^2T}{dz^2}$ )) and divided by the surface temperature ( $T_s$ ) to make it dimensionless. This stratification index is preferred to more conventional measures, such as the Brunt-Väisälä frequency, as it intrinsically takes into account the development time associated with upwelling events and associated changes in the phytoplankton community structure.

Algal community structure was quantified by classification analysis based on phytoplankton cell counts. The computer software package PRIMER (Plymouth Routines In Multivariate Ecological Research) was used in the assessment of community structure (Clarke and Warwick 2001). Classification analysis was used to group samples of similar phytoplankton composition. Root-root transformed abundance data, expressed in terms of number, were classified using the Bray–Curtis measure of similarity and group average sorting. In the resulting dendrograms, groups of samples were distinguished at arbitrary similarity levels. The species principally responsible for determining the sample groupings in the cluster or ordination analyses were identified by partitioning the contributions from each species to the separation of pairs of clusters. Ordination of samples by multidimensional scaling allowed the mapping or configuration of samples, attempting to satisfy all the conditions imposed by the rank similarity matrix, in two dimensions. Multidimensional scaling plots provide a clear indication of whether some groups in the cluster analysis are merely arbitrary subdivisions of a natural continuum. Community analyses were linked to the physical environment by superimposing the Stratification Index onto ordination plots, the degree of concordance between the index and the groupings of phytoplankton samples indicating the strength of linkage.

## Results

Observations made during the survey periods 18 February–11 March 2000 and 13–30 March 2001 are reported. Red tide dominated by a small previously unrecorded dinoflagellate, *Gyrodinium zeta*, formed inshore off Lambert's Bay during both the 2000 and the 2001 time series. *G. zeta* is a small (12–16  $\mu\text{m}$  long, 11–15  $\mu\text{m}$  wide) autotrophic dinoflagellate described by Larsen (1996). Cells contain several irregularly disc-shaped chloroplasts, and the outline of the cell is oval or obliquely oval in longitudinal section with the right part of the hyposome slightly larger than the left. No accounts of toxicity have been ascribed to *G. zeta*, and the observations off Lambert's Bay constitute the first reports of red tide attributed to this species.

**18 February–11 March 2000: Inshore time series**—The importance of local wind events in governing the observed hydrography and phytoplankton populations of the inshore environment is clearly evident from the 2000 time series (Fig. 2). Sea surface temperatures were tightly coupled to changes in the wind. Southerly winds dominated the time series but were interspersed with periods of wind relaxation or reversal each of which was associated with a rapid increase in sea surface temperature and phytoplankton biomass and shifts in phytoplankton composition. In addition to the observed temporal variability, considerable spatial variability was observed between the inshore station (S2) and the outer station (S4). Daily surface phytoplankton assemblages at station S3 revealed three groupings of samples for the 23-d time series (Fig. 2d), which were closely aligned to hydrographic

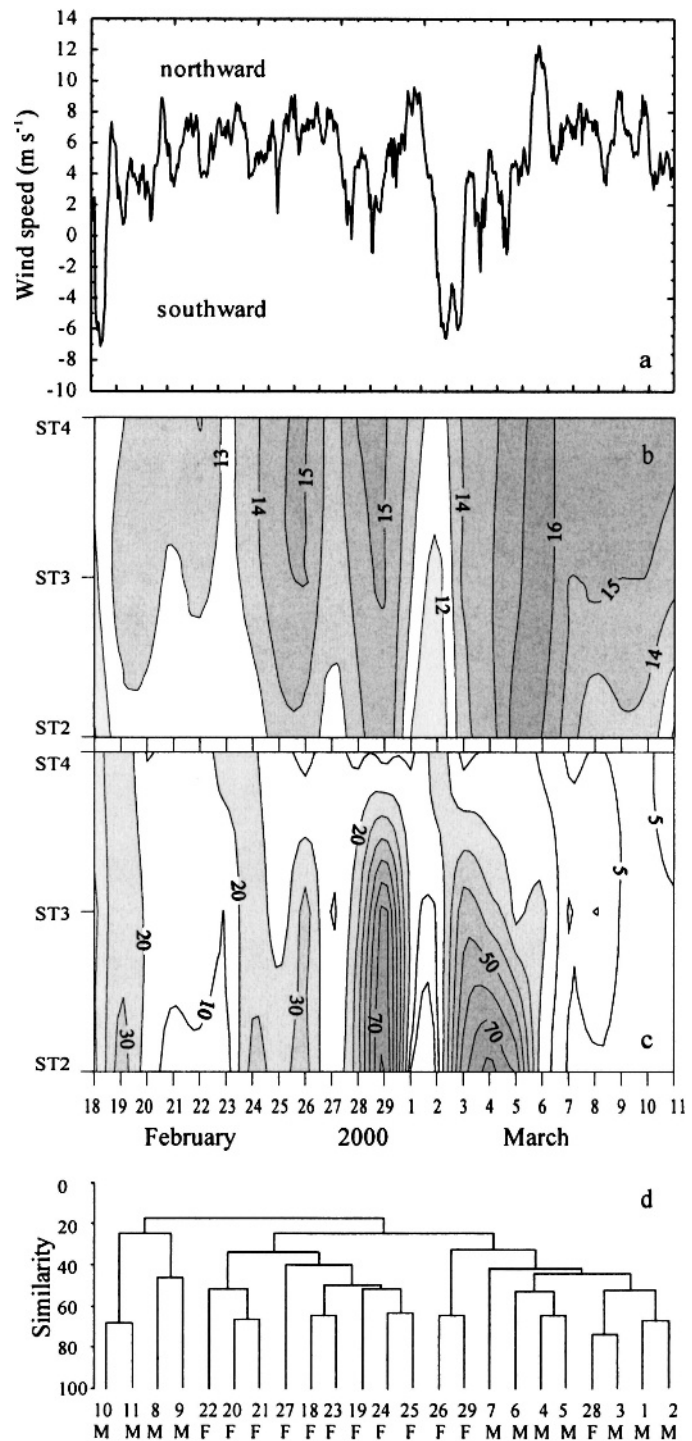
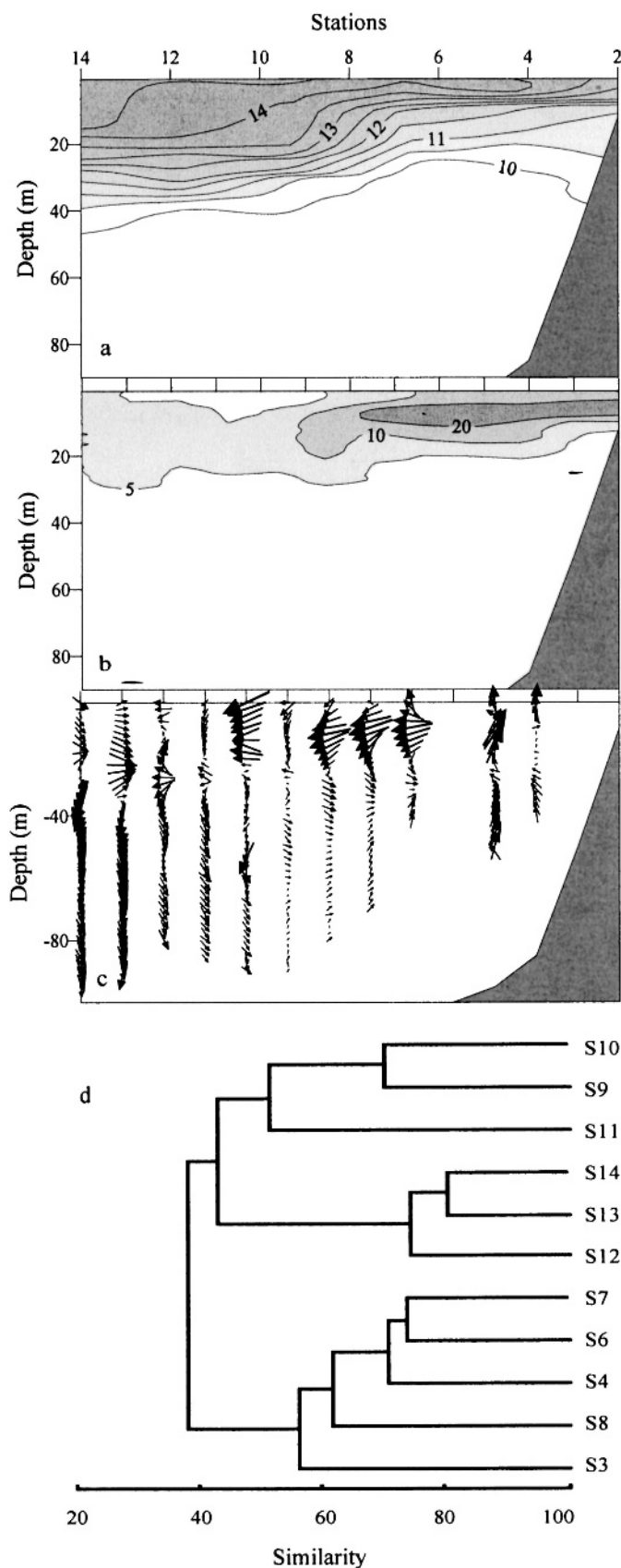


Fig. 2. Inshore time series for 18 February–11 March 2000 of (a) hourly alongshore wind, and (b) mean temperature ( $^{\circ}\text{C}$ ), and (c) mean chlorophyll *a* ( $\text{mg m}^{-3}$ ) in the upper 5 m of the water column at stations S2, S3, and S4. Daily surface phytoplankton samples from station 3 were grouped by means of a (d) dendrogram using group-average clustering from Bray–Curtis similarities on root-root-transformed abundance data.

observations. Assemblages of the first 8 d (18–25 February) were characterized by the dominance of diatom species of the genera *Pseudo-nitzschia* and *Chaetoceros* and *Skeleto-*



*nema costatum*. On 26 February, the assemblage changed to one dominated by dinoflagellates. Particularly prominent was the small dinoflagellate *G. zeta* and *Ceratium lineatum*, *Dinophysis acuminata*, two species of *Prorocentrum*, and *Ceratium furca*. Although the diatom community reappeared on 27 February, the dinoflagellate assemblage returned the following day, on 28 February, and persisted until 07 March. During this period, red tide developed inshore on two occasions, 29 February and 04 March, with concentrations of *G. zeta* exceeding  $40 \times 10^6$  cells  $\text{L}^{-1}$ . These blooms corresponded to periods of wind relaxation and inshore Chl *a* concentrations exceeded  $80 \text{ mg m}^{-3}$ . The final 4 d of the time series, from 08 to 11 March, were associated with the return of strong southerly winds, colder water, and declining levels of phytoplankton biomass, dominated once again by species of diatoms.

