AN ABSTRACT OF THE THESIS OF

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Title: RECENT MARINE DIATOM TAPHOCOENOSES OFF PERU AND OFF

SOUTHWEST AFRICA: REFLECTION OF COASTAL UPWELLING

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Abstract approved: _____

(Dr. Hans Schrader)

The phytoplankton of coastal upwelling areas is dominated by
diatoms. Sediments underlying two of the world's major coastal up-
welling areas, off Peru and off South West Africa, contain abundant
remains of diatoms. It is the premise of this thesis that the re-
mains of diatoms in underlying sediments constitute a history of
these highly productive waters. The analysis of the abundance of
diatom valves and of the diatom species composition, in sediment
samples from these coastal upwelling areas and from adjacent off-
shore areas, allows a characterization of the influence of coastal
upwelling on sediment composition.

The diatom fraction of sediment surface samples from off Peru
and off South West Africa was examined in order to identify in each
area the sediment record of coastal upwelling. Each chapter of this
thesis has been written as a separate paper. The first chapter

reports the findings from the study of 116 sediment surface samples from off Peru. This analysis shows a boundary in the sediments between upwelling-influenced sediments and sediments outside the highly productive coastal regime. Centers of high abundance of diatoms (>20 x 10^6 valves per gram of dry sediment) occur in water depths greater than 2000 meters. The distribution of meroplanktic species preserves in the sediments the sinuous pattern of surface water parameters off Peru. Chaetoceros species are an important component of the phytoplankton off Peru and resting spores of Chaetoceros contribute abundantly to the sediments, with high relative abundance in samples at the seaward edge of upwelling influence. The preservation in some samples of Delphineis karstenii, a specific indicator of coastal upwelling, and of Skeletonema costatum, a dissolution sensitive species, is additional evidence of the imprint of coastal upwelling on sediment composition. The basic data from the Peru study and the tabulated results of the statistical analyses are available from the School of Oceanography, Oregon State University, Corvallis, OR 97331, by requesting Data Report #73, Reference #79-8.

The second chapter reports the findings from the study of 124 sediment samples from the South East Atlantic, including 85 surface samples located within the coastal upwelling area. In this study the shallow water depths of the inner shelf off South West Africa allow the preservation of many diatom species prominent in the phytoplankton of the overlying surface waters. Diatom rich samples (75-800 x 10^6 valves per gram dry sediment) occur between 19° - 24°S

in water depths less than about 130 meters. The species composition of these samples contrasts markedly with that of the offshore sediment samples and is dominated by Chaetoceros resting spores and Delphineis karstenii.

Delphineis karstenii is characteristically found in newly upwelled waters and, correspondingly, it occurs in highest abundance in the sediments in nearshore patches. Chaetoceros resting spores generally occur in highest relative abundance outside these nearshore patches. The overlapping but distinct distribution patterns for these two dominant species may record a sequence of diatom assemblages which is related to the dynamics of coastal upwelling off South West Africa.

The final chapter is a comparison of the findings for the two areas and a characterization of coastal upwelling influence on sediment composition. Those features are discussed which are common to both upwelling areas and which differentiate upwelling-influenced diatom taphocoenoses: 1) abundant remains of well-preserved diatoms, 2) high percentages of meroplanktic species and species groups, and 3) coherent distribution patterns for diatom assemblages which represent subenvironments within the coastal upwelling area.

RECENT MARINE DIATOM TAPHOCOENOSES OFF PERU AND OFF SOUTHWEST AFRICA:

REFLECTION OF COASTAL UPWELLING

by

Gretchen Schuette

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CHAPTER I

DIATOM TAPHOCOENOSES IN THE COASTAL UPWELLING

AREA OFF WESTERN SOUTH AMERICA

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Diatom Taphocoenoses in the Coastal Upwelling Area off Western South America

by

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With 13 figures

Abstract: Diatom floral analysis of 116 sediment surface samples obtained off Peru reveals a boundary in the sediments between coastal upwelling influenced sediments and sediments outside the highly productive realm. Sinuous patterns of relative abundance for meroplanktic species (*Actinocyclus octonarius, Actinoptychus senarius,* and *Cyclotella striata/stylorum*) may preserve the meander-like patterns of surface water parameters off Peru. The occurrence of loci of high abundance of diatom valves per gram of dry sediment, and the limited occurrence of *Skeletonema costatum* and of a species of the genus *Delphineis* are additional pieces of evidence that upwelled tongues of cold water have a correspondingly patchy sediment signal.

Introduction

The diatom fraction of 116 sediment surface samples collected off western South America was studied in order to identify on the Peru continental margin the sediment record of coastal upwelling. The purpose was to differentiate sediments containing this record from those not influenced by the high rates of primary production associated with coastal upwelling (Ryther 1969).

Diatoms dominate the phytoplankton communities in coastal upwelling regions (Blasco 1971, Margalef 1973, Hart & Currie 1960, Berger 1976), and the preservation and abundance of their valves in hemipelagic sediments along the western coasts of continents has been documented (Calvert 1966, Calvert and Price 1971, Zhuse 1972). This study analyzes the distinct patterns of diatom distribution found in recent sediments preserving evidence of recurrent coastal upwelling off Peru.

The coastal upwelling process is described by Smith (1978). He estimates that the response to wind events off Peru occurs within 50 km from shore, with a depth of origin around 70 meters subsurface for the water found at the surface after favorable winds. A poleward undercurrent dominates the shelf with mean currents in a direction opposite to the mean wind, except in a shallow surface layer. The curvature of the midshelf bathymetry and of the shelf break are thought to influence the alongshore flow, its variability, and the magnitude of upwelling (SCOR Wg 36 1976). Maeda & Kishimoto (1970) have found upwelling centers to be present consistently at 5°, 11° and 15°S over a 17 year period, but further observational studies are needed to describe and locate the physical process of upwelling and to delineate its effect on plant and animal populations. This sediment study provides a testimony to the persistence of upwelling at certain locations.

Materials and Methods

Samples were taken from the uppermost sediments retrieved at the coring stations listed in Table I. The numbers in the first column will be used in the rest of this paper when referring to stations (see also Fig. 1). The ship and year of the cruise are registered in the OSU core numbers: e.g., W77- indicates the 1977 cruise of RV Wecoma; Y71-, the 1971 cruise of RV Yaquina; FD75-, the 1975 cruise of RV Francis Drake.

Those cores collected by the Reineck box (RB), the Kasten (K), the free fall (FF), and the gravity (G or MG) corers appeared to success-fully retrieve the surface layer of sediments. The uppermost sediments may have been lost in the recovery of some of the piston (P) cores.

The uppermost few centimeters (in some cases, only the first one cm; at most, the first 20 cm) of the Wecoma cores were placed in plastic bags when the cores were first opened aboard the ship. Samples were later taken from these bags of composite surface sediments. Thus, the nearshore samples, which may have been deposited at rates of about 66-140 cm/1000 years (see Discussion), represent from about 7 to 300 years of deposition.
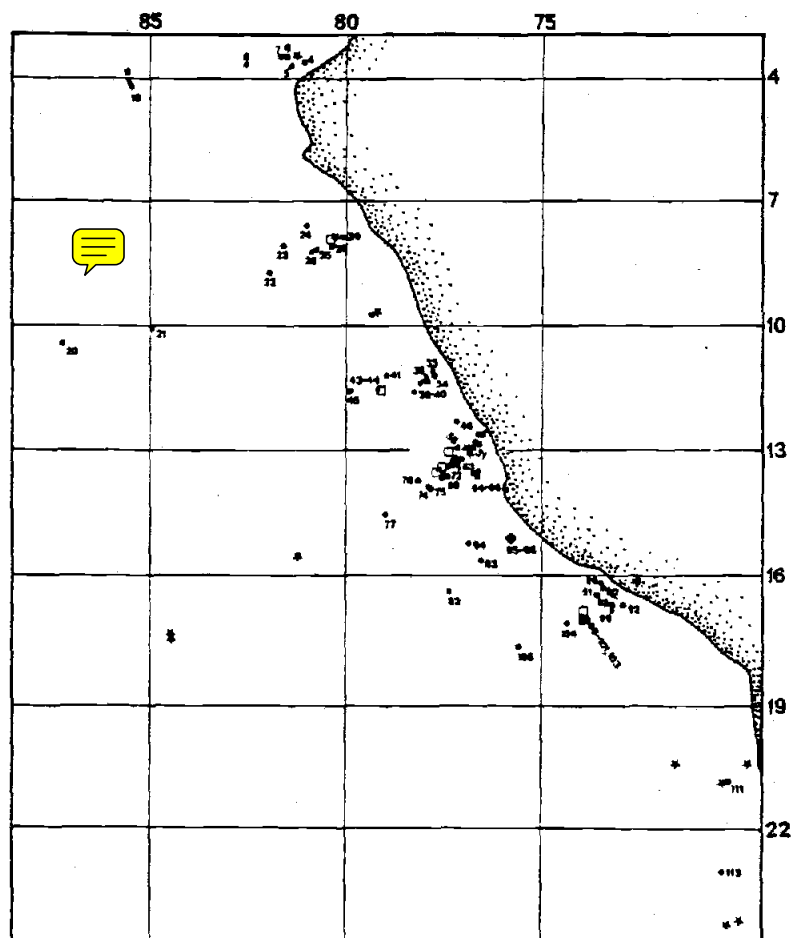
Fig. 1. Station locations, some stations are not numbered. □, stations not included in data analysis because of evidence of reworking of older floras; *, barren samples.

Samples were taken from bags as described above, or from the top sediments of cores stored in the OSU Core Repository. The procedure was to fill a bulk density ring of ca. 1.5 cm diameter (1 cm high) by pushing it into the soft sediments. Piston cores and gravity cores are split in half lengthwise for storage, and the tube samplers were pushed into the middle of the top of a core-half at a right angle to the long axis of the core-half, thus sampling the top 1.5 cm of the core. Downcore samples from W7706-64 were taken in the same way at selected depths in the core.

All samples were oven dried for 24 hours at 60°C in the sampling tubes and then extracted into the beakers used for the acid cleaning procedure. The dry weight of each sample was in a range from 0.5-2.0 grams.

Slide preparation followed the procedure outlined in Schrader (1974) and Schrader & Gersonde (1978) with the following exceptions: 1) Slides were made for all samples from a 50 ml dilution of the acid resistant residue remaining after cleaning and fractional sedimentation to remove the clay fraction. Automatic pipets were used for this subsampling. 25 μl were placed on slides for surface sediment samples; 50 μl for downcore samples. 2) Coverglasses were allowed to air dry.

The microscopical investigations were done on a Leitz-Orthoplan-Orthomat microscope using high power and high resolution apochromatic oil immersion objectives. Counts were made using the highest available magnification (Objective Apo oil 100×, n.A. 1.32, Ocular: Periplan GW 10× M) with counting procedures standardized in our lab after Schrader & Gersonde (1978). Each slide was counted in traverses randomly laid over the middle of the coverglass. About 300 valves were counted per slide, although, in some stations from the oceanic plate or outside the productive coastal region, limited preservation of diatoms in the sediments prohibited reaching this figure.

Observations

Numbers of diatom valves per gram of dry original sediment were calculated as described in Schrader & Gersonde (1978) and these values are listed in Table I. Barren and almost barren surface samples are indicated in this table by a zero value.

Approximately 110 different marine planktic and benthic species were identified. Some species represented reworked or exposed Pleistocene/Pliocene/Miocene floras. Some species were displaced freshwater diatoms. These occurred in greatest abundance (still less than 1% of the total assemblage) at sites 91, 94, 95, 99 and 104. Core tops with displaced shallow water marine benthics and with reworked older material are indicated in Table I.

Sixty-three species or species group categories were adopted for systematic counting and the relative abundance values in these categories were determined at 91 stations. From these 91 stations, 9 stations outside the coastal regime were eliminated from further analysis (stations 11-19), and 7 stations (27, 42, 58, 61, 70, 71, and 102) were eliminated because of evidence of reworking of older floras. The data from the following stations were combined because of proximity of the stations: 6+7, 9+10, 33+34, 35+36, 37+38, 39+40, 43+44, 48+49, 50+51, 54+56+57, 64+65+66, 69+72, 85+86+87+ 88, 89+90, 93+94, 95-101+103.

The original 63 species categories were altered in the following manner. Some species were left out of further data reduction because they are very rare in the samples (*Coscinodiscus A., C. asteromphalus, Lithodesmium undulatum, Thalassiosira gravida, Pseudotriceratium punctatum*), or because they are displaced benthics (*Triceratium alternans* and the category "marine benthics"), or because they represent reworked floras (i.e., *Cussia lancettula*). Some species were combined because similarity of morphology prevented consistent distinctions between species during routine counting procedures, i.e., *Actinocyclus curvatulus/Coscinodiscus rothii; Thallasiothrix mediterranea/T. longissima; Thalassiosira eccentrica/T. symmetrica/T. punctifera/T. spinosa;* and all *Chaetoceros* resting spores. To decrease the number of variables, species of similar distribution in our data set were combined as follows:

— *Cyclotella striata* + *Cyclotella stylorum*

— *Asteromphalus* group + *A. #1* + *A. #2*

— *Coscinodiscus africanus* + *C. tabularis*

— *Coscinodiscus nodulifer* + *C. radiatus*

— *Coscinodiscus obscurus* + *C. perforatus*

— *Stephanopyxis palmeriana* + *S. turris*

— *Thalassiosira* A + *Thalassiosira* B

— *Thalassiothrix* spp. + *T. mediterranea/T. longissima* + *T. frauenfeldii*

Further analysis then was based on the resulting 43 taxonomic categories. The matrix of 49 stations and 42 "species" (Table II) was the basis for a Q-mode (Fortran IV program CABFAC, Klovan &

Imbrie 1971, Imbrie & Kipp 1971) analysis of data. R-mode analysis (SPSS Subprogram FACTOR, PA2, Varimax Orthogonal Rotation) of the same data set (but without stations 111 and 113) was also accomplished.

Discussion

Interpretation of our data allows conclusions regarding the location of recurrent coastal upwelling off Peru and regarding the identification of species and species groups characteristic of sediments influenced by coastal upwelling. Preliminary data analysis supported the hypothesis that upwelling influenced sediments may be recognized and separated from adjacent regimes by the diatom composition of sediments. A factor analysis of species counts in 35 categories from 70 stations was undertaken to verify a sediment signal of the coastal upwelling process. This analysis produced 3 factors accounting for 93% of the variance in the data set and the factor loadings did generate interpretable distribution patterns for these factors.

Factor 1, accounting for 63% of the variance (Fig. 2), has high loadings in all continental margin stations. It is dominated by the resting spores of *Chaetoceros*. Factor 2, accounting for 20% of the variance (Fig. 3), has high loadings in the oceanic plate stations. It is dominated by *Coscinodiscus nodulifer*. It is not unexpected that 83% of the variance in our data set rests on the large differences between oceanic and coastal phytoplankton assemblages since Q mode analysis compares abundant species. Factor 3, accounting for 10% of the variance (Fig. 4), has highest loadings at stations 22, 27, 30, 40, 54, and 61, and is characterized by *Cyclotella striata/stylorum*. This factor did resolve distinct regions of importance for an assemblage which may be characteristic of coastal upwelling.