During this time series, four across-shelf transects (22 and 25 February and 03 and 08 March) and a single alongshore transect (23 February) were sampled placing the time series within a spatial context.

*Across-shelf transect: 22 February 2000*—Upper mixed layer characteristics varied over the length of the transect, and although sea surface temperatures were cooler inshore ( $<14^\circ\text{C}$ ), the outer half of the transect was characterized by deeper mixing (Fig. 3). This variation in the upper mixed layer corresponded to changes in phytoplankton biomass and assemblage. Phytoplankton biomass was considerably higher ( $>20 \text{ mg Chl } a \text{ m}^{-3}$ ) at the inner stations (S2–S8). These stations grouped together in terms of their species composition in a mixed assemblage, dominated by diatoms of the genus *Pseudo-nitzschia* and by the small dinoflagellate *G. zeta*. Few dinoflagellates were found further offshore, where two diatom communities were distinguished. Species of *Pseudo-nitzschia* and *Thalassiosira* were prominent at stations S9–S11, whereas species of the genus *Chaetoceros* and *S. costatum* dominated at stations S12–S14. In this instance, current patterns, as discerned from current profiles at each station along the transect, did not provide an entirely coherent picture. The inner stations were characterized by northward flow ( $>10 \text{ cm s}^{-1}$ ) at the surface. Offshore surface flow ( $>20 \text{ cm s}^{-1}$ ) dominated the middle stations, while weak onshore flow was observed at the outer two stations. Strong current shear was evident at approximately 25-m depth at most stations. At the outer stations, the bottom water was dominated by southerly flow. Weak onshore flow was detected further inshore, with northward bottom flow present at the inner stations.

*Alongshore transect: 23 February 2000*—Alongshore observations to the north of Lambert's Bay (Fig. 4) revealed considerable hydrographic and biological vari-

Fig. 3. Offshore transect 22 February 2000. Vertical sections derived from profiles at Stations S2–S14 of (a) temperature ( $^\circ\text{C}$ ), (b) chlorophyll *a* ( $\text{mg m}^{-3}$ ), and (c) current vectors ( $\text{cm s}^{-1}$ ). Surface phytoplankton samples were grouped by means of a (d) dendrogram using group-average clustering from Bray–Curtis similarities on root-root-transformed abundance data.

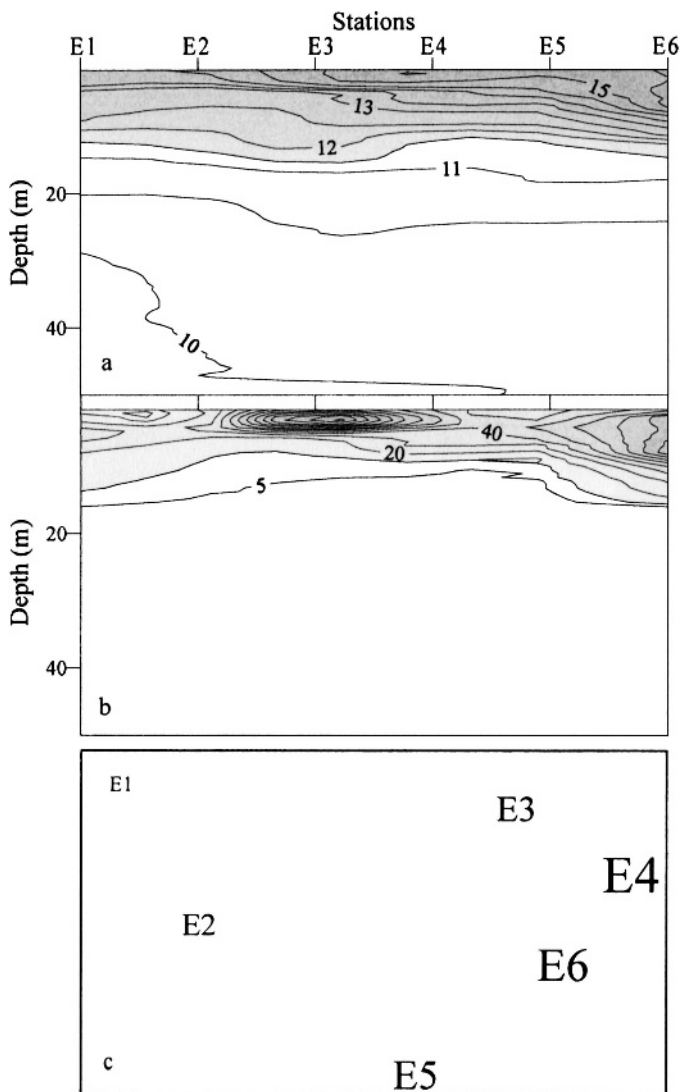


Fig. 4. Alongshore transect 23 February 2000. Vertical sections derived from profiles at Stations E1–E6 of (a) temperature ( $^{\circ}\text{C}$ ) and (b) chlorophyll *a* ( $\text{mg m}^{-3}$ ). Daily surface phytoplankton samples were grouped on the basis of phytoplankton species abundance. Ordination of phytoplankton samples by multidimensional scaling was based on root-root-transformed abundances and Bray–Curtis similarities (c). Fonts of increasing size reflect increasing stratification of the water column.

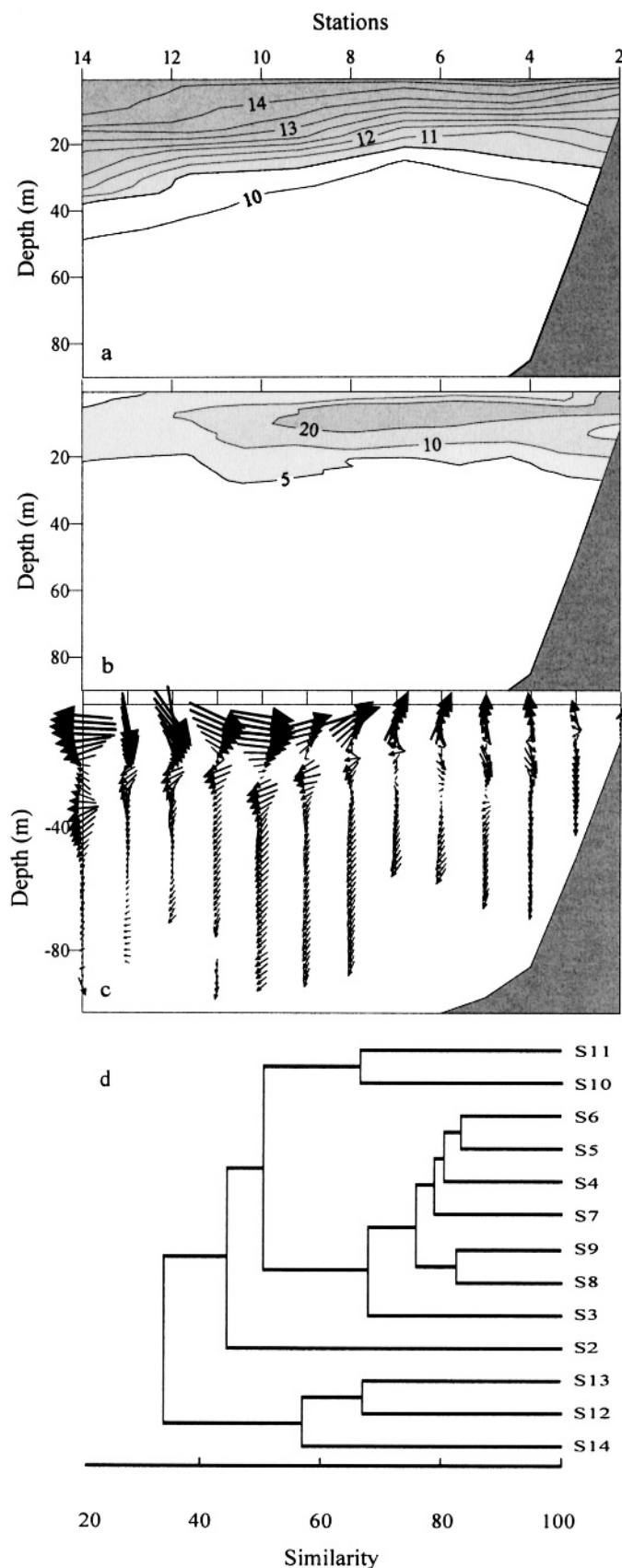
ability exceeding that observed across-shelf the previous day (Fig. 3). A very high biomass bloom ( $>100 \text{ mg Chl } a \text{ m}^{-3}$ ) characterized the warmer stratified waters of the northern stations. Ordination of the phytoplankton samples by multidimensional scaling revealed two clusters of samples, a southern community dominated by diatoms belonging to the genus *Pseudo-nitzschia* and a northern community dominated by the small dinoflagellate *G. zeta*. These community analyses were linked to the physical environment by superimposing an index of water column stratification, the results clearly indicating the association of the *G. zeta* bloom with highly stratified waters. Location of the bloom inshore to the north of Lambert's Bay on 23 February indicated in all likelihood that the bloom off

Lambert's Bay on 29 February did not originate offshore but rather from the north and was therefore a consequence of poleward flow inshore.

*Across-shelf transect: 25 February 2000*—Vertical sections of sea temperature and phytoplankton biomass on 25 February (Fig. 5) showed many similarities to those observations made on the 22 February (Fig. 3). Although sea surface temperatures were again marginally lower inshore ( $<14^{\circ}\text{C}$ ), mixing within the upper layer was more prevalent offshore. Phytoplankton biomass was higher inshore of station 10 ( $>20 \text{ mg Chl } a \text{ m}^{-3}$ ). Diatoms dominated all surface samples, and four groupings were identified that appeared to reflect current flow patterns in that assemblages were associated with current flow in a particular direction. Current flow was weak at station S2, where the diatom *Skeletonema costatum* dominated, with high concentrations of the dinoflagellates *C. lineatum* and *C. furca*. *Chaetoceros* species dominated stations S3–S9, where flow was entrained into a northward current ( $>20 \text{ cm s}^{-1}$ ) centered at stations S4 and S5. *Pseudo-nitzschia* species dominated stations S10 and S11, where flow was onshore ( $>30 \text{ cm s}^{-1}$ ). The outer stations (S12–S14) were discerned by offshore and southward flow and the prominence of *Thalassiosira* species. Current shear was again conspicuous between 20- and 25-m depth, with southwesterly flow dominating the cold bottom water.

*Across-shelf transect: 03 March 2000*—Red tide ( $>100 \text{ mg Chl } a \text{ m}^{-3}$ ) dominated by *G. zeta* was located inshore at stations S2 and S3 (Fig. 6) following the reversal of winds (Fig. 2). Cluster analysis of surface phytoplankton revealed a diatom population dominated by *Chaetoceros* species and *S. costatum* offshore of the dinoflagellate population dominated by *G. zeta*, *C. lineatum*, and *D. acuminata*. Strong onshore flow ( $>25 \text{ cm s}^{-1}$ ) of the surface water was evident at the outer stations. Moving inshore, the northward component of the surface flow ( $>25 \text{ cm s}^{-1}$ ) increased, and strong northward flow was centered at stations S4 and S5. Stations S2 and S3 were characterized by reduced flow, and at station S2 flow was reversed. The red tide was thus associated with a very narrow band of southward flow inshore, having been forced inshore by strong onshore and northward flow at the outer stations. Again, strong shear was evident at approximately 20-m depth, and southwesterly flow dominated in deeper water.

*Across-shelf transect: 08 March 2000*—Sampling followed the resumption of upwelling winds resulting in the cooling of inshore waters (Fig. 7). A lens of warm surface water separated the cooler inshore stations from cooler offshore water. Clustering of phytoplankton assemblages with observed current patterns was again evident. The inshore stations (S2–S8) were dominated by dinoflagellates, whereas diatoms dominated the offshore stations (S9–S14). The core of the bloom was now located further offshore and associated with strong northward flow ( $>25 \text{ cm s}^{-1}$ ) centered at stations S6 and S7. The highest biomass ( $>20 \text{ mg Chl } a \text{ m}^{-3}$ ) thus appeared to be located in an



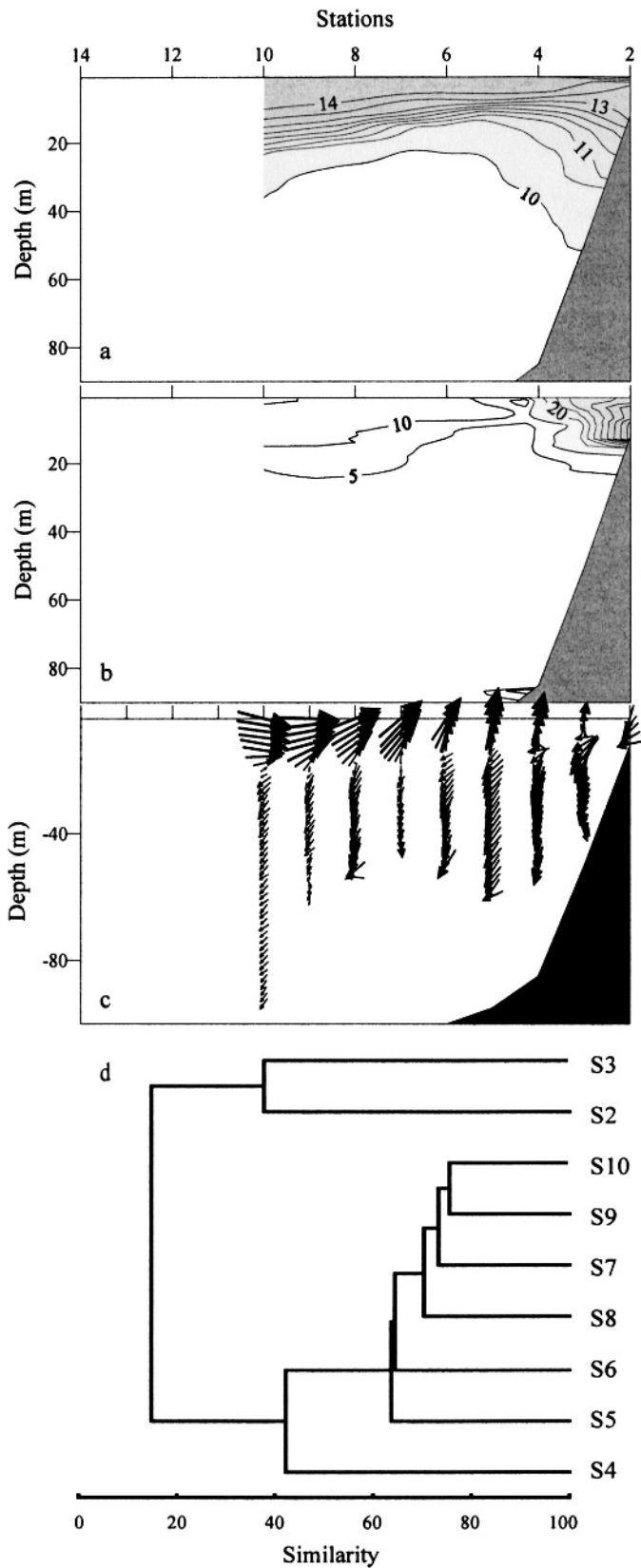
area of convergence of onshore flow at the outer stations and offshore flow at the inner stations. Offshore flow dominated the deeper water.

**13–30 March 2001: Inshore time series**—The first half of the 2001 time series was dominated by southerly winds (Fig. 8), and peaks in these upwelling-favorable winds corresponded to particularly low sea surface temperatures inshore (13, 16–18, and 20–21 March 2001). The latter half of the time series was marked by an extended period of wind relaxation or reversal that corresponded to strong downwelling and warming of the surface waters. Three groupings of surface phytoplankton samples collected daily from station S3 could be distinguished (Fig. 9a). The first group (13, 17, 18, and 20–22 March) reflected the assemblages present in cold water following upwelling and was distinguished by low cell concentrations in which *Thalassiosira* species were prominent. The second group of phytoplankton samples (14–16, 19, 23, and 24 March 2001) appeared to be characterized by intermediate cell composition and concentrations. Although species of *Thalassiosira* were still prominent, the small dinoflagellate *G. zeta*, present during the study in 2000, dominated the samples and was principally responsible for this grouping. The third group of phytoplankton samples (25–30 March) characterized the warm period, during which red tide developed inshore. Samples were dominated by *G. zeta* with surface cell concentrations attaining  $22 \times 10^6$  cells L<sup>-1</sup> and  $30 \times 10^6$  cells L<sup>-1</sup> on 25 and 29 March, respectively. The *Thalassiosira* species common in the former groups were virtually absent from this group.

The community analyses were again linked to the physical environment by superimposing an index of water column stratification on the ordination of daily phytoplankton samples (Fig. 9a). The high degree of concordance between the stratification index and the groupings of phytoplankton clearly demonstrated the importance of the upper mixed layer in determining species or life-form selection and development. These groups were also clearly identified in their environment as defined in terms of mixing and nutrient availability (Fig. 9b). The *Thalassiosira*-dominated community was characterized by a low index of stratification and high nutrient availability, the samples of intermediate composition were characterized by intermediate values, and the red tide dominated by the bloom of *G. zeta* was characterized by a high index of stratification and lower availability of nutrients.

Current meters deployed at station S3 at 10- and 35-m depth provided a useful account of current flow during the development of red tide (Fig. 10). The average current velocity during the study was notably higher at 10 m (10.8 cm s<sup>-1</sup>) compared to that at 35 m (7.0 cm s<sup>-1</sup>). Flow

← Fig. 5. Offshore transect 25 February 2000. Vertical sections derived from profiles at Stations S2–S14 of (a) temperature (°C), (b) chlorophyll *a* (mg m<sup>-3</sup>), and (c) current vectors (cm s<sup>-1</sup>). Surface phytoplankton samples were grouped by means of a (d) dendrogram using group-average clustering from Bray–Curtis similarities on root-root-transformed abundance data.



at this inshore station was found to be predominantly barotropic and southward, again indicating that the *G. zeta* bloom had been introduced from the north. The observed southward displacement or advection of the bloom during the course of the study averaged 6.5 km d<sup>-1</sup>. Although alongshore flow dominated currents, strong onshore flow from 20 to 24 March introduced the bloom to the coastal environment. During this period the bloom was advected shoreward at a rate of 3.8 km d<sup>-1</sup>. This period of onshore flow separated diatom domination of the inshore population during the first half of the time series from dinoflagellate domination of the phytoplankton during the latter half of the study.

Two across-shelf transects were sampled during this time series, on 16 and 24 March 2001, again placing the time series within a spatial context.

*Across-shelf transect: 16 March 2001*—Sampling followed a period of sustained upwelling-favorable winds. Consequently, cold water (<12°C) was observed inshore, and the highest phytoplankton biomass (>20 mg Chl *a* m<sup>-3</sup>) was associated with the upwelling front centered at station S6 (Fig. 11). Northward flow dominated the surface water at all stations, although an offshore component to the flow was observed at the inner stations and an onshore component at the outer stations. Surface phytoplankton samples clustered into two groups, an inshore group (stations S2–S7) dominated by the small *G. zeta* and several species of *Thalassiosira* and a group of outer stations (S8–S14) in which there was a marked decline in *G. zeta* concentrations. Surface current velocities were highest (>20 cm s<sup>-1</sup>) at these outer stations. Strong shear was evident in the region of the thermocline with southerly flow dominating the bottom water.

*Across-shelf transect: 24 March 2001*—Stratified conditions were observed following the onset of a period of wind relaxation and reversal (Fig. 12). Surface water exhibited particularly strong onshore flow (>40 cm s<sup>-1</sup>) at the outer stations and weaker offshore flow at the inner stations, entrained in northerly flow centered at stations S7–S9. The highest phytoplankton biomass (>30 mg Chl *a* m<sup>-3</sup>) was accumulated inshore of this core flow between stations S5 and S7. Phytoplankton samples were again clustered along an onshore–offshore continuum. The inner stations (S3 and S4) were characterized by notably higher concentrations of *G. zeta*.