Fig. 2. Factor 1. Contours in this figure and Figs 3, 4, 7-12 were drawn, in those places where there was poor sample control, so as to conform to the concept of a sinuous seaward boundary for upwelling influenced sediments. This concept is strongly supported in areas of good control. Fig. 3. Factor 2. Fig. 4. Factor 3.

2

Factor 1

- ■ >95
- ▨ 75-95
- ▦ 30-75
- □ <30

only margin stations contoured

3

Factor 2

- ▨ >90
- ▦ 10-90
- ▦ <10

4

Factor 3

- ■ >15
- ▨ >10-<15
- ▦ >3-<10
- ▦ <3
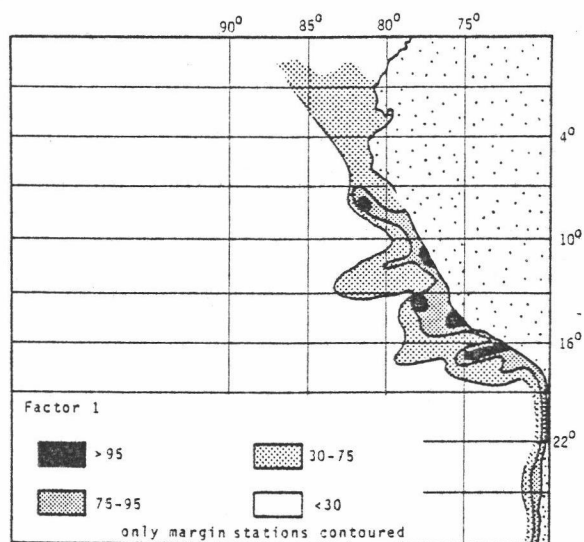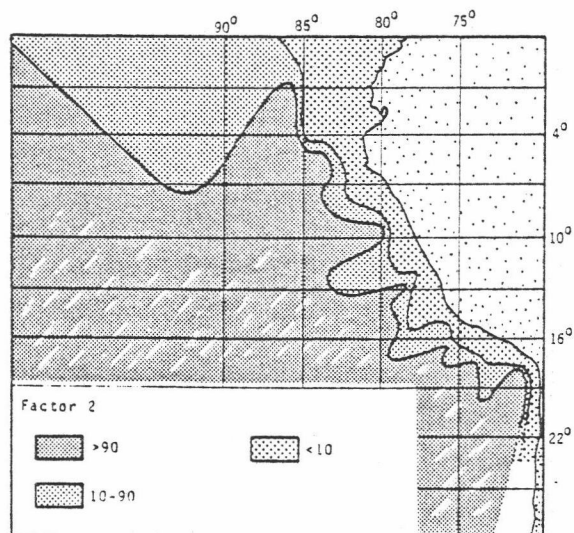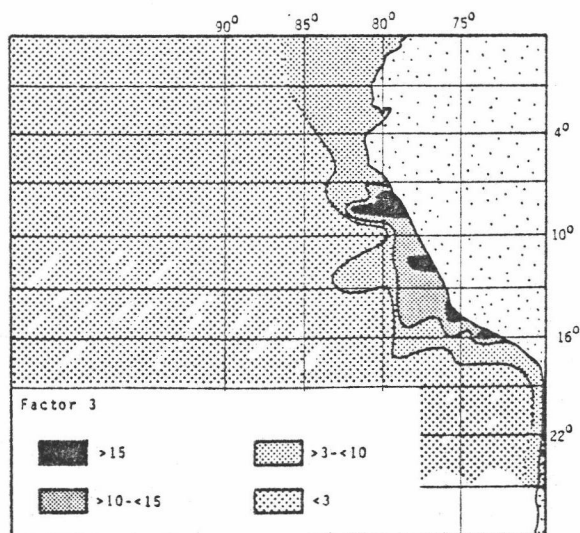
Meroplanktic Species

Cyclotella striata/stylorum, along with two other relatively abundant species, *Actinocyclus octonarius* and *Actinoptychus senarius,* are meroplanktic species, i.e., organisms which either produce a resting spore or possess a sedentary stage or dormant phase in their life cycle (Smayda 1958). Meroplanktic species are cosmopolitan in middle and low latitudes and occur in turbulent near-shore waters. Apparently none of the meroplanktic species abundant in sediments off Peru dominates phytoplankton assemblages in the surface waters (Strickland et al. 1969). But heavy silicification of the valves of these diatoms enhances their preservation, and the high supply of all diatoms to deposits underlying areas of high fertility and productivity accounts for the presence and abundance of meroplanktic species in these sediments.

When the abundance of the meroplanktic group of species (relative to all diatom species) is plotted in a depth-shore distance profile, the restriction of this component to a particular depth and shore-distance range becomes apparent (Fig. 5). Highest relative abundance occurs between 20 and 60 nautical miles from shore and in water depth of less than 2500 meters. *Chaetoceros* resting spores, which we have seen are also important in sediments underlying the near-shore productive region, have their peak in abundance further offshore and thus at greater water depths (Fig. 6). Formation of *Chaetoceros* resting spores may occur during a *Chaetoceros*-dominated stage of succession when nutrients are nearly exhausted in the euphotic zone (Guillard & Kilham 1977). Thus, the offshore distribution pattern for these spores may be interpreted to reflect the seaward edge of nutrient-replete surface waters.

Zhuse (1972) recorded *Chaetoceros* spore dominance on the shelf off Callao. She also found that diatom assemblages consisted of large "nertitic" species at some of her coastal stations. She characterized

Fig. 5. Distribution of relative abundance of the meroplanktic species group (*Actinocyclus octonarius* + *Actinoptychus senarius* + *A. splendens* + *Cyclotella striata/stylorum*). Sample stations were plotted according to their water depth and distance perpendicular to the coastline. Fig. 6. Distribution of relative abundance of the *Chaetoceros* resting spores. Sample stations plotted as in Fig. 5. Fig. 7. Occurrence of *Delphineis.*

5

180nm 120 60 0

>30

20-30

<20

Margin

Plate

Trench

1000

2000

3000

4000

5000

m

6

180nm 120 60 0

>50%

20-50%

<20%

Margin

Plate

Trench

1000

2000

3000

4000

5000

m

7

Delphineis spp. occurrence

>2%

present
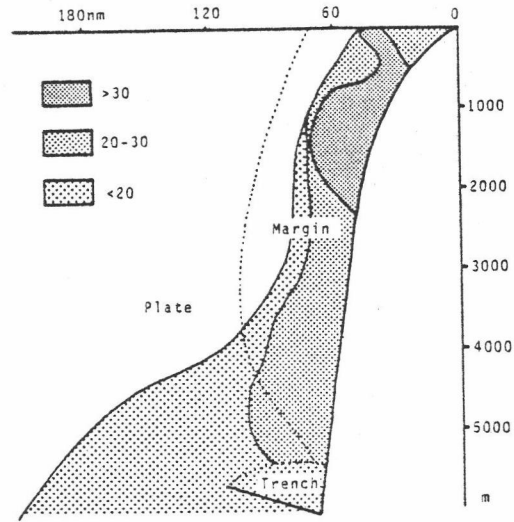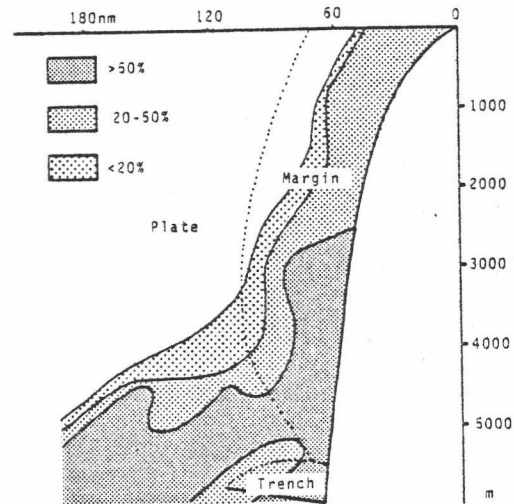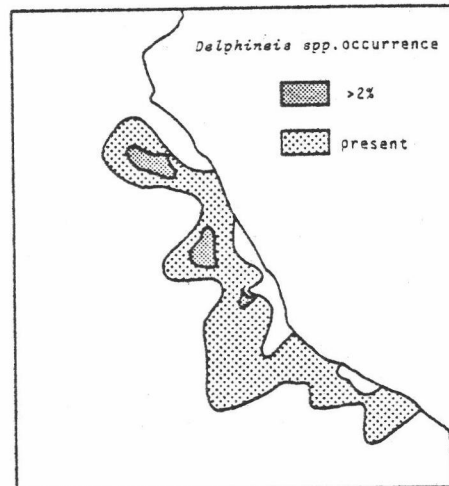
the distribution of her moderately-warm water — subtropical diatom complex, which consists chiefly of "neritic" species, as corresponding with the area of the cold Peru-Chile current. The extension of this complex away from the coast in the latitude of Callao (12° S) concurs in general with the high relative abundance of our meroplanktic complex at stations 39, 40, 54, 55, 57, 59-61, 63-65 and 69-71.

Diatom Abundance

The circulation within a coastal upwelling regime accounts for its anomalous character compared to adjacent regimes. The familiar profile or circulation (Hart & Currie 1960) includes wind induced offshore transport of surface water and compensating upwelling of nutrient rich deeper waters. This circumstance provides for high fertility and high primary productivity in a near-shore zone and concomitant preservation of siliceous microfossils in sediments under-lying this zone. There is a boundary, then, between the productive coastal upwelling region where nutrients upwell to the euphotic layer and the less productive oceanic realm where light energy is separated from deep nutrient reserves. This boundary is documented by our surface sediment data.

Our calculations of abundance of diatoms per gram of dry sediment reveal a sinuous boundary of the coastal upwelling region of high abundance with the oceanic realm, and discrete loci of highest abundance within a definite latitudinal range. Five clusters of high values occur at these stations: (1) 23, 24, 26; (2) 33, 34; (3) 42, 43, 44; (4) 48, 58, 61, 62, 63, 66, 68, 69, 70, 71, 72, 73, 74; (5) 91, 99, 102. Four areas are offset from the coastline suggesting offshore centers of upwelling influence, in addition, perhaps, to the near-shore region of high abundance evident at about 12° S. The inner shelf region is not well represented in the sample net; this study is predominantly of midshelf of oceanic plate sediments. Other inner shelf deposits were not sampled.

Available accumulation rates are in permissive agreement with the coarse distinction between diatom-rich sediments within the upwelling region and oceanic diatom-poor sediments. Pb 210 dating of the uppermost part of the cores from stations 34 and 65 gives sedimenta-

tion rates of 140 cm/1000 years and 66 cm/1000 years respectively. Accumulation rates calculated for these cores [dry bulk density (salt corrected) $\times$ sedimentation rate $\times$ number of diatoms/g] are 7.4 and 0.3 million diatoms/cm^2/year. On the other hand, accumulation rates for oceanic plate sediments range from zero to about 0.05 million diatoms/cm^2/year.

Zhuse (1972) also established the existence of a region of highly siliceous facies in a restricted area near Peru, and her figure of 20-50 million valves/gram of sediment on the shelf and trench near Callao is in general agreement with our data (her data did not include the area south of Pisco between 13 1/2° and 19° S). She also remarked that the quantitative distribution of diatoms in the surface layer of sediments is "highly uneven". Variations are indeed great in sediments at the coastal stations. Our data, as was stated above, could not be encompassed by simple contours parallel to the coast.

Occurrence of *Delphineis*

The distribution of one species of the genus *Delphineis* matches in its occurrence offshore areas of highest diatom abundance per gram (Fig. 7). Areas of greatest relative abundance (greater than 2%) are centered at station 23 and at station 60 matching the two major centers of diatom valve abundance, near 8° S, and between 13 and 14° S. *Delphineis* is present in greater than 1% relative abundance at stations 95 and 99, in the center of high abundance of diatoms per gram around 17° S. It is relatively abundant (1.4-3.3%) near station 42 where diatom abundance was also greater than 30 million valves/gram.

Delphineis is of particular interest as it may be a specific indicator of coastal upwelling. We have found that it occurs only in active coastal upwelling regions of the present and in deposits representing locations affected by very productive coastal surface waters of the past. The taxonomy of this genus is currently under revision. Simonsen (1974) described a form from the Indian Ocean as *Rhaphoneis surirelloides,* some specimens of which we feel belong into the genus *Delphineis* as defined by Andrews (1977). A similar form described by Fryxell & Miller (1978) from the west coast of South Africa as *Fragilaria karstenii* probably also belongs to this genus. In addition, *Rhaphoneis*

ischaboensis, found by Zhuse (1972) in sediments off Peru, and described by Mertz (1966) from the Pisco Formation, has strong affinities for *Delphineis.*

Relative Abundance Data

The relative abundance data for all 43 species categories (Table II) were examined in order to identify species, or groups of species, characteristic of coastal upwelling. The patterns produced by these basic data may also be used to characterize sediments underlying a coastal upwelling regime and to describe the geographic limits of influence of the coastal upwelling phenomenon on surface sediments. The sinuous pattern of sedimentation of important diatom species and species groups, and the localized high abundances of species and groups distinguishes this region.

Important species with highest abundance outside the coastal region between 7° and 18° S include: *Coscinodiscus nodulifer, Pseudoeunotia doliolus,* and *Thalassionema nitzschioides* v. *parva.* The category *Coscinodiscus nodulifer* + *C. radiatus* is present in greater than 20% at all stations west of 84°W with a high value of 61.1% at station 21. But it also has high abundance (greater than 15%) at these stations: 8, 22, 25, 35+36, 45, 55, 74, 76, 77; and occurs in all samples examined. As Zhuse suggested (1972), the distribution of a complex of diatoms associated with the "tropical" region may be illustrated by the distribution of *Coscinodiscus nodulifer.* The eastern boundary of this complex must be characterized, however, as approching and receding from the coast as it outlines the areas of upwelling influence mentioned above (Fig. 8).

Pseudoeunotia doliolus occurs in greater than 5% at almost all stations on the oceanic plate, but it also occurs in greater than 5% at stations 77, 82, and 84. *Thalassionema nitzschioides* v. *parva* occurs on the margin in greater than 5% at stations 4, 6+7, 8, 45, 64+65+

Figs 8-12. Relative abundances of *Coscinodiscus nofulifer/C. radiatus, Cyclotella striata/stylorum, Actinocyclus octonarius, Actinoptychus senarius,* and the *Thalassiosira eccentrica* group. — Fig. 13. Shannon-Wiener diversity values showing a displacement offshore of highest values.
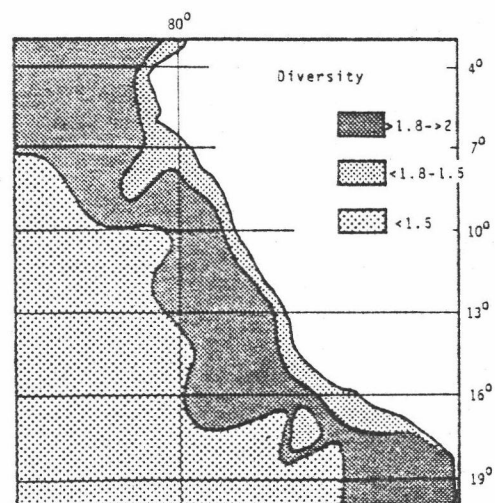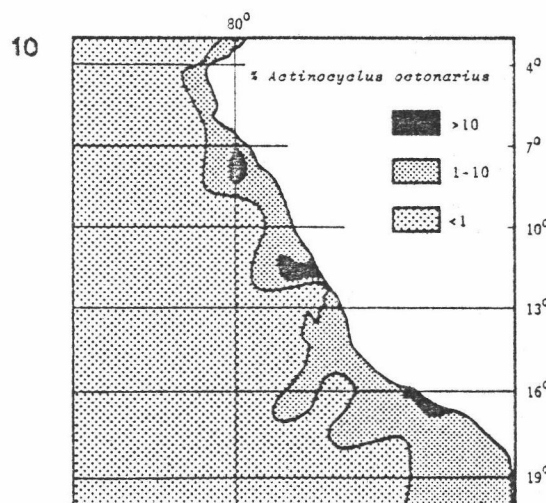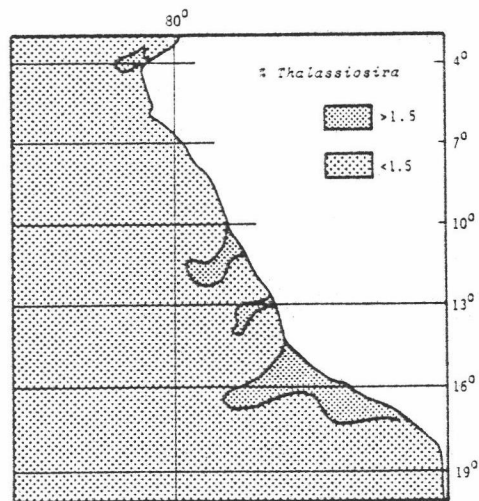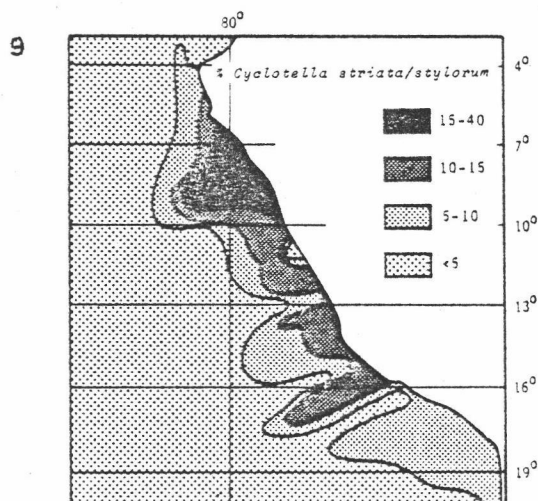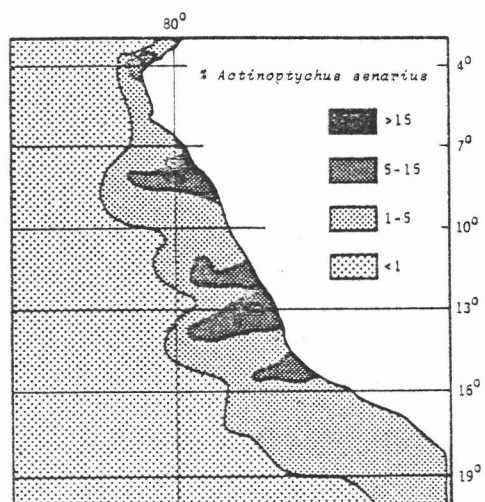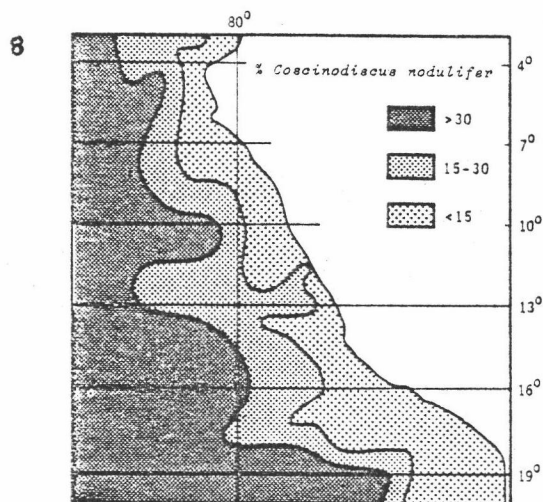
66, and 83. Other species identified as characteristic of tropical oceanic waters which are present in lesser percentages include *Thalassiosira oestrupii, Roperia tesselata,* and *Rhizosolenia bergonii.*

Important species east of 84°W include *Chaetoceros* resting spores, *Cyclotella striata/stylorum, Actinocyclus octonarius, Actinoptychus senarius, Thalassionema nitzschioides,* and the *Thalassiosira eccentrica* group.

Chaetoceros spores reach 75-85% of the entire population at our southernmost stations, 111 and 113, which is in agreement with Zhuse's (1972) data from off Antofagasta (23-24°S). However, we also found high percentages (greater than 50%) at stations 4, 23, 24, 33+34, 42, 48+49, and 62, as well as in 8 stations in the region not covered by the Russian survey: 74, 75, 85-88, 91, 93+94, 95-101+103, 104, and 105. In fact there are only 9 margin stations with values less than 30% *Chaetoceros* resting spores: 22, 25, 28, 30, 37+38, 39+40, 60, 82, and 92.

Cyclotella striata/stylorum has a maximum abundance of 35% at station 22, greater than 20% at 28 and 15-20% at 25, 26, 30 and 55. It is present at all margin stations and is greater than 5% at 32 stations (Fig. 9).

Actinocyclus octonarius occurs in greater than 10% relative abundance at 6 stations with a maximum of 30.8% at stations 89+90. High abundances occur in the following additonal stations: 28, 30, 37+38, 39+40, and 92 (Fig. 10).

Actinoptychus senarius occurs (with a maximum of 25.5% at station 60) in greater than 5% at 23 stations but in greater than 10% at only 9 stations: 5, 25, 28, 35+36, 46, 50+51, 55, 59, and 60 (Fig. 11).

The *Thalassiosira eccentrica* group occurs in 1-5% at many nearshore stations between 11 and 18°S (Fig. 12). Station 60 shows an especially high percentage of 26.5%.

Thalassionema nitzschioides occurs in margin samples at greater than 10% at 24 stations. This category includes all forms of this species as described by various authors (Heiden & Kolbe 1927, Hustedt 1959, Van Heurck 1880, Frenguelli 1949, Hasle & de Mendiola 1967, Hasle 1960, Kolbe 1954, 1955, 1957, and Mertz 1966) except the variety *parva.*

Factor Analysis of Samples in the Coastal Region

Q-mode factor analysis was applied to reveal the major patterns of variation within the coastal upwelling region itself. 98% of the total variance in the diatom taphocoenoses was accounted for by five factors. The species which were major contributors to these 5 factors are the *Chaetoceros* resting spore group already mentioned, *Coscinodiscus nodulifer/C. radiatus* characteristic of oceanic waters, and four other species: *Actinocyclus octonarius, Cyclotella striata/stylorum, Actinoptychus senarius,* and the *Thalassiosira eccentrica* species group (see Table III for the calculated factor scores showing the contributions of these species and groups to the five factors). The Varimax Factor matrix in Table IV indicates the importance of each factor at each site and the distribution of these factor loadings supports the major conclusions with regard to the character of the upwelling influenced region.

The sediments influenced by upwelling do indeed have a diatom flora which is distinct from that of sediments associated with adjacent oceanographic regimes. 69% of the variance in the data is located in two factors which define this distinction. The boundaries of the near-shore productivity region coincide with the area of highest loadings for Factor 1 in which the *Chaetoceros* resting spore group is dominant. The highest loadings for Factor 2 reflect the incursions of a more oceanic assemblage.

The characterization of the upwelling regime as producing tongue-like patterns of sedimentation for almost all diatom species and species groups found in sediments is also supported in this analysis. The loadings of those factors dominated by meroplanktic species illustrate the discontinuous nature of the upwelling signal in the sediments. That is, our findings are in permissive agreement with a concept in which high primary production as a result of coastal upwelling occurs in relatively stable plumes or areas of upwelling (SCOR Wg 36 1973, 1974, 1976). Our work can be considered along with other observations and efforts in modelling upwelling ecosystems which have modified the more conventional view of upwelling as a continuous band of nutrient- and phytoplankton-rich water parallel to the coast.

The Q-mode factor analysis satisfied our interest in the relationships among the samples. Interest in species associations or assem-

blages required R-mode analysis in which even the rarely encountered species would receive equal consideration along with the abundant forms that dominated the cross-products matrix analysis of CABFAC. 28 R-mode factors were necessary to account for 90% of the variance. This is not unexpected considering the patchy distribution of many species (see Fig. 13 for a map of the Shannon/Wiener diversity values for our samples). 66.5% of the variance, however, could be explained by 10 factors (Tables V and VI). Many of these factors pointed to a variety of distribution patterns within the two major realms recognized in the first two factors of the Q-mode analysis: Five factors (explaining together 60.0% of the variance explained by the 10 factors) are interpreted as describing relationships between oceanic diatom complexes and elements of the predominantly meroplanktic upwelling assemblages.

Some of these factors deserve special mention. The assemblage most characteristic of oceanic waters, and accounting for 25% of the variance explained by the 10 factors, included: *Coscinodiscus nodulifer/C. radiatus, Nitzschia marina, Pseudoeunotia doliolus, Rhizosolenia bergonii,* and *Thalassionema nitzschioides* v. *parva.* Important to negative loadings in this factor were *Chaetoceros* resting spores. Another factor explaining 14.4%, collected *Actinoptychus senarius, Stephanopyxis palmeriana/S. turris* and *Thallasiosira* species, including the *Thalassiosira eccentrica* group and *T. oestrupii. Actinoptychus curvatulus/Coscinodiscus rothii,* members of the genus *Asteromphalus, Coscinodiscus africanus/C. tabularis* form an assemblage which has a pattern of distribution which, loosely, is inverse to that of *Actinocyclus octonarius. Cyclotella striata/stylorum* and *Coscinodiscus obscurus/C. perforatus* are important in a distribution pattern occurring mainly north of 13° S.

The distribution of the *Delphineis* species was also highlighted in one factor (Factor 10, accounting for 5% of the variance explained by the 10 factors) in which this species dominated the factor loadings. It is significant that this relatively rare species helps account for a portion of the variance, from an objective statistical viewpoint as well as from our more subjective view.

Of special interest was a factor (Factor 7) accounting for 6.5% of the variance explained by the 10 factors. The highest factor loadings

define an area coinciding with offshore regions of high abundance of diatoms in the sediments. *Skeletonema costatum*, a dissolution sensitive species, is important in this factor. Its occurrence in the sediments (Table II) corresponds to the area of the highest factor loadings, and its presence in sediments below even 3000 meters water depth is a reflection of the abundant supply which enhances diatom preservation over this narrow region. *Skeletonema costatum* is, then, another indicator species for coastal upwelling off Peru as it also points to the influence of high productivity induced by coastal upwelling.

In summary, we have established a base line for coastal upwelling off Peru which can be described by: (1) the sinuous pattern of relative abundance of individual species and species groups, and of species collected by factor analysis to describe the variation between samples, and (2) the occurrence of discrete centers of upwelling influence, marked by high abundances of some indicator species, including the "endemic" *Delphineis* species. Areas of upwelling influence occur off Peru at about 8°, 13-14°, and about 17° S.

Comparison of our surface base line with surface samples from another upwelling area will help verify a common response of biogenous components to coastal upwelling in other geographic areas. Historical variation in the location and intensity of upwelling may be determinable by downcore studies of the fluctuation in the abundance of diatoms and in the relative abundance of species groups that we have shown to testify to the influence of coastal upwelling. Preliminary analysis of downcore samples from one core (W7706-64) within the coastal upwelling influenced region strongly suggests that historical variation in the abundance of the oceanic versus the meroplanktic component is of significance. The parallel occurrence of *Delphineis* supports an interpretation of hemipelagic and pelagic intervals based on sediment color change. Further analysis of downcore samples from this and other stations within the upwelling region will establish the persistence of the phenomenon over time and the reoccurrence of parameters that we have shown to be evidence of the influence of coastal upwelling.

Acknowledgements

Tables

Because of their size the tables could not be included in this publication. These may be obtained by writing to School of Oceanography, Oregon State University, Corvalis, OR 97331, and requesting Data Report No. 73, Oregon State University, School of Oceanography, Reference No. 79-8. — The tables: Table I. List of sediment surface samples. — Table II. Relative abundance of 43 species at 49 stations. — Table III. Varimax Factor Matrix (Q-Mode). — Table IV. Varimax Factor Score Matrix (Q-Mode). — Table V. Rotated Factor Matrix (R-Mode). — Table VI. Factor Score Matrix (R-Mode).

References

ANDREWS, G.W. (1977) - Morphology and stratigraphic significance of Delphineis, a new marine diatom genus. Nova Hedwigia, Beih. 54, 243-260.

BERGER, W.H. (1976) - Biogenous deep sea sediments: production, preservation and interpretation. In: Chemical Oceanography (J.P. Riley and R. Chester, eds.), 5, 265-388. London: Academic Press.

BLASCO, D. (1971) - Composicion y distribucion del fitoplankton en la region del afloramiento de las costas perunas. Investigacion Pesquera 35, 61-112.

CALVERT, S.E. (1966) - Accumulation of diatomaceous silica in the sediments of the Gulf of California. Geol. Soc. Amer. Bull. 77, 569-596.

CALVERT, S.E. & N.B. PRICE (1971) - Recent sediments of the South-West African shelf. ICSU/SCOR, Working Party 31, Symp. Cambridge, 1970; Inst. of Geol. Sc., Rep. No. 70/16, 175-185.

FRENGUELLI, J. (1949) - Diatomeas fosiles de los yacimientos chilenos de Tiltil y Mejillones. Darwiniana 9(1), 97-157.

FRYXELL, G.A. & W.J. MILLER III (1978) - Chain-forming diatoms: Three araphid species. Bacillaria 1, 113-136.

GUILLARD, R.L. & P. KILHAM (1977) - The ecology of marine planktic diatoms. In: The Biology of Diatoms (D. Werner, ed.), Bot. Monogr. 13, 372-469.

HART, T.J. & R.J. CURRIE (1960) - The Benguela Current. Discovery Rept. 31, 123-298.