Discussion

The development of red tide during the two time series of observations (18 February–11 March 2000 and 13–30

← Fig. 6. Offshore transect 03 March 2000. Vertical sections derived from profiles at Stations S2–S10 of (a) temperature (°C), (b) chlorophyll *a* (mg m<sup>-3</sup>), and (c) current vectors (cm s<sup>-1</sup>). Surface phytoplankton samples were grouped by means of (d) dendrogram using group-average clustering from Bray–Curtis similarities on root-root-transformed abundance data.

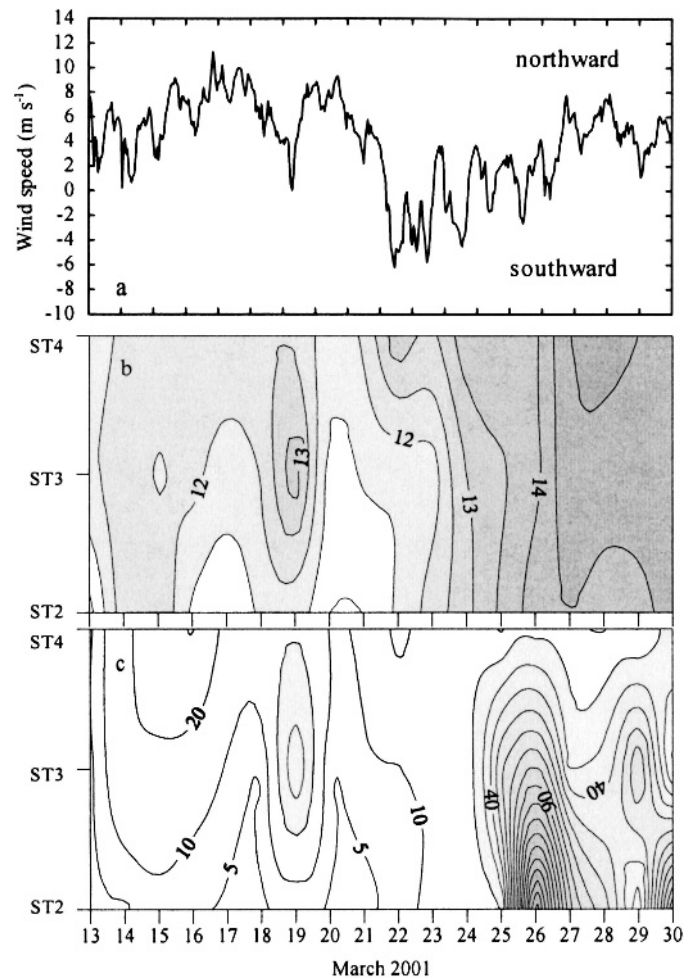
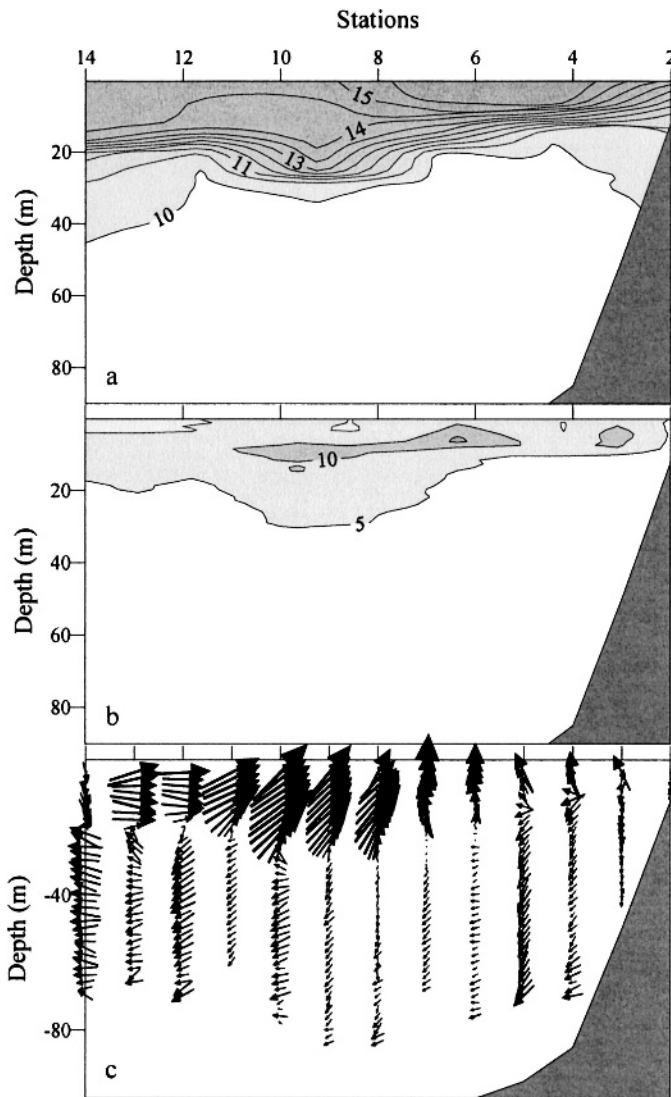
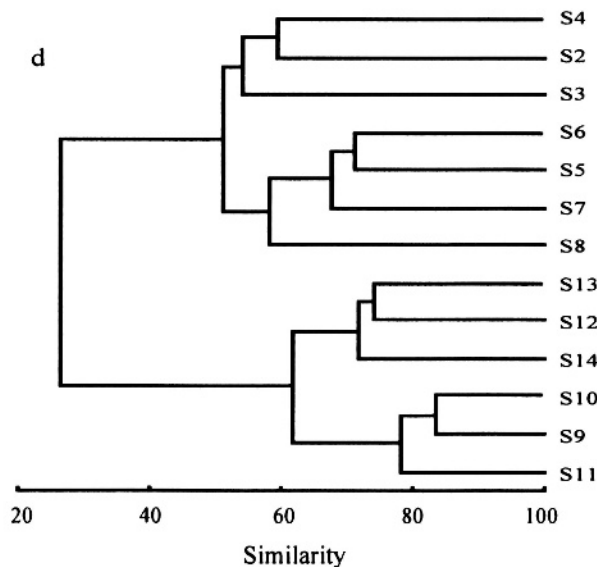


Fig. 8. Inshore time series for the period 13–30 March 2001 of (a) hourly alongshore wind speed and (b) mean temperature ( $^{\circ}\text{C}$ ), and (c) mean chlorophyll *a* ( $\text{mg m}^{-3}$ ) in the upper 5 m of the water column at stations S2, S3, and S4.



March 2001) at station S3 off Lambert’s Bay provided insight into the upper mixed layer conditions favoring dinoflagellates and the advective regime responsible for the shoreward accumulation of blooms.

### Life-forms and upper mixed layer dynamics

The causes of shifts in phytoplankton community structure favoring flagellate taxa and their blooms remain poorly resolved (Smayda and Reynolds 2001). The composition of phytoplankton communities is considered to reflect two fundamental selection features, notably, life-form and species-specific selection, and the importance of small-scale physical processes in effecting selection is

Fig. 7. Offshore transect 08 March 2000. Vertical sections derived from profiles at Stations S2–S14 of (a) temperature ( $^{\circ}\text{C}$ ), (b) chlorophyll *a* ( $\text{mg m}^{-3}$ ), and (c) current vectors ( $\text{cm s}^{-1}$ ). Surface phytoplankton samples were grouped by means of a (d) dendrogram using group-average clustering from Bray–Curtis similarities on root-root-transformed abundance data.

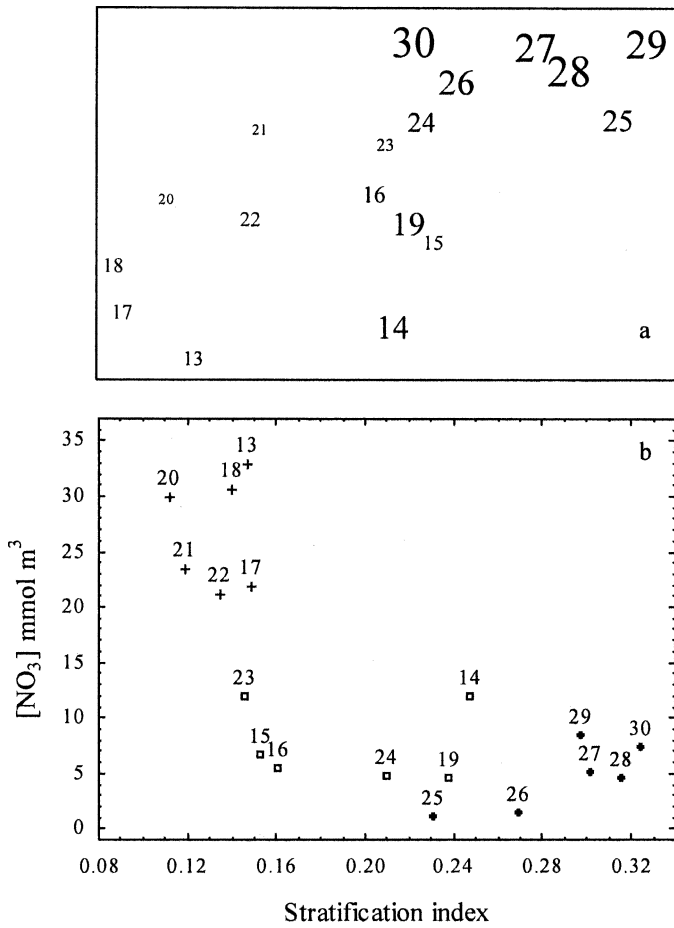


Fig. 9. Daily surface phytoplankton samples from station S3, for the period 13–30 March 2001, were grouped on the basis of phytoplankton species abundance. Ordination of phytoplankton samples by multidimensional scaling (a) was based on root-root-transformed abundances and Bray–Curtis similarities. Fonts of increasing size reflect increasing stratification of the water column. Groupings of phytoplankton samples were also identified in their environment as defined in terms of mixing and nutrient availability (b).