HASLE. G.R. (1960) - Phytoplankton and ciliate species from the tropical Pacific. Skrifter Utgitt av Det Norske Videnskaps-Akademi i Oslo, I. Mat.-Naturv. Klasse 1960(2), 5-50.

HASLE, G.R. & B.R. DE MENDIOLA (1967) - The fine structure of some Thalassionema and Thalassiothrix species. Phycologia 6(2/3), 107-125.

HEIDEN, H. & R.W. KOLBE (1927) - Die marinen Diatomeen der Deutschen Südpolar-Expedition 1901-1903. Deutsche Südpolar-Expedition VIII, Botanik, 450-745.

HUSTEDT, F. (1959) - Die Kieselalgen Deutschlands, Österreichs und der Schweiz, Band 7 of Rabenhorst, G.L., Kryptogamenflora - Teil 2, 845 pp. Leipzig: Akademische Verlagsgesellschaft.

IMBRIE, J. & N.G. KIPP (1971) - New method for quantitative paleo-climatology: Application to a late Pleistocene Caribbean core. In: The Late Cenozoic Glacial Ages (K. Turekian, ed.), 71-181. New Haven: Yale University Press.

KLOVAN, J.E. & J. IMBRIE (1971) - An algorithm and Fortran IV program for large scale Q mode factor analysis. J. Int. Assoc. Mathem. Geol. 3(1), 61-77.

KOLBE, R.W. (1954) - Diatoms from Equatorial Pacific cores. In: Reports of the Swedish Deep-Sea Expedion, vol VI, 3-49.

KOLBE, R.W. (1955) - Diatoms from Equatorial Atlantic cores. In: Reports of the Swedish Deep-Sea Expedition, vol. VII, 151-184.

KOLBE, R.W. (1957) - Diatoms from Equatorial Indian Ocean cores. In: Reports of the Swedish Deep-Sea Expedition, vol. IX, 3-50.

MAEDA, S. & R. KISHIMOTA (1970) - Upwelling off the coast of Peru. J. Oc. Soc. Jap. 26, 300-309.

MARGALEFF, R. (1973) - Fitoplankton marino de la region de affloramiento del NW de Africa. Res. Exp. Cient. B/0 Cornide 2, 65-94.

MERTZ, D. (1966) - Mikropaläontologische und sedimentologische Untersuchung der Pisco-Formation Südperus. Palaeontographica Abt. B, 118(1-3), 1-51.

RYTHER, J.H. (1969) - Photosynthesis and fish production in the sea. Science 166, 72-76.

SCHRADER, H.-J. (1974) - Proposal for a standardized method of cleaning diatom bearing deep-sea and land-exposed marine sediments. Nova Hedwigia, Beih. 45, 403-409.

SCHRADER, H.-J. & R. GERSONDE (1978) - Diatoms and silicoflagellates. Utrecht Micropaleo. Bull. 17, 129-176.

SCOR Wg 36 (1973) - SCOR Wg 36 Coastal upwelling processes, Report 1st meeting, Corvallis, Oregon. Proc. of the Scientific Committee on Oceanic Research 9, 25-33.

SCOR Wg 36 (1974) - SCOR Wg 36 Coastal Upwelling Processes, Report 2nd Meeting, Kiel FRG. Proc. of the Scientific Committee on Oceanic Research 10, 120-128.

SCOR Wg 36 (1976) - SCOR Wg 36 Coastal Upwelling Processes, Report 3rd Meeting, Banyuls-sur-Mer, France. Proc. of the Scientific Committee on Oceanic Research 11, 30-36.

SIMONSEN, R. (1974) - The diatom plankton of the Indian Ocean Expedition of RV "Meteor" 1964-1965. "Meteor" Forschungsergebnisse, Reihe D, 19, 1-107.

SMAYDA, T.J. (1958) - Biogeographical studies of marine phytoplankton. Oikos 9, 158-191.

SMITH, R.L. (1978) - Physical oceanography of coastal upwelling regions. A comparison: Northwest Africa, Oregon, and Peru. Symposium on the Canary Current: Upwelling and Living Resources. No. 4, 10 pp.

STRICKLAND, J.D.H., R.W. EPPLEY & B.R. DE MENDIOLA (1969) - Phytoplankton populations, nutrients and photosynthesis in Peruvian coastal waters. Bot. Inst. Mar. Peru. 2, 4-45.

VAN HEURCK, H. (1880-1885) - Synopsis des Diatomées de Belgique. Anvers: 235 pp.

ZHUSE, A.P. (1972) - Diatoms in the surface sediment layer of the Chilean-Peruvian region of the Pacific Ocean. Okeanologiia 12(5), 831-841. Moscow (in Russian).

CHAPTER II

DIATOM TAPHOCOENOSES

IN THE COASTAL UPWELLING AREA OFF SOUTH WEST AFRICA

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ABSTRACT

The diatom floral composition of one hundred twenty-four sediment samples from the South East Atlantic records the influence of coastal upwelling on sediment composition off South West Africa. Inner shelf samples between 19° and 24° S are rich in diatom valves and the patterns of diatom species distribution in these samples are related to the coastal upwelling process. Comparison with recent phytoplankton data shows that the sediment assemblages preserve many of the important species of the diatom biocoenoses, including Chaetoceros (resting spores), Delphineis karstenii, Thalassiosira eccentrica, and Thalassionema nitzschioides. Delphineis karstenii, a pioneer species in enriched coastal water, occurs nearshore and Chaetoceros resting spores are widespread, with highest relative abundance values in some more offshore samples. The abundance of the Thalassiosira eccentrica group and of Thalassionema nitzschioides in sediment samples in and near Walvis Bay reflects the recurrence of intense upwelling off this part of the coast. An abundance of large centric species has been reported in hydrological conditions characteristic of newly upwelled waters and, correspondingly, Actinocyclus octonarius and some large Coscinodiscus species occur in the sediments in nearshore patches or belts.

INTRODUCTION

The physical oceanography and biology of coastal upwelling have recently been the objects of multidisciplinary research efforts. The objectives of these studies are summarized in the introduction to the collected reports from the first expedition of the CUEA (Coastal Upwelling Ecosystems Analysis) program (Barber, 1977). Two of these objectives may be stated in the following way: 1) description in space and time of the distribution of variables defining the ecosystem--wind, nutrients, phytoplankton, zooplankton, etc., and 2) documentation of the interaction of physical and biological processes that result in high biological production. The broader goal, gaining a predictive knowledge of the coastal upwelling ecosystem, is also served by understanding the consequences of differences among the world's major upwelling regimes (Barber, 1977).

This study stands outside the space and time framework of most reported (or indeed anticipated) coastal upwelling research. Empty diatom shells in sediments are "outside the box" in most conceptual diagrams of the ecosystem, and the use of our samples, which collapse perhaps a decade of deposition, (Meyer, 1973) assumes that there is value in such a representation of "average" conditions. Nonetheless, our analysis addresses the objectives of mainstream coastal upwelling research. We can identify from the abundant occurrence of remains of diatoms in sediments, locations of recurrent high concentrations of diatoms in surface waters. Sediment patterns of diatom species

distribution can be related to the physical processes which repeatedly introduce nutrient rich waters to the photic zone.

Eighty-five surface sediment samples from the coastal upwelling area off South West Africa (the inner shelf between 19⁰24°S), were examined in order to identify in the sediments the influence of coastal upwelling. Thirty-nine offshore samples were also examined in order to verify an expected contrast with the coastal upwelling area, a contrast both in species composition and in abundance of diatoms preserved in sediments.

Diatom analysis of the inner shelf samples and comparison with recent phytoplankton data from this area show that the sediments off South West Africa contain, for many species which regularly occur in surface waters, a parallel record of abundance and distribution. In addition, the abundance in some samples of species characteristically found in newly upwelled waters, documents the repeated occurrence of these waters at sites along the coast and in Walvis Bay. Principal components analysis indicates that several different associations of species have coherent distribution patterns in the sediments off South West Africa. This result is interpreted as a reflection of recurring diatom assemblages, which are in turn related to the dynamics of coastal upwelling.

MATERIAL AND METHODS

The inner shelf sample set consisted of 84 grab samples (two of which were barren) and one piston core top sample (V 12-64) (Figure 1;

Table I). The offshore sample set consisted of thirty-nine core tops
from trigger weight, gravity and piston cores (Figure 2; Table II). All
samples were oven dried for 24 hours at 60°C. The dry weight of each
sample ranged from 0.1 to 2.4 grams. Slide preparation followed the
procedure of Schrader (1974) and Schrader and Gersonde (1978). Samples
were placed in 400 ml (13 cm tall) beakers for acid cleaning. These
beakers were repeatedly filled (to 10 cm in height) with deionized water
for fractional sedimentation to remove the clay component of the samples.
Ninety minute settling times were allowed before aspiration of the over-
standing water. Slides were prepared from 25 μl or 50 μl splits by
automatic pipeting.

The microscopical investigations were carried out on a Leitz-
Orthoplan Orthomat microscope using high power and high resolution
apochromatic oil immersion objectives. Counts were made using the
highest available magnification (Objective: Pl Apo/Oil 100 x/1.32;
Ocular: Periplan GW 10 x M) with counting procedures after Schrader
and Gersonde (1978). Each slide was counted in traverses randomly
laid over the middle of the coverglass. More than 300 valves were
counted per slide, although limited preservation in 8 offshore samples
prevented reaching this figure. Twenty-three of the offshore samples
had no diatoms or insufficient density of diatoms to justify species
counts.

Forty-one species or species group categories were adopted for
systematic counting of the offshore sample set (see Appendix A). Counts

were converted to relative abundance values (% of total valves in a sample, values for all species at all sites are presented in Appendix A).

Of the eighty-five inner shelf samples, eighty-three were rich in diatoms. The flora of the core top sample (V 12-64, see Figure 1) was similar to some of the inner shelf grab samples, with 80% of the total valves accounted for by Chaetoceros resting spores (36.1%), Actinocyclus octonarius (25.7%), Delphineis karstenii (11.0%), and the Thalassiosira eccentrica group (7.2%). However, this sample was not included in the statistical analysis. Sedimentation rates on the South African shelf may be as high as 0.15 cm y^{-1} (Meyer, 1973). The core top collected in 1957 thus may represent an earlier time period than the grab samples collected in the early 1970's and thus was excluded for that reason.

Thirty-nine species or species group categories were adopted for systematic counting of the 82 inner shelf samples (see Appendix B). Species counts were converted to relative abundance values (% of total valves in a sample, values for all species at all sites are presented in Appendix B). Species which did not occur in greater than 2% relative abundance at least at one site, were excluded from further data reduction. Sixteen species were thus selected for further analysis. The correlations for these species at 82 sites were computed (Table III) and the principal components solution for the correlation matrix was determined. The statistical approach was that described in Cooley and Lohnes (1971). The eigen solution was found using IMSL computer program EIGERS (IMSL, 1979).

The factors are uncorrelated and give equal weight to each variable (species). Varimax rotation of the factors was performed using the method of Kaiser (1958). Seven factors were rotated accounting for 82% of the variance in the data. The factor structure matrix which shows the correlations of species to the factors suggested several associations of species (see Table IV). The apportionment of variance in the factors is expressed as % values below each factor on Table IV. The factor matrix was calculated to reveal the distribution of these "associations" at the sediment sites.

HYDROLOGY

The seasonal movements of water masses and the distribution of surface temperature and salinity for the South West African coastal upwelling area have been outlined by Hart and Currie (1960) and Stander (1964). Recently, O'Toole (1977) has analyzed the results of monthly hydrographic surveys between ~18° - 24°S for August 1972 to March 1973 (late winter-early autumn) and August 1973 to April 1972 (late winter-mid autumn). In addition, vertical temperature profiles (0-50m) provided information on the vertical stratification of waters in the same area for the same period. In general, the water movements reported by O'Toole (l.c.) concur with the findings of Hart and Currie (1960) and Stander (1964) who noted two distinct surface masses off the South West Africa coast with relatively sharp boundaries between inshore cold, low salinity waters and offshore warm waters of higher salinity. O'Toole's analysis, however, shows that the water movements in this region are best summarized as a

complex series of advances and withdrawals of three water masses with mixing at the boundaries of these masses, and with cyclonic and anti-cyclonic eddies as prominent features during summer months, particular-ly between 20° - 22°S latitude.

The three fairly distinct bodies of surface water are: 1) A cold, low salinity water characteristic of upwelled water, occurring mainly between 21° - 24°S (surface temperatures: 12° - 16°C in spring; 14° - 18°C in summer; salinities: 34.9°/oo - 35.1°/oo); 2) A warm, highly saline water mass (17° - 22°C; 35.5°/oo - 35.9°/oo) which periodi-cally advances into the northwest sector of the research area off Cape Frio (18°S), and 3) Surface water with intermediate temperature and salinity properties (16° - 20°C, 35.2°/oo -35.5°/oo) which usually advanced toward the coast from the west between 19° - 22°S. Conditions considered typical of late winter and early spring are shown in Figures 3, 4, and 5, modified from O'Toole (1977, 1978). Lowest temperatures occur inshore south of Walvis Bay. But, cold water (11° - 14°C, hatch-ed area in figures, water type #1) is widespread in late winter and early spring with temperatures isothermal in the upper 50 meters characteristic of strong upwelling (O'Toole, 1978). Warm highly saline water (water type #2 in figures) may be present offshore near 18°S and advances mainly in summer (figure 6) in a south to southeasterly direc-tion. Oceanic water of intermediate properties (water type #3) may be "drawn inshore" between centers of upwelling in spring (Figure 4), but the greatest inshore movement takes place in summer (Figure 6). Figure

4 also shows an example of the periodic intrusions of warm water from the southwest at about 24°S.

PHYTOPLANKTON COMPOSITION, DISTRIBUTION AND RELATION TO HYDROLOGY

The R.S. William Scoresby covered seven lines of stations off South West Africa between 20° and 29°S, on two surveys during March and September-October 1950. Hart and Currie (1960) reported observations on the hydrology and microplankton encountered on these surveys. Their estimates of total microplankton for both surveys support the idea that upwelling activity proceeds, with fluctuations in intensity, throughout most of the year and over a major part of the area. Hart and Currie (l.c.) state that the cool low salinity water moving offshore clearly does not originate uniformly along the coast, but is produced in localized regions and they implicate the dominating effect of local winds. Variable coastal winds prevail some 80 miles from the coast which is about the maximum width of the inner shelf off South West Africa. Upwelling waters of the Benguela Current were found to meet warm oceanic waters in the vicinity of the shelf edge (defined at 200 m in this study).

A coastal zone with abundant phytoplankton was sampled on both surveys. Incursions of offshore water were recorded by contrastingly poorer plankton catches. Tongue-like intrusions of sparsely populated oceanic water also occurred in the north on the Möwe Point line of stations (∿20°S). The Chaetoceros group was by far the most important

component of the nearshore diatom flora. Delphineis karstenii and Asterionella japonica dominated at many inshore stations on both surveys. Delphineis karstenii was not observed more than 30 miles from land. In warmer more saline oceanic waters, Rhizosolenia spp., Thalassiothrix and Planktoniella sol were prominent members of the diatom flora.