observed in the vertical dimension (i.e., dynamics of the upper mixed layer). Thus, changes in water column stratification and mixing depth are known to be important by altering competitive conditions through changes in light and nutrient availability. Because of these factors, stratification was identified during this study as a habitat feature operative in regulating spatial and temporal differences in phytoplankton assemblages by clustering taxa with shared features. These observations are consistent with the conceptual model of Margalef (1978), in which functional groups of phytoplankton, sharing various life-form properties, are variously adapted to a turbulent environment, defined in terms of nutrient availability and turbulence. The model therefore combines the interactive effects of habitat mixing and nutrient conditions on the selection of phylogenetic morphotypes. In this context, the typical phytoplankton succession, from fast-growing diatoms to motile dinoflagellates, is driven by changes leading from a well-mixed, nutrient-rich water column to a nutrient-poor

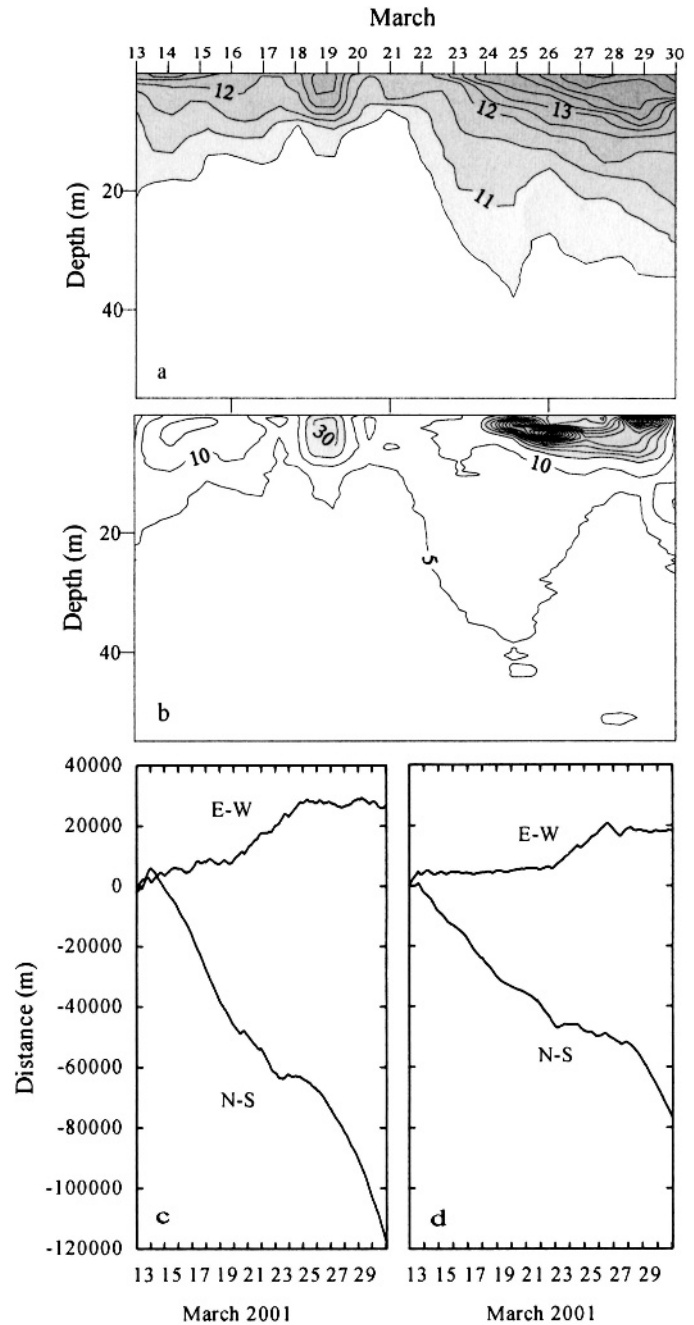
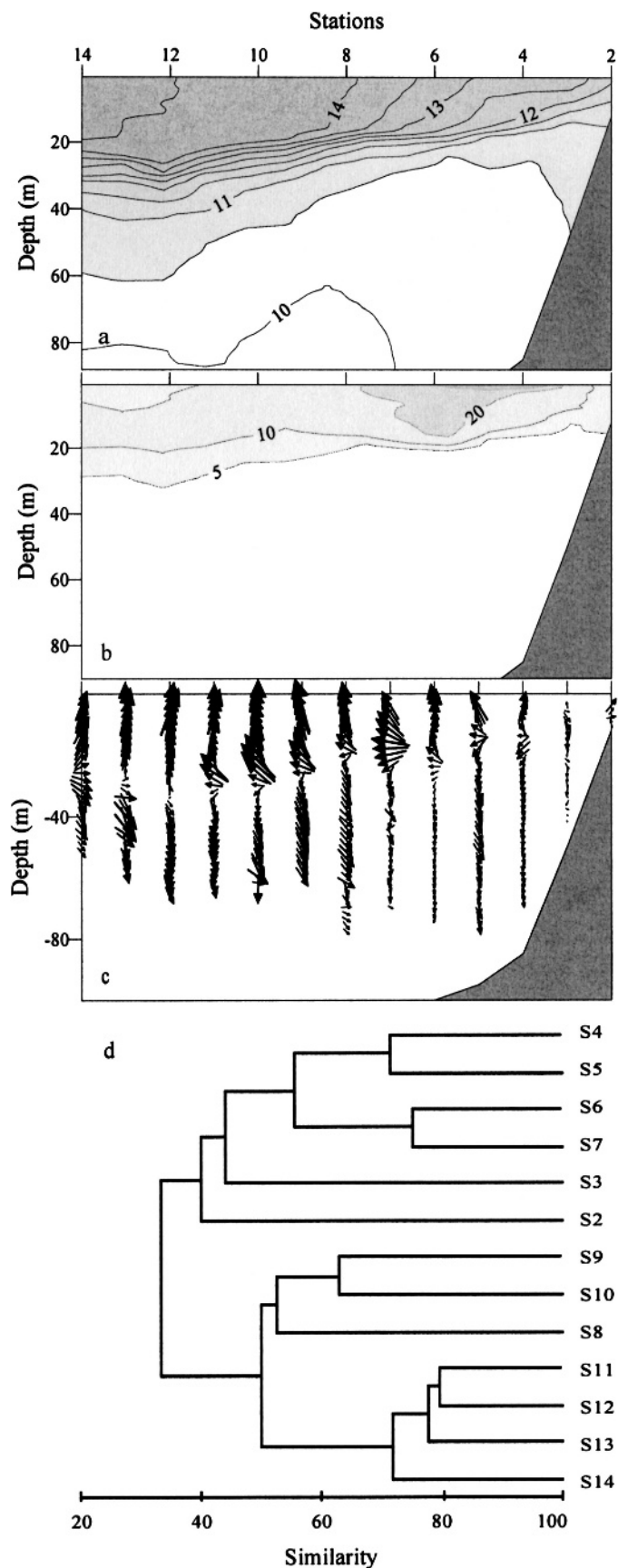


Fig. 10. Inshore time series for 13–30 March 2001. Vertical sections derived from daily profiles at station S3 of (a) temperature ( $^{\circ}\text{C}$ ) and (b) chlorophyll *a* ( $\text{mg m}^{-3}$ ) and progressive current vectors from (c) 10- and (d) 35-m depth.

stratified environment as observed in this study (Fig. 9b). Diatom- and dinoflagellate-dominated communities on the southern Namaqua shelf tend therefore to be spatially and temporally segregated and predictable in terms of their response to different regimes of turbulence. The introduction off Lambert’s Bay of red tide dominated by *G. zeta* in both 2000 (Fig. 2) and 2001 (Fig. 10) was clearly associated with the introduction of warmer water and increasingly stratified conditions. Similarly, both across-shelf (Fig. 3) and alongshore (Fig. 4) transects revealed the association



of dinoflagellate-dominated assemblages with more stratified environments. These observations demonstrated an ability to describe the sequence of phytoplankton dominance across temporal and spatial sequences of waterbodies.

Complex wind and current flow patterns induced by Cape Columbine resulted in unexpected spatial patterns in the upper mixed layer characteristics and in the consequent distribution of phytoplankton. Ordination of the surface phytoplankton samples from each of the across-shelf transects revealed a very consistent banded pattern, with dinoflagellates typically dominating inshore of diatom-dominated assemblages (Fig. 13). In most cases this distinction of an inshore dinoflagellate community corresponded approximately to the inner half of the transect. These patterns correspond in turn to an offshore deepening of the surface mixed layer (Fig. 14) considered to be driven by strong wind-stress shear in this region (Jury 1985). As expected, from the distribution of phytoplankton, changes in surface mixed layer depth appeared greatest midtransect. Increased wind mixing and greater shear instabilities at the base of the mixed layer, due to stronger surface currents, are considered to enhance entrainment and deepen the mixed layer offshore.

Although prediction of precise community composition is presently unlikely, as the predictability of individual species is consistent with stochastic selection in that species are often selected as a result of fortuity of presence, the formulation of functional groups does provide the potential for limited prediction because of the distinctive ecophysiological properties of various life forms significant to their bloom dynamics, habitat selection, and successions. Smayda and Reynolds (2001) have thus distinguished the habitat preferences of dinoflagellate bloom species along a continuum of progressively decreasing nutrient levels, increasing inertia of water masses against mixing, and deepening of the stratified layer. They claim success in distinguishing nine types of harmful algal bloom species reflecting an array of harmful algal bloom species with distinct morphotype features and specific habitat preferences along an onshore-offshore mixing-nutrient gradient. Their Type I species are considered to occur in relatively shallow, highly nutrient-enriched habitats having reduced water-mass exchange with offshore waters, and the predominant dinoflagellate blooms tend to be those of small to intermediate-sized gymnodinioid species. Intermediate-sized peridiniids (*Scropsiella trochoidea*) and prorocentroids (*Prorocentrum micans*) characterize Type II species found in habitats where nutrient levels are somewhat lower but still elevated. Type III blooms of morphologically complex ceratians extend offshore into stratified coastal waters but remain responsive to nutrient loading. They

← Fig. 11. Offshore transect 16 March 2001. Vertical sections derived from profiles at Stations S2–S14 of (a) temperature ( $^{\circ}\text{C}$ ), (b) chlorophyll *a* ( $\text{mg m}^{-3}$ ), and (c) current vectors ( $\text{cm s}^{-1}$ ). Surface phytoplankton samples were grouped by means of a (d) dendrogram using group-average clustering from Bray–Curtis similarities on root-root-transformed abundance data.

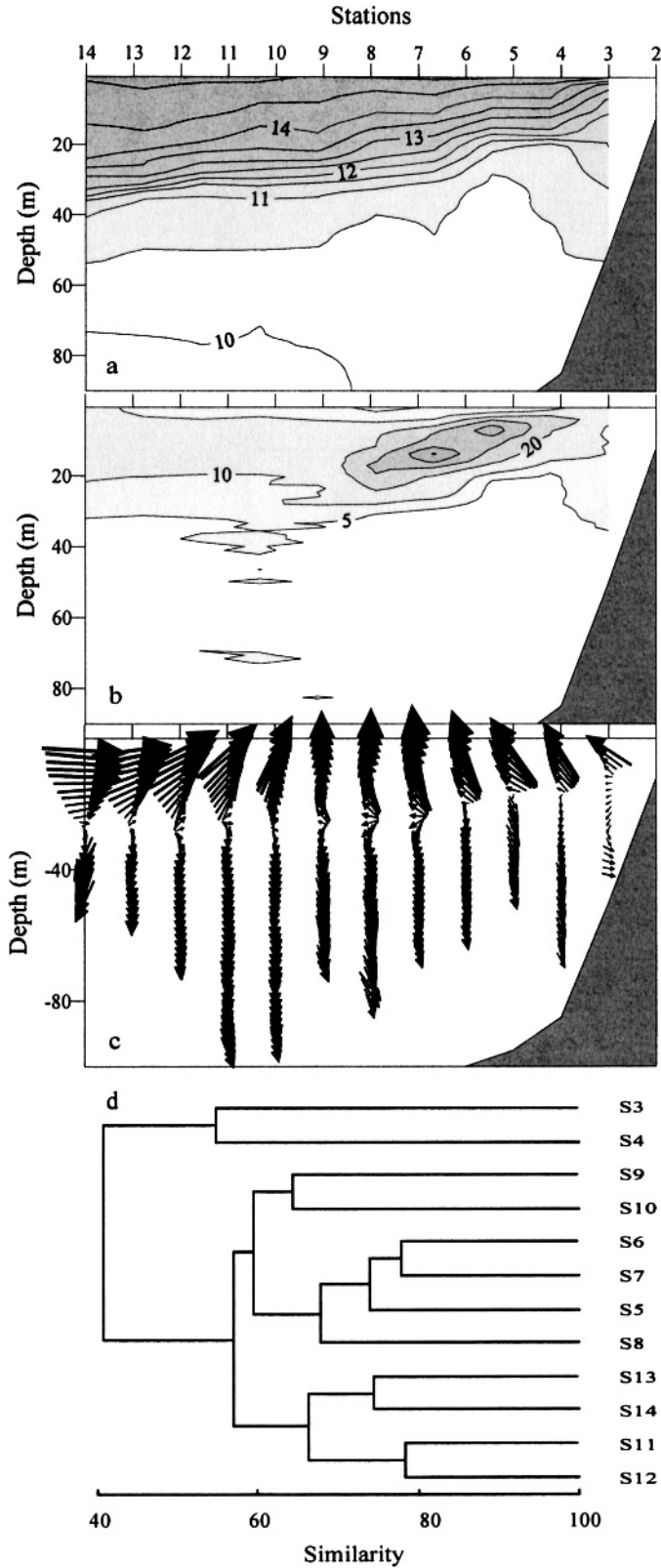


Fig. 12. Offshore transect 24 March 2001. Vertical sections derived from profiles at Stations S3–S14 of (a) temperature ( $^{\circ}\text{C}$ ), (b) chlorophyll *a* ( $\text{mg m}^{-3}$ ), and (c) current vectors ( $\text{cm s}^{-1}$ ). Surface phytoplankton samples were grouped by means of a (d) dendrogram using group-average clustering from Bray–Curtis similarities on root-root–transformed abundance data.

develop during late summer or autumn in temperate coastal habitats and often culminate in anoxia. Type IV species are adapted to the increased velocities associated with frontal zones (*Gymnodinium mikimotoi*, *Alexandrium catenella*), Type V species are adapted to the dampened but still elevated vertical mixing during relaxations in coastal upwelling (*Gymnodinium catenatum*, *Lingulodinium polyedra*), and Type VI assemblages are typically entrained within coastal currents (*Gymnodinium breve*, *C. furca*). Type VII species are characterized by the dinophysoids, which appear to represent transitional life forms, tolerating coastal upwelling sites but also common in offshore coastal waters of lower nutrient levels and more pronounced seasonal stratification. Two dinoflagellate life-form types are recognized within the very oligotrophic, highly stratified, and deepened trophogenic zone of the subtropical and tropical oceanic provinces—Type VIII, a tropical oceanic flora (*Ornithoceros* spp.), and Type IX (*Pyrocystis* spp.), a tropical shade flora—both characterized by very large ornamented dinoflagellates.

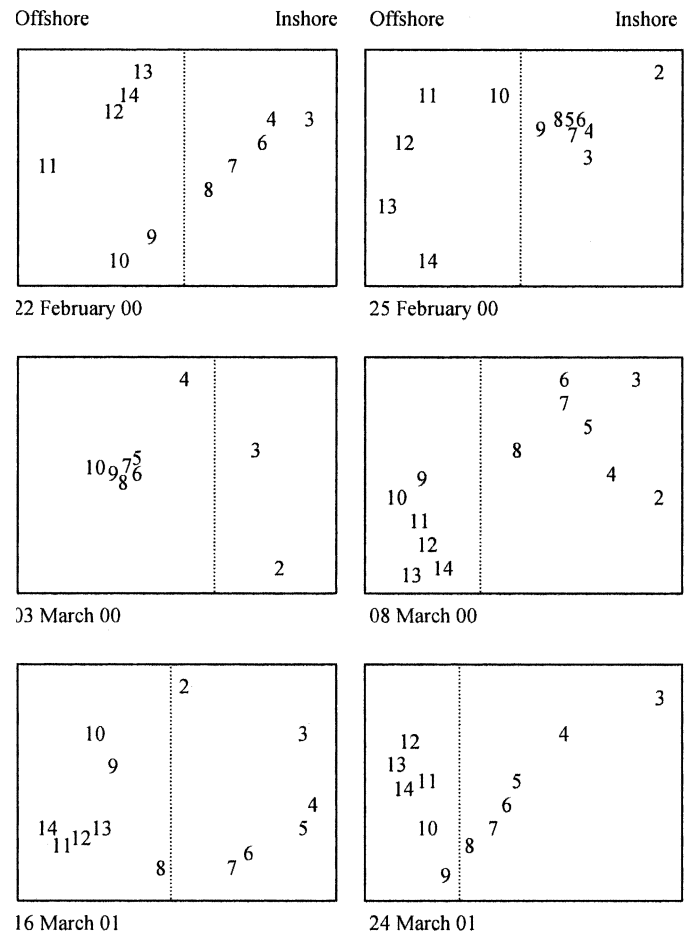


Fig. 13. Ordination of surface phytoplankton samples along each of the offshore transects by multidimensional scaling based on root-root–transformed abundances and Bray–Curtis similarities. The consistent distribution of an inshore and offshore grouping of phytoplankton assemblages is demarcated.

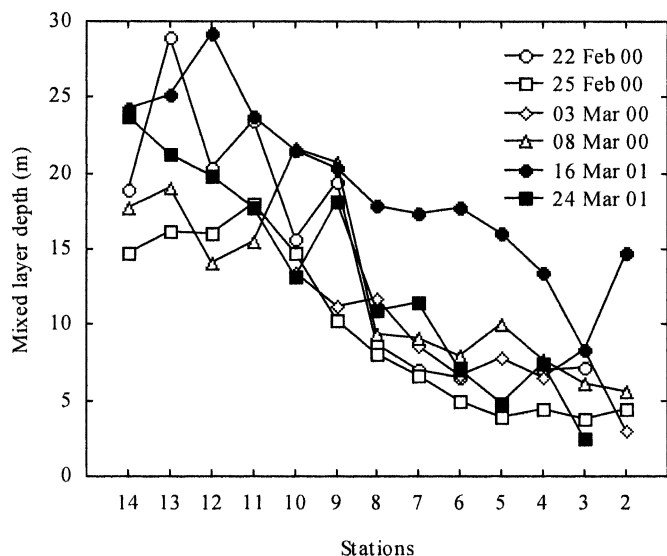


Fig. 14. Surface mixed layer depth along each of the offshore transects. Mixed layer depth is defined here as the maximum depth over which the observed temperature is within 1°C of the water temperature observation closest to the surface (<1-m depth).

This and other studies (Horstman 1981; Pitcher and Calder 2000) have identified a variety of bloom-forming dinoflagellate species on the southern Namaqua shelf representing a range of life-form types (I–VII): *Akashiwo sanguinea*, *A. catenella*, *Ceratium dens*, *C. furca*, *C. lineatum*, *D. acuminata*, *Gonyaulax polygramma*, *G. zeta*, *Noctiluca scintillans*, *Prorocentrum balticum*, *P. micans*, *Prorocentrum triestinum*, *Protoceratium reticulatum*, and *S. trochoidea*. These observations tend therefore to indicate a high degree of overlapping and intergrading of the traits or preferences of Type I–VII species and/or a diversity of habitats on the southern Namaqua shelf in terms of their nutrient-mixing characteristics, incorporating nearshore, coastal, and shelf environments and fronts, coastal currents, and upwelling events. Therefore, prediction, based on the physical environment, beyond the switch between diatoms and dinoflagellates, is not easily achieved. It may be that the diversity of dinoflagellates on the southern Namaqua shelf is explained not by external factors alone but by the dynamics of competition between species. Modeling by Huisman and Weissing (1999) has shown, for example, that competitive interactions may generate oscillations and chaotic behavior of species abundances, thus allowing the persistence of a greater diversity of competitors.

#### Advective control of blooms

The analysis of spatial and temporal patterns in planktonic ecosystems differs fundamentally from that in benthic or terrestrial ecosystems because, by definition, planktonic organisms are passively transported around by the fluid medium in which they exist. The first attempts to explain horizontal patterns in the distributions of plank-

tonic organisms (Skellam 1951; Kierstad and Slobodkin 1953) considered the coupled effects of biological growth and physical fields of flow. Many other explanations have followed incorporating at one extreme those of Gower et al. (1980) that consider the phytoplankton as a passive scalar being advected about by variable ocean currents. Ultimately, physical and biological processes are tightly coupled, and it is often difficult to discern their individual effects on species successions and changes in biomass and production.