The restriction of the coastal plankton nearshore and an abundance of zooplankton feeding on the edges of phytoplankton concentrations distinguished the second or spring survey. Chaetoceros species, along with Delphineis karstenii were abundant and confined to the innermost stations in upwelled water. Largest concentrations of phytoplankton were found at these stations with an abrupt diminution in concentrations before the shelf edge was reached. Few resting spores of Chaetoceros were reported on the spring survey.

In autumn, the rich concentrations of phytoplankton between 23° 26°S, included vast numbers of Chaetoceros resting spores and lines of surface foam which were presumed to be accumulations of dying phytoplankton. Whether these are persistent seasonal features or the more transient effects associated with heating and mixing with more saline waters could not be determined. Hart and Currie speculated that they represented merely a quiescent stage of upwelling, succeeding a more active phase such as encountered on the spring survey. They interpret their survey data as documenting the ephemeral nature of coastal upwelling off South West Africa, where

upwelling depends on the relative effects of the trade winds and coastal winds.

Kollmer's studies (1962, 1963) provide additional data with regard to phytoplankton concentrations and species composition in and near Walvis Bay. Defining a bloom as a temporarily limited increase of the phytoplankton standing stock, Kollmer remarks on the great number of minor fluctuations in phytoplankton concentration, especially at stations northwest of Walvis Bay. Even weak easterly to south westerly winds are found to cause upwelling. The resulting minor blooms are almost rhythmical in their reoccurrence at intervals of approximately six weeks. Changes retarding phytoplankton abundance could occur before considerable quantities of phytoplankton were propagated and before large spatial extensions were achieved. The fluctuations in phytoplankton concentration were related to changes in hydrographical and meteorological factors. Grazing, however, was also implicated as possibly limiting standing stocks and restricting the seaward extension of phytoplankton concentrations (Kollmer, 1962).

The neritic community in these studies was mainly represented by the genus Thalassiosira and some species of the genus Chaetoceros as well as Delphineis karstenii. These species were most abundant from autumn to spring.

Thalassiosira was the most important genus recorded by Pieterse and van der Post (1967) in bi-monthly samples during a two year study (1964-1966) of red tide conditions in Walvis Bay. Diatoms appeared

in approximately equal numbers with dinoflagellates, but some species, notably _Thalassiosira_ species periodically developed concentrations nearly equal to that of the dinoflagellates. Of the 65 diatom species encountered, _Thalassiosira_ species were the most important (including _T. subtilis_, _T. eccentricus_, _T. rotula_, _T. decipiens_, and _T. condensata_) followed by _Nitzschia_, _Leptocylindrus_, _Chaetoceros_ and _Thalassionema nitzschioides_. _Thalassionema nitzschioides_ was considered an important subdominant in this study, apparently blooming in spring and summer.

Survey data from the Sea Fisheries Branch in South Africa collected during the Cape Cross Programme includes phytoplankton data and associated hydrographic data (temperature, salinity, dissolved oxygen) for May-November 1971 (Cape Cross Programme Phase II), for January, April, June, August and October 1972 (Phase III), and for June and July 1973 (Phase IV, Wessels et al., 1974).

Monthly records of temperature, salinity and dissolved oxygen for 1971 (DeVos and Visser, 1972) show changing locations and extent of oxygen-poor zones (newly upwelled waters) and the intrusions of warm saline waters. Phytoplankton was collected (N50V net hauls) in association with these hydrographic data. "Mean surface hydrological conditions" were calculated for each species using the temperature, salinity and dissolved oxygen data at stations where the species had maximum abundance (Kruger, in preparation).

Dominant species for May-November 1971 ($\sim$ 17° - 24°S) were Delphineis karstenii (34.11% of total cell counts), Chaetoceros socialis (22.30%), Chaetoceros constrictus (10.00%), other Chaetoceros species (16.89%), Asterionella japonica (6.07%) and Nitzschia species (2.71%). Large celled Coscinodiscus species also occurred from May to November and were recorded inshore as well as offshore forming continuous belts and patches from Dune Point to Conception Bay (20° - 24°S). Thalassiothrix species, Stephanopyxis turris, Corethron criophilum, and Thalassiosira decipiens also occurred year round.

Chaetoceros species constituted with Delphineis karstenii 83.3% of total cell counts, and occurred in maximum abundance in waters with the following properties: 5.91 ml/l O_2, 13.76°C temperature and 35.13°/oo salinity. The mean hydrological conditions for Delphineis karstenii were: 3.19 ml/l O_2, 12.69°C temperature, 35.12°/oo salinity. The Coscinodiscus species (Coscinodiscus centralis var. pacifica, Coscinodiscus gigas var. praetexta, and others) were characterized as occurring in hydrological conditions similar to those where Delphineis karstenii was in maximum abundance. That is, Delphineis karstenii and the Coscinodiscus species tended to occur nearshore and were characterized as "pioneers" in newly upwelled water.

Data from 1972 (N5OV phytoplankton samples collected from 19° - 23°S; Kruger, in prep.) again show the dominance of Delphineis karstenii in cool water with low dissolved oxygen content. Chaetoceros species were the sub-dominant to Delphineis karstenii. The other

important phytoplankton species, as in 1971, are concentrated further offshore in warmer and more oxygenated waters. Changes in diatom assemblages are suggested by changes in abundance of some important species. Contributing higher concentrations than in other months were Actinocyclus octonarius and C. centralis var. pacifica in January, Nitzschia species, Rhizosolenia setigera and Asterionella japonica in August, and Thalassiosira subtilis and Stephanopyxis turris during October.

OFFSHORE SAMPLE SET: RESULTS

Only samples from the nearshore upwelling area and the sample V 16-45 (31°42'S, 08°37'E) had more than 2 million diatom valves per gram of dry sediment. The value calculated for the core top within the coastal upwelling area of the inner shelf (V 12-64) was 78×10^6 diatom valves/g. Even higher values, $300-820 \times 10^6$ valves/g, have been recorded in sediments between about 70-120 m water depth (Mukhina, 1974). Richert's calculations (Richert, 1976) for our samples were $50 - 150 \times 10^6$/mg sediment between 90-130 meters water depth.

V 16-45 had 88×10^6 valves/g and is composed of an allochthonous flora dominated by Nitzschia kerguelensis (66%), Coscinodiscus lentiginosus (16%) and Coscinodiscus tabularis (6%). The composition of this sample is explained by selective dissolution of the autochthonous flora and displacement of primarily endemic Antarctic species.

Eight samples in the offshore sample set were barren in siliceous microfossils. The other thirty one samples had from 0.002 - 2.0 x 10^6 diatom valves/gram dry sediment (Figure 2). Sixteen samples were analyzed for species composition (counted samples are underlined in Table II and circled in Figure 2).

Offshore sites from latitudes 18° - 26°S provide two sets of samples with which to compare the species composition of the offshore region to the inner shelf. One set forms a transect at about 25°S latitude, from V 12-62 (#19) at 12°27'E, westward to CIRC 142 (#23) at 7°00'E (Transect A on Figure 2). Table V lists for two samples on this transect, the numerically dominant species and their relative abundances. These two samples (#19 and #22) which fall on an east-west line, suggest a seaward enrichment of the dissolution-resistant species, e.g., Coscinodiscus nodulifer. In the more offshore sample (#22), a high relative abundance of other oceanic species (Hemidiscus cuneiformis and Coscinodiscus africanus) was recorded along with a marked representation of partially dissolved, unidentifiable fragmented valves.

The second set of samples falls near a line extending northwest from CIRC 211 (#11; 19°58'S, 10°42'E) to CIRC 212 (#7; 18°12'S, 7°36'E) (Transect B on Figure 2). The most abundant taxa in these samples (Table IV) include species more common in the neritic environment (Chaetoceros resting spores, Thalassiosira eccentrica, Actinoptychus splendens, A. senarius) as well as species representing an oceanic influence (Coscinodiscus nodulifer, Roperia tesselata, Hemidiscus cuneiformis).

INNER SHELF SAMPLE SET: RESULTS

The species composition of the inner shelf samples can be summarized by an abbreviated and reorganized version of the matrix of species relative abundance at each site. At each site the four most abundant species constitute from 72-98% of the total valves. Table VII lists the four most abundant species or species groups at each site and illustrates the recurrent dominance of Chaetoceros resting spores, Delphineis karstenii, Thalassiosira eccentrica group, Thalassionema nitzschioides, and Actinocyclus octonarius. The distribution of these species and species groups is discussed below. Thalassiosira aestivalis, Paralia sulcata, and Navicula species are also discussed as additional examples of distributional patterns.

Chaetoceros Resting Spores

There is considerable infraspecific variation in surface structure and morphology of Chaetoceros resting spores and a prior knowledge of the variability in spore morphology is necessary for accurate species determinations (Hargraves, 1979). Reported observations on the morphology of diatom resting spores remain inadequate and widely scattered in the literature and justify our consideration of the Chaetoceros resting spores as a group.

Chaetoceros resting spores occurred at all sites, ranging from 18 - 88% of the total valves in a sample (mean 60.6; standard deviation, 20.3). Chaetoceros spores were the most abundant species in 72 of the samples and represented >30% of the total valves in each sample from sites 1-49. From sites 50 - 82, they occured at $\leq$ 30%

in 11 samples. The distribution of these resting spores is shown in Figure 7.

Delphineis karstenii

At least three morphotypes occur in our sediment samples, each with morphologic characteristics of Delphineis karstenii (Boden) Fryxell (Fryxell and Miller, 1978). These morphotypes correspond to three species identified by Mukhina (1974) in her sediment samples off South West Africa. She labeled these taxa Rhaphoneis wetzelii Mertz, R. simonseni Mertz, and R. ischaboensis Grun. Delphineis karstenii was described by Fryxell and Miller (1978) from material collected in a net haul off South West Africa and their description applies to the specimens we observed in our samples and fits well with Mukhina's photographs of R. wetzelii and R. simonseni. The more elliptical outline in valve view of "R. ischaboensis" specimens may perhaps exclude these forms from Delphineis karstenii. The shape of the valve in valve view as described for Delphineis karstenii is linear with rounded apices ("R. wetzelii") to slightly inflated in center and ends with rounded apices ("R. simonseni"). I tried to differentiate all three forms in our routine counting. However, distinctions between long "R. ischaboensis" specimens and short "R. wetzelii" specimens were often arbitrary and my feeling is that these two forms intergrade. In any event, of the three forms counted, those designated "R. wetzelii" were far more abundant than the other forms. The relative abundance patterns show no distinct differences in distribution. The decision to 'lump' the three morphotypes into a single category was based on this result, on the judgment that intergrades of "ischaboensis" and "wetzelii"

occur in our samples, and on the judgment of Fryxell and Miller (1978) to include in Delphineis karstenii specimens of "simonseni" valve outline, as well as those of "wetzelii" outline.

The Delphineis complex, hereafter referred to as Delphineis karstenii, occurs within a range from < 1 - 49% relative abundance (mean, 14.5; standard deviation, 11.7). It is one of the top four dominants in all but 16 samples and is >30% of the total diatoms in the samples from 10 sites. It is the most dominant species recorded at Sites 50, 51, 53, 54, 56, 65, and 66. It is second only to Chaetoceros spores, or subdominant, at forty-one sites. The distribution of Delphineis karstenii is shown in Figure 8.

Thalassiosira eccentrica

The similarity of specimens in sediment samples prevented a consistent distinction between several species during routine counting procedures. This category includes T. symmetrica (Grunow) Fryxell, T. punctifera Fryxell and Hasle, T. spinosa Simonsen, as well as T. eccentrica (Ehr.) Cleve. Thalassiosira eccentrica, so defined, occurs at all sites and with a range of <1 - 31% (mean, 5.6; standard deviation, 5.8). It is the most abundant diatom at two sites, 60 and 64. It is dominant (one of the four most abundant species) at all but 14 sites and is subdominant at sites 12, 29, 39, 49, 51, 59, 66, 68, and 80. The relative abundance of Thalassiosira eccentrica group is shown in Figure 9.

Thalassionema nitzschioides Grunow

Thalassionema nitzschioides occurs at all but 11 sites with a range from 0-29% relative abundance (mean, 4.59; standard deviation, 6.60). It is one of the dominant diatoms at 30 sites and subdominant at sites 23, 37, 43, 57, 62, and 79. The distribution of relative abundance is shown in Figure 10. No subdivision into varieties has been attempted.

Actinocyclus octonarius Ehr.

Actinocyclus octonarius occurs in all samples (Figure 11). It is one of the dominant diatoms in 53 samples. The range of relative abundance is 1-32% (mean, 5.38; standard deviation, 6.20). It is the most abundant diatom at site 67 and subdominant at sites 9, 10, 11, 17, 21, 22, 24, 26, 30, 35, 36, 41, 45, 70, 77, 78, and 81.

Thalassiosira aestivalis Gran

Hasle (1978) has provided an amended description of Thalassiosira aestivalis Gran which fits well with our specimens. She reports the occurrence of diatoms similar to T. aestivalis in samples from Chile, Cape Town, South Africa, Sylt, the North Sea and the Oslofjord, Norway. However, she identified the species with certainty only from northwest American coastal waters and reserves judgment on whether the diatoms observed from the southern hemisphere belong to a separate taxon or to T. aestivalis. T. aestivalis occurs in about half of our samples. Most often only a single specimen was found in the fraction of the sample counted. However, in and near Walvis Bay, it occurs from 1-10% in 12 samples (Figure 12).

Paralia sulcata (Ehr.) Cleve

Paralia sulcata occurs in highest abundance inshore at Walvis Bay and at a few other areas along the coast (Figure 13).

Navicula: Sect. Navicula = Lineolatae (Hendey, 1964)

Most occurrences of the Navicula species were as single specimens. The only sites where Navicula records values >2% are in Walvis Bay, sites 54, 55 and 56.

FACTOR ANALYSIS

The results of the factor analysis are to present in one factor the overlapping but opposing distribution patterns of Chaetoceros and Delphineis karstenii. The Chaetoceros-Delphineis Factor (Table IV, Factor 4) includes Paralia sulcata in the nearshore patchy distribution (Figure 14). The Large Centrics Factor (Table IV, Factor 1) suggests that there is an association of relatively large centric species which occurs in belts and patches overlaying the Delphineis patches between 20°30' and 23°30' (Figure 14). The Chaetoceros resting spores are in highest abundance on the outskirts of these patches (Figure 14).

Thalassiosira aestivalis, T. eccentrica group and Navicula spp. are correlated with the Thalassiosira Factor (Table IV, Factor 2, Figure 15). Thalassiosira eccentrica has its greatest concentration of high values in Walvis Bay and in other sites at about 23°S (Figure 9). Thalassiosira aestivalis and Navicula spp. also occur predominantly in Walvis Bay. The Thalassiosira Factor thus summarizes the distribution of these three species and groups which have concentrations of highest abundances in Walvis Bay.