Donaghay and Osborn (1997) combined fluid continuity equations with a conservation equation for population dynamics to quantify the role of biological and physical processes in the population dynamics of harmful algae and in their potentially harmful impact. The change in concentration of phytoplankton in a given parcel of water is given by a term for the biological generation and disappearance of phytoplankton (the net growth rate, which equates to the sum of the rate of cell division and the rate of mortality) and by a term for the motion of phytoplankton relative to the water (either convergent or divergent). However, the change in concentration of phytoplankton at a fixed point must also include a term for advection. This advective term may be an important source of variation with time, and it is important not to interpret the appearance of a bloom as the result of rapid growth of a local population when it is in fact the result of advection from elsewhere. Physical processes are therefore fundamental to the transport, concentration, and dissipation of harmful blooms.

The importance of advective processes dictated by meteorological forcing in controlling rapid shifts in the biomass and species composition of the inshore phytoplankton community of the southern Benguela has been previously demonstrated (Pitcher et al. 1996, 1998) and is again clearly apparent from the findings of this study. Both the 2000 and the 2001 time series demonstrated the role of alongshore poleward flow in the introduction of the *G. zeta* bloom off Lambert's Bay. In 2000, an alongshore transect revealed the presence of the bloom to the north of Lambert's Bay 6 d prior to its introduction off Lambert's Bay, while across-shelf transects revealed the absence of *G. zeta* offshore. In 2001, the deployment of current meters at station S3 revealed the dominance of poleward and onshore flow in the introduction of *G. zeta* off Lambert's Bay. Also evident from these time series was the rapidity at which blooms can be introduced, concentrated, and dissipated from any single station. Observations of greater alongshore physical and biological variability (Fig. 4) than that observed across shelf (Fig. 3), and knowing that alongshore flow dominates coastal currents, substantiates the importance of alongshore flow in determining these rapid changes in the composition of the phytoplankton. The appearance of red tide was clearly associated with increasingly stratified conditions, driven by alongshore flow of warmer water from the north, following periods of wind relaxation and consequent reversal of surface currents. The ability to predict red tide in inshore coastal waters is therefore dependent on understanding the mechanisms that control the transport and, to a lesser extent, the dynamics of blooms in offshore waters.

## Role of coastal topography in the distribution and transport of blooms

Whereas continental shelf bathymetry and equatorward winds provide large-scale upwelling mechanisms, variable local topography and meteorology create complex time- and space-dependent three-dimensional circulation. Consequently, the existence of pronounced capes or headlands and coastal embayments has been considered to give rise to upwelling shadows where phytoplankton can be accumulated through different retention mechanisms (Graham and Largier 1997; Roughan et al. 2005). Physical evidence for increased retention within bays associated with headlands is provided by the presence of warmer water in the bay, a lag between change of water temperature inside and outside the bay, increased water column stratification in the bay, or a reversal of current direction in the bay from predominant flow. The area downstream of Cape Columbine, incorporating the greater St. Helena Bay region, is clearly characterized by warmer water and higher phytoplankton biomass, as identified from remotely sensed NOAA AVHRR and SeaWiFS ocean color data, respectively (Pitcher and Weeks 2006). Here phytoplankton biomass is highest during the latter half of the upwelling season, when the contribution of dinoflagellates to the phytoplankton community is greatest and the region is particularly prone to harmful blooms. These areas may also favor bloom initiation, as they may allow species to reach threshold cell concentrations for bloom development and may function as sedimentary basins accumulating benthic cysts that will later serve as bloom inocula (Joyce et al. 2005).

Wind-driven circulation is well known to be important in the transport of harmful blooms in many parts of the world, but trying to understand the effects of temporally fluctuating and spatially variable winds in complicated coastal regions with capes, bays, and subsurface topography is a challenging problem. Nevertheless, observations during this study have allowed better conceptualization of the processes important to the development of harmful blooms in the greater St. Helena Bay region (Fig. 15) and are supported by the barotropic model of Penven et al. (2000) in the simulation of a coastal jet retention mechanism.

During upwelling (Fig. 15a), alongshore currents form a coastal jet that is interrupted by the topographic discontinuity of Cape Columbine. Although cyclonic curvature of the wind into St. Helena Bay is considered to influence the orientation of the coastal jet (Taunton-Clark 1985), the jet is separated from the coast to the north of the Cape. The predominantly northward flow adjacent to the Columbine headland, where the shelf is narrow and steep, has been observed by means of both drift-card returns (Duncan and Nell 1969) and radio-tracked drifters (Holden 1985). To the north of Cape Columbine, the bottom relief is more gently sloping and featureless, the bathymetric influence is less conspicuous, and although the surface drift is predominantly northerly, across-shelf, tidal, and inertial flow is more evident. In addition to the upwelling off Cape Columbine, a narrow band of upwelling may extend along the coast to the north of Dwarskersbos (Jury 1985). The

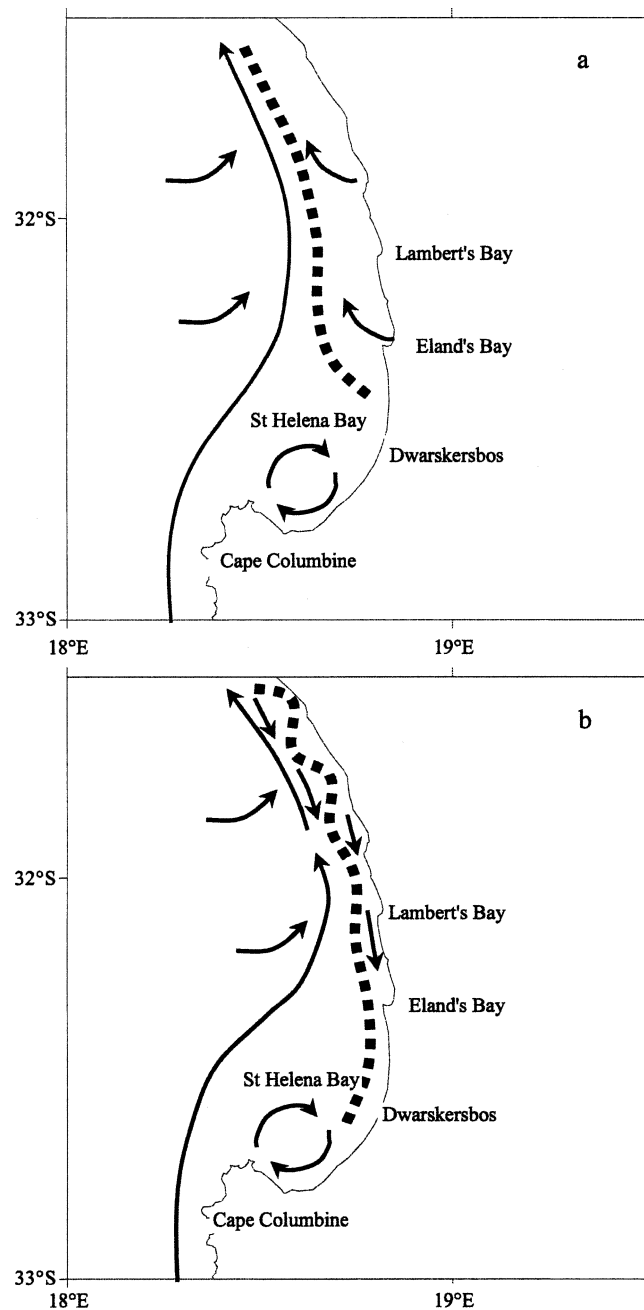


Fig. 15. Conceptualization of harmful bloom events in the greater St. Helena Bay region during periods of (a) upwelling and (b) relaxation or downwelling. The broken line demarcates the area of highest dinoflagellate abundance.

transects conducted during this study, offshore of Lambert's Bay, reflect not only these flow patterns but also the phytoplankton assemblages associated with them and with water of different origin. The coastal jet is often seen to separate an inshore assemblage in which dinoflagellates are abundant from an offshore population typically dominated by diatoms (Fig. 13). Under conditions of upwelling, the dinoflagellate population tends to accumulate offshore in a region of convergence, created by the narrow belt of upwelling and the core northward flow (Fig. 7).

These observations are supported by the patterns of circulation within the model domain of Penven et al. (2000) whereby equatorward wind forcing produces a cyclonic eddy in the lee of Cape Columbine that contributes to create a dynamic boundary between the coastal and the offshore domains. The wind-induced upwelling plume tends to isolate the nearshore area from the offshore domain, thereby inducing retention on the coastal side of the plume. A positive coupling between upwelling and retention may be provided by such structures, with stronger upwelling-favorable winds enhancing retention within the nearshore area despite the intensification of offshore flow associated with upwelling. The limited across-shelf exchange of water is depicted in the clear and consistent delineation of phytoplankton assemblages representing the offshore and nearshore regions, with phytoplankton representing latter stages of succession dominating the nearshore region (Fig. 13).

Wind relaxation or reversal (Fig. 15b) is typically associated with the shoreward accumulation of dinoflagellate blooms, and the development of an inshore countercurrent results in the general southward progression of these blooms (Fig. 6). Of the earlier models that describe time-variable upwelling, most present an upwelling cycle as a symmetric two-dimensional process. In such cases the warming of inshore waters following the relaxation of upwelling-favorable winds is described as an across-shelf advection of heat. However, subsequent studies have shown that reversed alongshore flow may be responsible for observed warming inshore and in many cases this alongshore flow is clearly related to features in the coastline topography (Send et al. 1987). Gan and Allen (2002a and 2002b) have demonstrated the dominant role of coastal capes in determining alongshore variability of flow within upwelling systems, by the establishment of an alongshore pressure gradient, indicated in the surface elevation field, that forces poleward currents near the coast during relaxation of upwelling-favorable winds. These inshore current reversals and consequent poleward flow are likely to have an important influence on the transport of coastal blooms in upwelling systems (Sordo et al. 2001; Pitcher et al. 2004). The presence of a nearshore countercurrent to the north of Cape Columbine was first detected by drift card returns, and this inshore poleward current was found to be most pronounced during late summer and autumn (Duncan and Nell 1969). Application of the Gan and Allen (2002a,b) model to the Cape Columbine–St. Helena system would suggest that the separation of the equatorward jet from the coast by Cape Columbine results in the development of a negative pressure gradient to the north of the Cape. During relaxation, this pressure gradient may drive poleward currents and strengthen cyclonic circulation to the north of Cape Columbine, thereby contributing to the retentive nature of circulation within the region and to the poleward transport of coastal blooms.