The Walvis Bay Factor (Table IV, Factor 5) is positively correlated with Chaetoceros resting spores and negatively with Thalassiosira eccentrica group and Thalassionema nitzschioides. The Walvis Bay Factor summarizes the distributions of the two negatively correlated species which occur everywhere, but in highest concentrations in and near Walvis Bay. Chaetoceros spores on the other hand occur everywhere in abundance, but are less in relative abundance in Walvis Bay. The distribution of the Walvis Bay Factor is given in Figure 16.

The factor associated with Thalassiosira lineata, Actinocyclus curvatulus and Coscinodiscus radiatus expresses really the non-occurrence of these species, or occurrence of only one or two specimens, at most sites. Communalities are somewhat low for A. curvatulus and T. lineata (Table IV, Factor 3). However, the distribution of C. radiatus is well explained by the principal components analysis and this species is highly correlated with this factor. The "offshore" distribution of the C. radiatus Factor (Figure 17) with high values appearing both in the north and south of the study area, as well as around 21°S, may represent an oceanic influence. C. radiatus is an oceanic species with a world wide distribution and has been frequently observed off the coast of South Africa (Hendey, 1937).

Factor 6 was primarily the distribution of Planktoniella sol, Factor 7 was primarily that of Coscinodiscus curvatulus.

DISCUSSION

The contrast in numbers of diatom valves per gram of sediment between the offshore and inner shelf sample sets was extreme. The low

primary productivity of offshore waters and poor preservation associated with low supply of silica to the sea floor accounts for the absence of diatoms or low abundance values in offshore samples. These factors also account for the enrichment of solution resistant species in offshore samples with preserved populations. The species composition of the offshore set includes in abundance species which are rare or absent in the inner shelf samples: Coscinodiscus africanus, Coscinodiscus nodulifer, Rhizosolenia spp., Roperia tesselata, Pseudoeunotia doliolus, Asteromphalus spp., Hemidiscus cuneiformis, and Thalassiothrix. Of these species, Rhizosolenia spp. and Thalassiothrix species have been prominent in records of oceanic intrusions into the nearshore upwelling area.

The influence of coastal upwelling dominates the composition of the inner shelf sample set. High abundance of well preserved diatom remains reflects the high productivity of surface waters and the abundant supply of diatom valves to the sediments. The species composition contrasts markedly with the offshore set and is dominated by Chaetoceros resting spores, and Delphineis karstenii. These species are dominant in phytoplankton records for the coastal waters. Although there is apparent dissolution of some species reported as prominent in the phytoplankton (notably, Asterionella japonica), the sediment assemblages on the inner shelf preserve many of the other important species of the diatom biocoenoses.

Sediment patterns of abundance of diatom species and groups of species on the inner shelf are related to the dynamics of coastal

upwelling off South West Africa. The species characteristic of newly upwelled water (Delphineis karstenii) is predominant in some sediment samples, especially at sites in the southern half of the survey area where newly upwelled waters regularly occur. High relative abundance of Chaetoceros spores occurs outside the nearshore patches of Delphineis karstenii. These patterns may record a sequence of diatom assemblages in waters moving offshore: initial blooms of Delphineis and Chaetoceros and later, widespread formation of Chaetoceros resting spores.

Hydrological and phytoplankton data document the recurrence of upwelling off Walvis Bay. An extended area of cold, diatom rich waters, is periodically characteristic of this part of the coast. Species which have been reported in bloom concentration in and near Walvis Bay (Thalassiosira spp., Thalassionema nitzschioides) have a sediment record in that area which attests to the repeated occurrence of favorable conditions for such blooms. Their high abundance at other sites along the coast may be evidence of similar processes occurring in other portions of the coastal upwelling region.

The sea-bed distribution of some large-celled diatom species is interpreted as reflecting periodic concentrations of these diatoms in patches or belts between 20° - 24°S. Winnowing of smaller species could account for concentrations in the sediments of these larger specimens (>∿100μm). However, the phytoplankton data off South West Africa include some observations of the abundant occurrences of

Actinocyclus octonarius and large-celled Coscinodiscus species.
High abundance in the sediments of these large cells overlaps areas
with high abundance of Delphineis karstenii. The reported occurrence
of Delphineis karstenii and of the Coscinodiscus species in hydrolog-
ical conditions characteristic of coastal upwelling supports the inter-
pretation that these sediment compositions reflect "real" phytoplankton
assemblages.

CONCLUSIONS

This study and previous studies of sediments from coastal upwell-
ing areas (Round, 1967, 1968; Koopmann et al., 1978; Diester-Haass and
Schrader, 1979; Schuette and Schrader, 1979) support the following
conclusions:

1. Diatoms, which are absent or in low abundance in adjacent off-
shore sediments, may be extremely abundant in sediments influenced by
coastal upwelling. The preservation of weakly silicified diatom valves
is enhanced by this influence.

2. Short term variations in diatom assemblages of overlying sur-
face waters are not resolved by diatom floral analysis of sediment
samples. However, the repeated abundant occurrence of diatom species
or groups, and the long term overprinted spatial patterns of species
distributions are well recorded in diatomaceous sediments underlying
the coastal upwelling areas.

3. The diatom species composition of sediment samples influenced by coastal upwelling is not uniform. Rather, diatom species distribution patterns preserve the lobe or patch-like structure of coastal upwelling regimes and thus record a history of coastal upwelling in specific locations.

4. Periodic nutrient enrichment of surface waters allows for the reinitiation of species succession. Species preserved in the sediments--from pioneer species representing newly upwelled waters to those representing nutrient-depleted waters--record the evolution of the upwelling system. The occurrence of large diameter diatoms is also a characteristic feature of upwelling influenced sediments and reflects their recurrent abundance in surface waters.

5. The species composition and the abundance and preservation of diatom remains in sediment samples allows for a differentiation of "coastal upwelling-influenced" sediments from "oceanic" diatomaceous sediments. In addition to providing information about features of recent coastal upwelling regimes, the characterization of recent (surface) upwelling-influenced sediments will allow recognition of other sites of recurrent coastal upwelling in subsurface sediments and thus allow paleoecological interpretation of older diatomaceous material.

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REFERENCES

Barber, R.T., 1977. The JOINT-I expedition of the Coastal Upwelling Ecosystems Analysis program. Deep-Sea Research, 24: 1-6.

Cooley, W.W. and Paul R. Lohnes, 1971. Multivariate Data Analysis. John Wiley and Sons, Inc., New York, 364 pp.

DeVos, J.E. and G.A. Visser, 1972. Hydrology, Cape Cross Programme (Phase II). Sea Fisheries Branch South Africa Internal Report, unpublished.

Diester-Haass, L. and H.J. Schrader, 1979. Neogene coastal upwelling history off Northwest and Southwest Africa. Marine Geology, 29: 39-53.

Fryxell, G.A. and W.J. Miller III, 1978. Chain-forming diatoms: Three araphid species. Bacillaria, 1: 113-136.

Hargraves, P.E., 1979. Studies on marine plankton diatoms IV. Morphology of Chaetoceros resting spores. Nova Hedwigia, Beiheft 64: 99-120.

Hart, T.J. and R.J. Currie, 1960. The Benguela Current. 'Discovery' Report, 31: 123-398.

Hasle, G.R., 1978. Some Thalassiosira species with one central process (Bacillariophyceae). Botany, 2: 77-110.

Hendey, N.I., 1937. The plankton of southern seas. 'Discovery' Report, 16: 151-364.

IMSL, 1979. The IMSL Library: Fortran subroutines in the areas of Mathematics and Statistics, Vol. 1. International Mathematical and Statistical Libraries, Inc., GNB Building, 7500 Bellaire Blvd., Houston, Texas.

Kaiser, H.F., 1958. The varimax criterion for analytic rotation in factor analysis. Psychometrika, 23: 187-200.

Kollmer, W.E., 1962. The pilchard of South West Africa (Sardinops ocellata Pappé): The annual cycle of phytoplankton in the waters off Walvis Bay 1958. South West Africa Administration Marine Research Laboratory Investigational Report, 4: 1-44.

Kollmer, W.E., 1963. The pilchard of South West Africa (Sardinops ocellata Pappé): Notes on zooplankton and phytoplankton collections made off Walvis Bay. South West Africa Administriation Marine Research Laboratory, Investigational Report, 8: 1-78.

Koopmann, B., M. Sarthein and H.J. Schrader, 1978. Sedimentation influenced by upwelling in the subtropical Baie du Lévrier. In: R. Boje and M. Tomczak (Editors), Upwelling Ecosystems. Springer-Verlag, Berlin, pp. 282-288.

Kruger, I., in prep. Geographical distribution and abundance of phytoplankton in South West African waters and its relation to the environment (I. Kruger, Sea Fisheries Branch, Cape Town, South Africa).

Meyer, K., 1973. Uran-Prospektion vor Südwestafrika. Erzmetall, 26 (7): 313-317.

Mukhina, V., 1974. Diatoms in the suspension and surface sedimentary layer of the shelf of South Western Africa. In: A.P. Zhuse (Editor), The Micropaleontology of Oceans and Seas. Nauka, Moscow, pp. 94-105. (in Russian).

O'Toole, M.J., 1977. Investigations into some important fish larvae in the South-East Atlantic in relation to the hydrological environment. Ph.D. thesis, University of Cape Town, South Africa.

O'Toole, M.J., 1978. Aspects of the early life history of the hake Meluccius capensis Castelnau off South West Africa. Fisheries Bulletin South Africa, 10: 20-36.

Pieterse, F. and D.C. van der Post, 1967. The pilchard of South West Africa (Sardinops ocellata): Oceanographical conditions associated with red-tides and fish mortalities in the Walvis Bay region. South West Africa Administration Marine Research Laboratory, Investigational Report, 4: 1-125.

Richert, P., 1976. Relationship between diatom biocoenoses and taphocoenoses in upwelling areas off West Africa (abstract). 4th Symposium on Recent and Fossil Diatoms, Oslo.

Round, F.E., 1967. The phytoplankton of the Gulf of California. Part I. Its composition and contribution to the sediments. Journal of Experimental Marine Biology and Ecology, 1: 76-97.

Round, F.E., 1968. The phytoplankton of the Gulf of California. Part II. The distribution of phytoplanktonic diatoms in cores. Journal of Experimental Marine Biology and Ecology, 2: 64-86.

Schrader, H.-J., 1974. Proposal for a standardized method of cleaning diatom bearing deep-sea and land-exposed marine sediments. Nova Hedwigia, Beiheft 45: 403-409.

Schrader, H.-J., and R. Gersonde, 1978. Diatoms and silicoflagellates. Utrecht Micropaleontological Bulletin, 17: 129-176.

Schuette, G., and H. Schrader, 1979. Diatom taphocoenoses in the
coastal upwelling area off western South America. Nova Hedwigia,
Beiheft 64: 359-378.

Stander, G.H., 1964. The pilchard of South West Africa (Sardinops
ocellata): The Benguela current off South West Africa. South
West Africa Administration Marine Research Laboratory, Investi-
gational Report, 12, 1-22.

Wessels, G.F.S., D.F. Coetzee and I. Kruger, 1974. The environment,
Cape Cross Programme (Phase IV). Sea Fisheries Branch South
Africa Internal Report, unpublished.

Table I: Inner shelf sediment surface sample set and water depths (m).

Site #[1]	Water Depth	Site #[1]	Water Depth	Site #[1]	Water Depth
1	115	29	82	57	125
2	105	30	65	58	100
3	100	31	118	59	91
4	93	32	86	60	76
5	82	33	75	61	40
6	122	34	106	62	132
7	100	35	66	63	102
8	92	36	51	64	98
9	96	37	102	65	80
10	77	38	68	66	60
11	63	*	130	67	38
12	95	39	115	68	127
13	93	40	96	69	88
14	75	41	61	70	77
15	106	42	49	71	103
16	96	43	121	72	93
17	93	44	103	73	82
18	100	45	63	74	140
19	82	46	122	75	89
20	63	47	99	76	78
21	87	48	125	77	86
22	73	49	110	78	72
23	66	50	69	79	90
*	48	51	56	80	79
24	110	52	50	81	109
25	89	53	35	82	88
26	80	54	21	V12-64[2]	73
27	65	55	16		
28	90	56	15		

[1]Corresponding to location on Figure 1.

[2]Top sample of trigger weight core. Location: 22°34'S, 14°12'E.

Table II. Offshore sediment samples.

	Core	Type of Core[2]	Latitude	Longitude	Level in core (cm)	Water Depth (m)	Repository[3]
1	V 27-227	TW	12°19'S	09°02'E	1-2	4422	LDGO
2	V 19-267	TW	13°23'S	02°13'E	top	5585	LDGO
3	V 19-266	TW	14°36'S	03°40'E	top	5543	LDGO
4	V 27-225	TW	16°32'S	03°54'E	top	5495	LDGO
5	V 19-262	TW	18°20'S	08°23'E	top	4918	LDGO
6	CIRC 212	PG	18°12'S	07°36'E	2-3.5	5142	OSU
7	V 19-261	TW	18°59'S	09°12'E	top	4662	LDGO
8	V 19-260	TW	19°20'S	09°37'E	top	3585	LDGO
9	CIRC 211	Gb	19°58'S	10°42'E	2-3.5	1377	OSU
10	V 29-135	TW	19°42'S	08°53'E	top	2675	LDGO
11	RC 13-227	TW	21°53'S	08°52'E	12	4301	LDGO
12	RC 13-228	TW	22°19'S	11°12'E	5	3204	LDGO
13	V 12-65	TW	22°59'S	08°06'E	top	4118	LDGO
14[1]	CIRC 157	P	24°50'S	13°52'E	0-1.5	216	OSU
15	V 29-134	TW	24°13'S	07°25'E	0.5-1.5	3804	LDGO
16	V 19-248	P	24°34'S	04°50'E	top	3321	LDGO
17	V 12-62	TW	25°30'S	12°27'E	top	3038	LDGO
18	RC 13-229	TW	25°30'S	11°18'E	top	4191	LDGO
19	CIRC 144	G	25°46'S	09°26'E	6-7.5	4677	OSU
20	CIRC 143	PG	25°40'S	07°10'E	0-1.5	4196	OSU
21	CIRC 142	PG	25°40'S	07°00'E	0-1.5	4099	OSU
22[1]	V 19-246	P	25°46'S	04°06'E	top	4244	LDGO
23	V 20-204	TW	26°38'S	08°40'E	top	4352	LDGO
24[1]	CIRC 136	P	26°13'S	05°50'E	0-1.5	1410	OSU
25	V 20-203	TW	28°39'S	12°19'E	5	3860	LDGO
26[1]	V 19-243	TW	28°16'S	07°41'E	top	4967	LDGO
27	V 19-241	TW	29°37'S	10°36'E	top	4493	LDGO
28	V 19-242	TW	29°31'S	09°35'E	top	4881	LDGO
29[1]	V 20-202		30°32'S	15°22'E	top	327	LDGO
30	V 19-240	TW	30°35'S	13°17'E	top	3103	LDGO
31	RC 12-303	TW	30°29'S	11°33'E	top	4250	LDGO
32[1]	V 12-58		32°16'S	16°21'E	top	459	LDGO
33[1]	V 12-59		32°16'S	16°20'E	top	424	LDGO
34[1]	V 18-182	TW	32°20'S	15°01'E	top	2941	LDGO
35	V 16-45	G	31°42'S	08°37'E	top	4817	LDGO
36	RC 12-300	TW	32°53'S	02°50'E	~1-2	4652	LDGO
37	RC 12-299	TW	34°05'S	01°00'E	2-3	4296	LDGO
38	V 22-117	TW	34°39'S	16°06'E	top	4144	LDGO
39	V 12-57	G	35°20'S	10°43'E	top	5011	LDGO

[1]Samples barren in siliceous microfossils.

[2]Type of core: TW = triggerweight; PG, Gb or G = gravity; P = piston.

[3]Repositories: LDGO = Lamont-Doherty Geological Observatory; OSU = Oregon State University.

Table III. Correlation Matrix for 16 Species*(high correlations between species are underlined)

	AOCT	ACUR	CHAE	CAST	CCUR	CGIG	CRAD	CPER
AOCT	1.0000							
ACUR	-.1214	1.0000						
CHAE	-.3017	.0207	1.0000					
CAST	.6965	-.2115	-.1421	1.0000				
CCUR	-.0189	.2066	.0209	-.0207	1.0000			
CGIG	.6274	-.1751	-.1353	.8060	-.0131	1.0000		
CRAD	.2031	.4378	-.0858	-.0629	.1540	-.0028	1.0000	
CPER	.8739	-.1264	-.3209	.8039	-.0052	.7712	.0658	1.0000
DLPH	-.2297	-.1000	-.6736	-.2440	-.0940	-.2527	-.1289	-.1516
PSUL	.4347	-.0409	-.4915	.0383	-.0599	.0783	.2061	.3341
TNIT	-.1486	.0079	-.5307	-.1816	-.0276	.1669	-.0940	-.1625
TECC	-.0253	.1424	-.7153	-.1213	.0306	-.0330	.2057	.0024
TAES	-.0493	-.0558	-.5278	-.0646	-.0672	-.0488	-.0521	-.0447
TLIN	-.0056	.3911	.1663	-.0365	.1892	-.0483	.2266	-.0641
NAVI	-.1657	.0114	-.3308	-.1603	-.1288	-.1756	-.1748	-.1516
PSOL	.1594	-.0714	-.1662	-.0213	-.1642	-.0208	-.0037	.1126
	AOCT	ACUR	CHAE	CAST	CCUR	CGIG	CRAD	CPER

	DLPH	PSUL	TNIT	TECC	TAES	TLIN	NAVI	PSOL
AOCT								
ACUR								
CHAE								
CAST								
CCUR								
CGIG								
CRAD								
CPER								
DLPH	1.0000							
PSUL	.2697	1.0000						
TNIT	.2253	.0086	1.0000					
TECC	.3258	.2146	.4785	1.0000				
TAES	.3073	.2042	.2127	.6892	1.0000			
TLIN	-.2813	-.0897	-.1496	.0108	-.0889	1.0000		
NAVI	.3919	.0252	.1461	.2816	.5202	-.1283	1.0000	
PSOL	.0571	.2162	.0348	.1508	.0582	-.0123	-.0446	1.0000
	DLPH	PSUL	TNIT	TECC	TAES	TLIN	NAVI	PSOL

*See Appendix B for explanations of abbreviations.

Table IV.   Factor Structure Matrix*(high correlations of species to factors are underlined).

Species	*	Factors						
		1	2	3	4	5	6	7
AOCT	.862	.8637	.0947	.1149	.2535	.0573	-.1579	-.0288
ACUR	.683	-.1694	-.0380	.7901	-.0976	-.0354	.0977	.0932
CHAE	.954	-.2505	.4558	-.0214	-.5663	.5947	.0739	-.0574
CAST	.874	.9130	.0243	-.1397	-.1168	.0463	.0667	.0049
CCUR	.950	-.0097	.0896	.1243	-.0039	-.0106	.1121	.9558
CGIG	.819	.8914	.0239	-.0792	-.1115	.0007	.0707	-.0058
CRAD	.762	.0690	.1550	.8204	.2390	-.0345	.0414	-.0229
CPER	.914	.9342	.0385	-.0013	.1835	.0254	-.0702	.0126
DLPH	.750	-.2824	-.3711	-.2373	.6500	-.2097	.0963	.0178
PSUL	.773	.2195	-.0706	.1577	.7922	.0359	-.2553	-.0191
TNIT	.876	-.1545	-.0477	-.0786	.0068	-.9178	.0135	-.0329
TECC	.845	.0127	-.5654	.2523	.1477	-.6364	-.1740	.0681
TAES	.786	.0075	-.8439	-.0052	.0959	-.2328	-.1039	.0019
TLIN	.654	-.0132	-.0840	.5569	-.3962	.1849	-.2585	.2808
NAVI	.749	-.1659	-.8097	-.1120	.0963	.0507	.1587	-.1269
PSOL	.879	.0146	.0167	-.0715	.1243	-.0608	-.9180	-.1078
		22%	13%	11%	11%	11%	7%	7%

Factors: 1 = Large centrics   * = Communalities
           2 = Thalassiosira spp.
           3 = C. radiatus
           4 = Chaetoceros-Delphineis
           5 = Walvis Bay

*See Appendix B for explanations of abbreviations.

Table V.   Relative abundance of dominant species for samples from sites
           on Transect A (Figure 2).

V 12-62   (3038 m water depth)   C 143   (4196 m water depth)

Thalassiosira eccentrica   20%   Coscinodiscus nodulifer   65%

Coscinodiscus nodulifer   19   Thalassiosira eccentrica   5

Thalassionema nitzschiodes   17   Pseudoenotia doliolus   5

Coscinodiscus curvatulus   15   unidentifiable diatoms   4

Actinocyclus octonarius   6   Hemidiscus cuneiformis   3

Actinocyclus curvatulus   4   Coscinodiscus africanus   2
                                ___   ___
                                81%   84%

Table VI. Relative abundance of dominant species for samples from
           sites on Transect B (Figure 2).

C 211 (1377 m water depth)

Coscinodiscus nodulifer	42%
Actinoptychus splendens	9
Actinoptychus senarius	8
Thalassionema nitzschiodes	6
Thalassiosira eccentrica	6
	74%

V 19-260 (358 m water depth)

Coscinodiscus nodulifer	34%
Thalassiosira eccentrica	11
Chaetoceros resting spores	10
Actinoptychus senarius	7
Coscinodiscus curvatulus	7
	66%

V 19-261 (4662 m water depth)

Coscinodiscus nodulifer	50%
Actinoptychus senarius	18
Chaetoceros resting spores	7
Thalassiosira oestrupii	5
Actinocyclus curvatulus	4
Thalassiosira eccentrica	3
	87%

V 19-262 (4918 m water depth)

Thalassiosira eccentrica	30%
Coscinodiscus nodulifer	12
Pseudoeunotia doliolus	11
Chaetoceros resting spores	7
Roperia tesselata	7
Coscinodiscus curvatulus	6
	73%

C 212 (5142 m water depth)

Thalassiosira eccentrica	17%
Pseudoeunotia doliolus	17
Coscinodiscus nodulifer	14
Roperia tesselata	9
Coscinodiscus curvatulus	8
Hemidiscus cuneiformis	4
	69%

Table VII. Four most abundant species at each inner shelf site and their relative abundance values.

Site	1	% abundance	2	% abundance	3	% abundance	4	% abundance	Sum
1	Chaetoceros	50	Delphineis	25	T. eccentrica	8	Thalassionema	7	90
2	Chaetoceros	76	Delphineis	8	Paralia	4	T. eccentrica	3	91
3	Chaetoceros	50	Delphineis	24	T. eccentrica	10	Thalassionema	8	92
4	Chaetoceros	41	Delphineis	26	Thalassionema	22	T. eccentrica	6	95
5	Chaetoceros	62	Delphineis	26	T. eccentrica	4	Thalassionema	2	94
6	Chaetoceros	59	Delphineis	22	T. eccentrica	4	A. octonarius Thalassionema	3	88
7	Chaetoceros	66	Delphineis	16	T. eccentrica	5	A. curvatulus	3	90
8	Chaetoceros	54	Delphineis	40	T. eccentrica	2	A. octonarius A. curvatulus	1	97
9	Chaetoceros	68	A. octonarius	9	T. eccentrica	5	T. lineata	4	86
10	Chaetoceros	44	A. octonarius	20	C. asteromph.	13	T. eccentrica	6	83
11	Chaetoceros	63	A. octonarius	12	Delphineis	8	T. eccentrica	5	88
12	Chaetoceros	75	T. eccentrica	8	T. lineata	6	A. octonarius A. curvatulus	3	92
13	Chaetoceros	61	Delphineis	15	T. eccentrica	7	Thalassionema	5	88
14	Chaetoceros	69	Delphineis	12	A. octonarius	8	T. eccentrica	4	93
15	Chaetoceros	63	Delphineis	17	T. eccentrica	6	A. octonarius	5	91
16	Chaetoceros	60	Delphineis	12	T. eccentrica	9	A. octonarius	8	89
17	Chaetoceros	85	A. octonarius	5	Thalassionema	3	T. eccentrica C. asteromph.	2	95
18	Chaetoceros	68	Delphineis	22	T. eccentrica	3	A. octonarius	1	94
19	Chaetoceros	50	Delphineis	28	A. octonarius	4	T. eccentrica	4	86
20	Chaetoceros	64	Delphineis	8	A. octonarius	6	Paralia	5	83
21	Chaetoceros	70	A. octonarius	8	T. eccentrica	7	Delphineis	6	91
22	Chaetoceros	71	A. octonarius	13	T. eccentrica	4	A. curvatulus	2	90
23	Chaetoceros	45	Thalassionema	15	T. eccentrica	13	Delphineis	10	83
24	Chaetoceros	81	A. octonarius	5	T. eccentrica	4	C. radiatus	3	93
25	Chaetoceros	70	Delphineis	20	T. eccentrica	4	C. curvatulus A. curvatulus	1	95
26	Chaetoceros	88	A. octonarius	4	T. eccentrica	2	Delphineis	1	95
27	Chaetoceros	82	Delphineis	8	T. eccentrica	3	A. octonarius	2	95
28	Chaetoceros	84	Delphineis	8	T. eccentrica	3	A. octonarius	1	96
29	Chaetoceros	72	T. eccentrica	10	A. octonarius	8	Delphineis	3	93
30	Chaetoceros	75	A. octonarius	8	T. eccentrica	7	A. curvatulus	2	92
31	Chaetoceros	80	Delphineis	7	T. eccentrica	6	C. curvatulus	2	95
32	Chaetoceros	86	Delphineis	6	T. eccentrica	4	A. octonarius	1	97
33	Chaetoceros	74	Delphineis	10	A. octonarius	6	Thalassionema	1	91
34	Chaetoceros	76	Delphineis	14	T. eccentrica	3	A. octonarius	2	95
35	Chaetoceros	61	A. octonarius	17	C. asteromph.	7	C. perforatus	4	89
36	Chaetoceros	62	A. octonarius	27	C. perforatus	4	C. asteromph.	4	97
37	Chaetoceros	59	Thalassionema	23	Delphineis	7	T. eccentrica	5	94
38	Chaetoceros	72	Delphineis	16	A. octonarius	5	C. asteromph.	2	95
39	Chaetoceros	87	T. eccentrica	5	A. octonarius Delphineis	2			96
40	Chaetoceros	76	Delphineis	12	T. eccentrica	7	A. octonarius	2	97
41	Chaetoceros	39	A. octonarius	32	C. asteromph.	12	C. perforatus	9	92

Table VII. (continued)