Time-varying wind forcing and spatially variable coastal topography provide local modulation of the upwelling process, influencing the characteristics of the surface boundary layer, both upper mixed layer characteristics and flow patterns, both of which have a pronounced effect

on harmful bloom dynamics. These effects are clearly evident in the greater St. Helena Bay region, an area characterized by elevated phytoplankton biomass and prone to red tide. Spatial patterns in upper mixed layer characteristics correspond to predictable patterns in the distribution of phytoplankton in response to different regimes of turbulence. Complex three-dimensional circulation forced by local topography and winds was decisive in the introduction, concentration, and dissipation of blooms from any single locality. At the event scale, the population dynamics model of red tide, particularly in potentially affected local areas, may therefore be reduced to the advective term, and at this scale, hydrodynamic models may be very useful in developing a predictive capability.

### References

- CLARKE, K. R., AND R. M. WARWICK. 2001. Change in marine communities: An approach to statistical analysis and interpretation, 2nd ed., PRIMER-E.
- COCKCROFT, A. C., D. S. SCHOEMAN, G. C. PITCHER, G. W. BAILEY, AND D. C. VAN ZYL. 2000. A mass stranding, or “walkout” of west coast rock lobster *Jasus lalandii* in Elands Bay, South Africa: Causes, results and implications. In J. C. Von Kaupel Klein and F. R. Schram [eds.], *The biodiversity crises and Crustacea*. Crustac. Issues, **11**: 362–688.
- CULLEN, J. J., AND J. G. MACINTYRE. 1998. Behaviour, physiology and the niche of depth-regulating phytoplankton, p. 559–579. In D. M. Anderson, A. D. Cembella and G. M. Hallegraeff [eds.], *Physiological ecology of harmful algal blooms*. Springer-Verlag, NATO ASI Series, Vol. **G 41**.
- DONAGHAY, P. L., AND T. R. OSBORN. 1997. Toward a theory of biological-physical control of harmful algal bloom dynamics and impacts. *Limnol. Oceanogr.* **42**: 1283–1296.
- DUNCAN, C. P., AND J. H. NELL. 1969. Surface currents off the Cape Coast. Investigational Report Division of Sea Fisheries South Africa **76**: 1–19.
- ESTRADA, M., AND E. BERDALET. 1998. Effects of turbulence on phytoplankton. In D. M. Anderson, A. D. Cembella and G. M. Hallegraeff [eds.], *Physiological ecology of harmful algal blooms*. Springer-Verlag, NATO ASI Series, Vol. **G 41**, p. 601–618.
- GAN, J., AND J. S. ALLEN. 2002a. A modeling study of shelf circulation off northern California in the region of the Coastal Ocean Dynamics Experiment: Response to relaxation of upwelling winds. *J. Geophys. Res.* **107**: 3123 [doi: 10.1029/2000JC000768]
- , AND ———. 2002b. A modeling study of shelf circulation off northern California in the region of the Coastal Ocean Dynamics Experiment 2. Simulations and comparisons with observations. *J. Geophys. Res.* **107**: 3184 [doi: 10.1029/2001JC001190]
- GOWER, J. F. R., K. L. DENMAN, AND R. J. HOLYER. 1980. Phytoplankton patchiness indicates the fluctuation spectrum of mesoscale oceanic structure. *Nature* **288**: 157–159.
- GRAHAM, W. M., AND J. L. LARGIER. 1997. Upwelling shadows as nearshore retention sites: The example of the northern Monterey Bay. *Continental Shelf Research* **17**: 509–532.
- HASLE, G. R. 1978. The inverted-microscope method, p. 88–96. In A. Sournia [ed.], *Phytoplankton manual*. UNESCO.
- HOLDEN, C. J. 1985. Currents in St Helena Bay inferred from radio-tracked drifters, p. 97–109. In L. V. Shannon [ed.], *South African Ocean Colour and Upwelling Experiment*. Sea Fisheries Research Institute.

- HORSTMAN, D. 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.
- HUISMAN, J., AND F. J. WEISSING. 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* **402**: 407–410.
- JOYCE, L. B., G. C. PITCHER, A. DU RANDT, AND P. M. S. MONTEIRO. 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.
- JURY, M. R. 1985. Mesoscale variations in summer winds over the Cape Columbine–St Helena Bay regions, South Africa. *S. Afr. J. Mar. Sci.* **3**: 77–88.
- KIERSTEAD, H., AND L. B. SLOBODKIN. 1953. The size of water masses containing plankton blooms. *J. Mar. Res.* **12**: 141–147.
- LAMBERTH, R., AND G. NELSON. 1987. Field and analytical drogue studies applicable to the St Helena Bay area off South Africa's west coast. *In* A. L. L. Payne, J. A. Gulland and K. H. Brink [eds.], *The Benguela and comparable ecosystems*. *S. Afr. J. Mar. Sci.* **5**: 163–169.
- LARSEN, J. 1996. Unarmoured dinoflagellates from Australian waters II. Genus *Gyrodinium* (Gymnodiniales, Dinophyceae). *Phycologia* **35**: 342–349.
- MARGALEF, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta* **1**: 193–509.
- MOSTERT, S. A. 1983. Procedures used in South Africa for the automatic photometric determination of micronutrients in seawater. *S. Afr. J. Mar. Sci.* **1**: 189–198.
- PARSONS, T. R., Y. MAITA, AND C. M. LALLI. 1984. *A manual of chemical and biological methods for seawater analysis*. Pergamon Press.
- PENVEN, P., C. ROY, A. COLIN DE VERDIERE, AND J. LARGIER. 2000. Simulation of a coastal jet retention process using a barotropic model. *Oceanol. Acta* **23**: 615–634.
- PITCHER, G., J. AGENBAG, D. CALDER, D. HORSTMAN, M. JURY, AND J. TAUNTON-CLARK. 1995. Red tides in relation to the meteorology of the southern Benguela upwelling system, p. 657–662. *In* P. Lassus, G. Arzul, E. Erard, P. Gentien and C. Marcaillou [eds.], *Harmful marine algal blooms*. Intercept Ltd.
- , AND A. J. BOYD. 1996. Across-shelf and alongshore dinoflagellate distributions and the mechanisms of red tide formation within the southern Benguela upwelling system, p. 243–246. *In* T. Yasumoto, Y. Oshima and Y. Fukuyo [eds.], *Harmful and toxic algal blooms*. Intergovernmental Oceanographic Commission of UNESCO.
- , D. A. HORSTMAN, AND B. A. MITCHELL-INNES. 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.
- , AND D. CALDER. 2000. Harmful algal blooms of the southern Benguela current: a review and appraisal of monitoring from 1989–1997. *S. Afr. J. Mar. Sci.* **22**: 255–271.
- , P. MONTEIRO, AND A. KEMP. 2004. The potential use of a hydrodynamic model in the prediction of harmful algal blooms in the southern Benguela, p. 11–13. *In* K. A. Steidinger, J. H. Landsberg, C. R. Tomas and G. A. Vargo [eds.], *Harmful algae 2002*. Florida Fish and Wildlife Conservation Commission, Florida Institute of Oceanography, and Intergovernmental Oceanographic Commission of UNESCO.
- , A. J. RICHARDSON, AND J. L. KORRUBEL. 1996. The use of sea temperature in characterizing the mesoscale heterogeneity of phytoplankton in an embayment of the southern Benguela upwelling system. *J. Plankton Res.* **18**: 643–657.
- , AND S. J. WEEKS. 2006. The variability and potential for prediction of harmful algal blooms in the southern Benguela ecosystem, p. 125–146. *In* V. Shannon, G. Hempel, P. Malanotte-Rizzoli, C. Moloney and J. Woods [eds.], *The Benguela: Predicting a large marine ecosystem*. Elsevier.
- PROBYN, T. A., G. C. PITCHER, P. M. S. MONTEIRO, A. J. BOYD, AND G. NELSON. 2000. Physical processes contributing to harmful algal blooms in Saldanha Bay, South Africa. *S. Afr. J. Mar. Sci.* **22**: 285–297.
- ROUGHAN, M., A. J. MACE, J. L. LARGIER, S. G. MORGAN, J. L. FISHER, AND M. L. CARTER. 2005. Sub-surface recirculation and larval retention in the lee of a small headland: A variation on the upwelling shadow theme. *J. Geophys. Res.* **110**: C10027 [doi: 10.1029/2005JC002898].
- SEND, U., R. C. BEARDSLEY, AND C. D. WINANT. 1987. Relaxation from upwelling in the Coastal Ocean Dynamics Experiment. *J. Geophys. Res.* **92**: 1683–1698.
- SKELLAM, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**: 196–218.
- SMAYDA, T. J., AND C. S. REYNOLDS. 2001. Community assembly in marine phytoplankton: Application of recent models to harmful dinoflagellate blooms. *J. Plankton Res.* **23**: 447–461.
- SORDO, I., E. D. BARTON, J. M. COTOS, AND Y. PAZOS. 2001. An inshore poleward current in the NW of the Iberian Peninsula detected from satellite images, and its relation with *G. catenatum* and *D. acuminata* blooms in the Galician Rias. *Estuar. Coast. Shelf Sci.* **53**: 787–799.
- TAUNTON-CLARK, J. 1985. The formation, growth and decay of upwelling tongues in response to the mesoscale wind field during summer, p. 47–61. *In* L. V. Shannon [ed.], *South African Ocean Colour and Upwelling Experiment*. Sea Fisheries Research Institute.
- WEEKS, S. J., G. C. PITCHER, AND S. BERNARD. 2004. Satellite monitoring of the evolution of a coccolithophorid bloom in the southern Benguela ecosystem. *Oceanography* **17**: 83–89.

Received: 7 October 2005

Accepted: 14 June 2006

Amended: 17 July 2006