Site	1	% abundance	2	% abundance	3	% abundance	4	% abundance	Sum
42	Chaetoceros	48	Delphineis	18	Thalassionema	10	A. octonarius	10	86
43	Chaetoceros	49	Thalassionema	24	Delphineis	15	T. eccentrica	8	96
44	Chaetoceros	86	Delphineis	6	T. eccentrica	2	A. octonarius	2	96
45	Chaetoceros	82	A. octonarius	5	T. eccentrica	2	C. curvatulus	2	91
46	Chaetoceros	67	Delphineis	11	T. eccentrica	6	Thalassionema	4	88
47	Chaetoceros	50	Delphineis	39	T. eccentrica	5	Thalassionema	2	96
48	Chaetoceros	74	Delphineis	18	T. eccentrica	2	Navicula	1	95
49	Chaetoceros	82	T. eccentrica	4	A. octonarius	3	A. curvatulus	2	91
50	Delphineis	49	Chaetoceros	44	T. eccentrica	2	A. octonarius	1	96
51	Delphineis	30	T. eccentrica	21	Chaetoceros	20	Thalassionema	15	86
52	Chaetoceros	42	Delphineis	32	A. octonarius	8	T. eccentrica	5	87
53	Delphineis	31	Chaetoceros	21	T. eccentrica	20	Thalassionema	9	81
54	Delphineis	38	Chaetoceros	29	T. eccentrica	15	Thalassionema	6	88
55	Chaetoceros	32	Delphineis	24	T. eccentrica	16	T. aestivalis	10	82
56	Delphineis	43	Chaetoceros	29	T. eccentrica	10	Thalassionema	6	88
57	Chaetoceros	33	Thalassionema	29	T. eccentrica	18	Delphineis	10	90
58	Chaetoceros	56	Delphineis	19	Thalassionema	14	T. eccentrica	7	96
59	Chaetoceros	25	T. eccentrica	23	Delphineis	18	A. octonarius	12	78
60	T. eccentrica	21	Chaetoceros Delphineis	21			Thalassionema	11	74
61	Chaetoceros	33	Delphineis	32	T. eccentrica	12	A. octonarius	6	83
62	Chaetoceros	51	Thalassionema	20	Delphineis	17	T. eccentrica	8	96
63	Chaetoceros	65	Delphineis	23	T. eccentrica	5	Thalassionema	4	97
64	T. eccentrica	31	Delphineis	24	Chaetoceros	23	Thalassionema	11	89
65	Delphineis	33	Chaetoceros	28	Thalassionema	13	A. octonarius	9	83
66	Delphineis	22	T. eccentrica	20	Chaetoceros	18	A. octonarius	15	75
67	A. octonarius	29	Delphineis	24	Chaetoceros	20	Paralia	11	84
68	Chaetoceros	74	T. eccentrica	11	C. curvatulus	4	T. lineata	3	92
69	Chaetoceros	47	Delphineis	21	Thalassionema	16	A. octonarius	6	90
70	Chaetoceros	83	A. octonarius	7	T. eccentrica	4	A. curvatulus Thalassionema	1	95
71	Chaetoceros	71	Delphineis	15	T. eccentrica	4	A. octonarius	2	92
72	Chaetoceros	83	Delphineis	12	A. curvatulus	2	A. octonarius	1	98
73	Chaetoceros	72	Delphineis	21	A. octonarius	2	T. eccentrica	2	97
74	Chaetoceros	87	T. lineata	3	T. eccentrica	3	A. octonarius	2	95
75	Chaetoceros	86	Delphineis	10					96
76	Chaetoceros	84	Delphineis	12	Navicula	1			97
77	Chaetoceros	81	A. octonarius	8	T. eccentrica	2	Thalassionema A. curvatulus C. curvatulus	1	92
78	Chaetoceros	70	A. octonarius	11	Delphineis	4	T. eccentrica	3	88
79	Chaetoceros	61	Thalassionema	20	Delphineis	9	T. eccentrica	6	96
80	Chaetoceros	82	T. eccentrica	5	Delphineis	5	A. octonarius	2	94
81	Chaetoceros	88	A. octonarius	4	Thalassionema Delphineis	1			94
82	Chaetoceros	30	Delphineis	22	T. eccentrica	12	A. octonarius	8	72
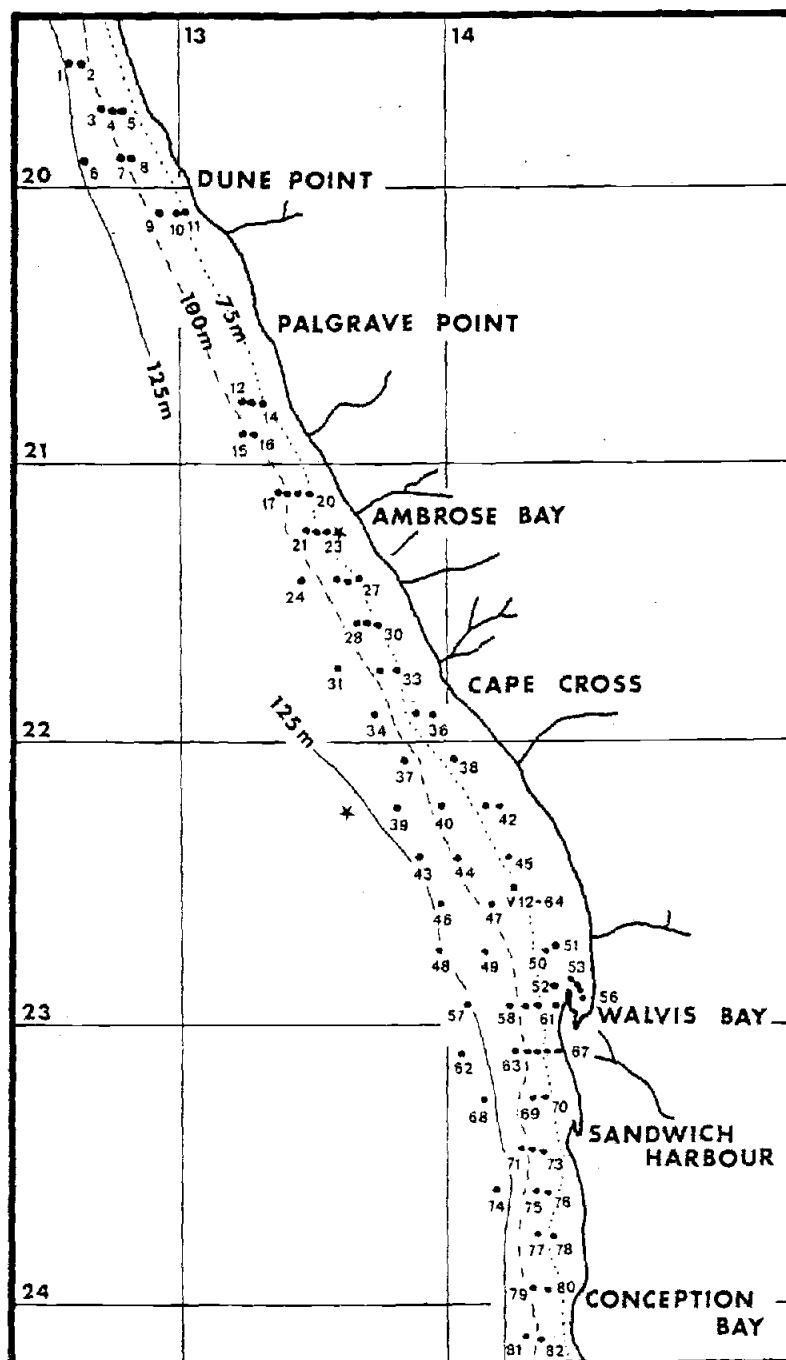
Figure 1: Locations of inner shelf sample sites. The two barren sites are marked by asterisks.

Figure 2: Locations of offshore sample sites and inner shelf sample
set, and abundance of diatom valves/gram dry sediment. The
location of the inner shelf sites is inset; shading indicates
areas of highest abundance (with over 300×10^6 valves/gram dry
sediment) in $\sim$90-130 m water depth (Richert, 1976). Lines connect
the two transects discussed in text. Counted samples are circled.

Figure showing a distribution map with numbered sampling sites (1–39, A, B) and legend:

> 300×10⁶ (solid black)
2–300×10⁶ (dotted)
0.002–2 ×10⁶ (light stipple)
Barren (white)
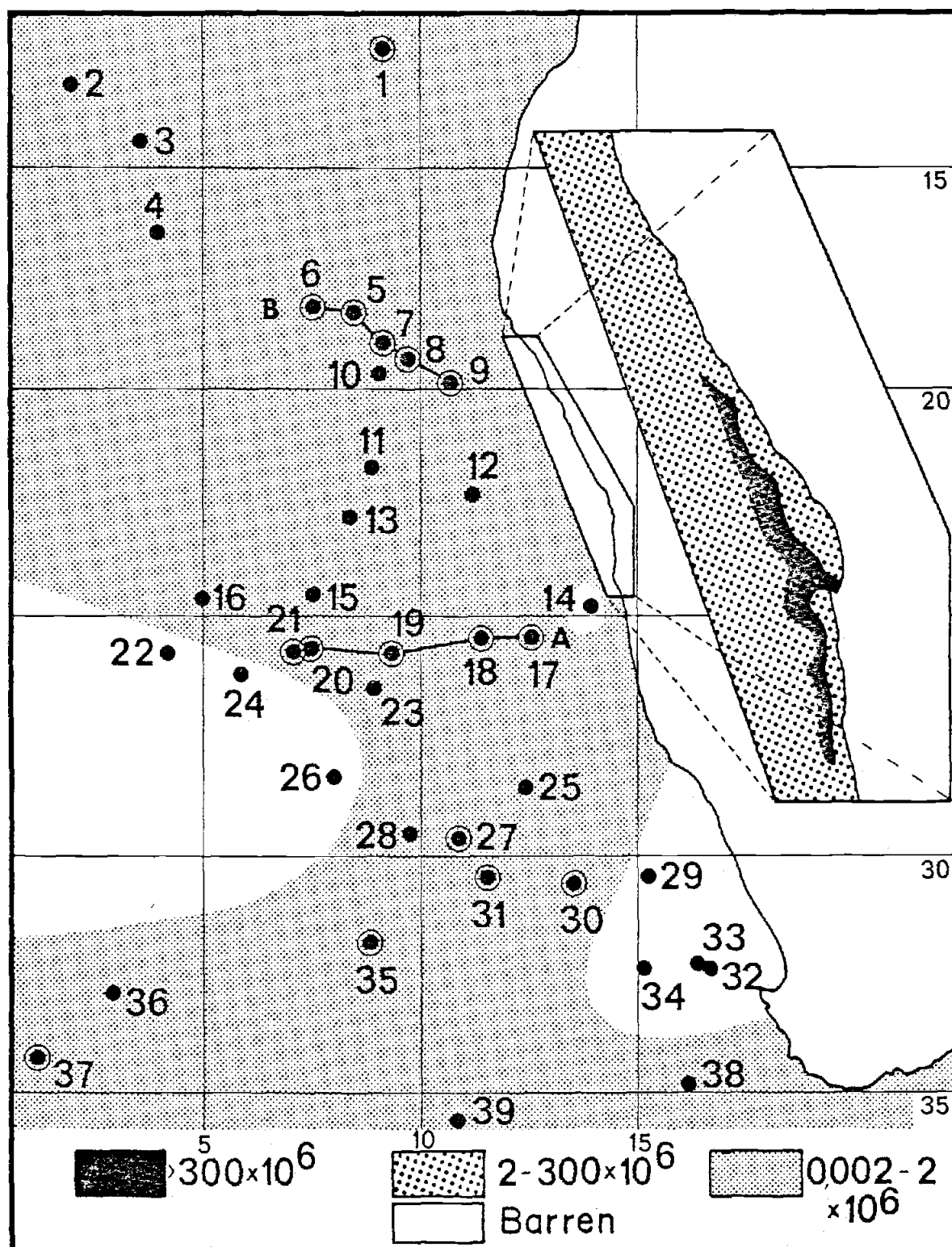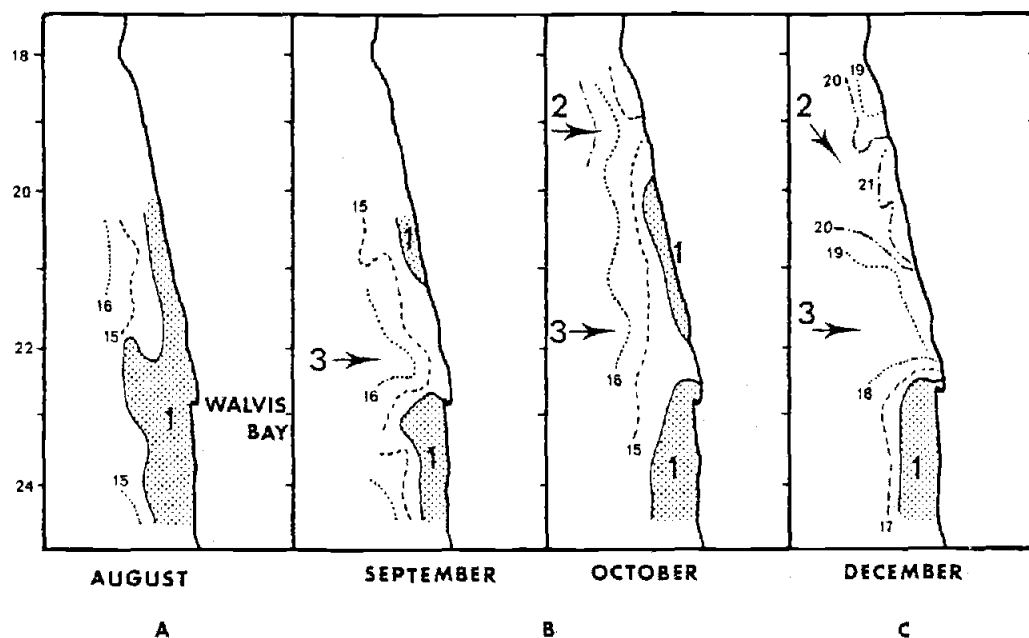
Figure 3-6: Distribution of surface temperature and locations of
surface water masses, August-October (A, late winter; B, spring),
and December (C, summer), 1972 (after O'Toole, 1977, 1978). For
definition of water masses 1-3, compare the text. Figure 3:
August surface water masses and surface temperatures. Figure 4:
September surface water masses and surface temperatures.

Figure 5: October surface water masses and surface temperatures.

Figure 6: December surface water masses and surface temperatures.
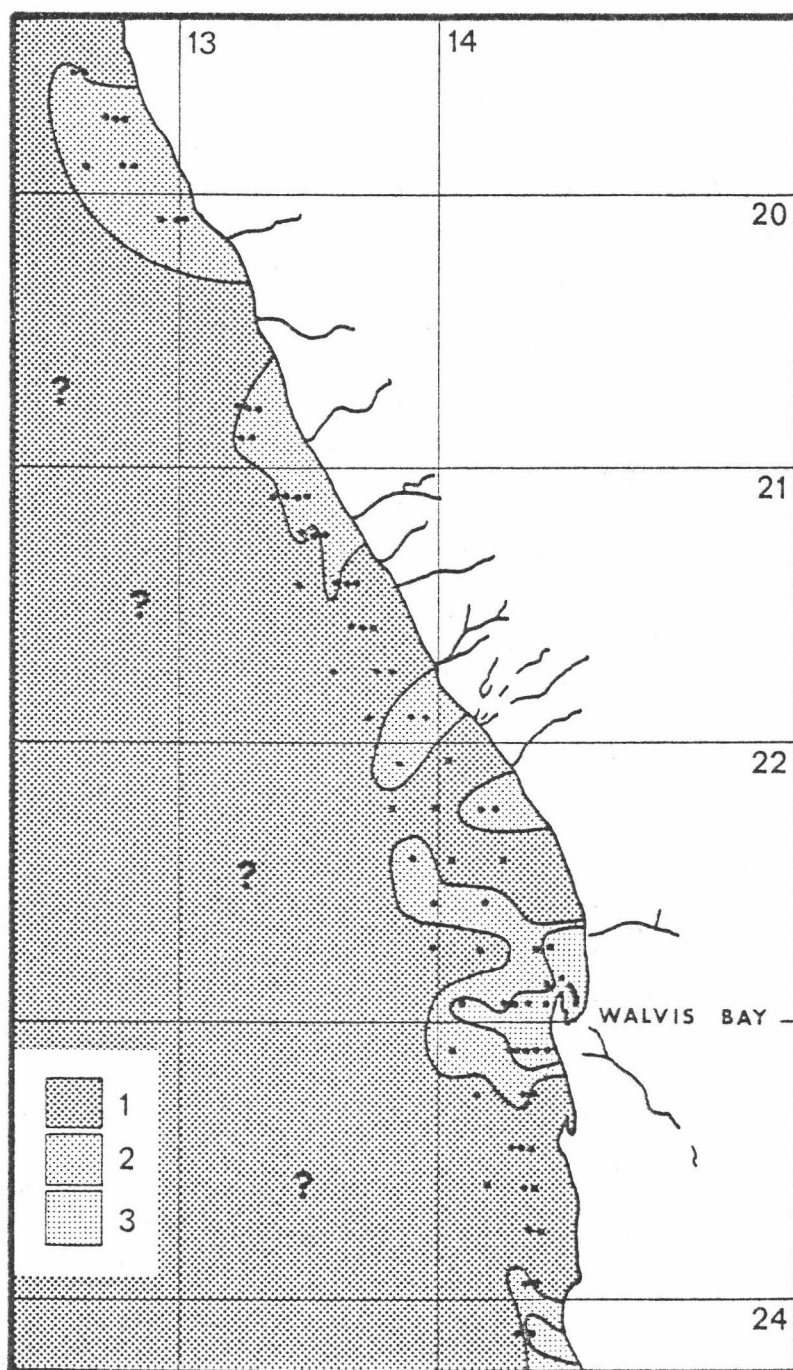
Figure 7: Distribution of relative abundance of _Chaetoceros_ resting
spores. 1: >70%. 2: 35-70%. 3: 18-35%.
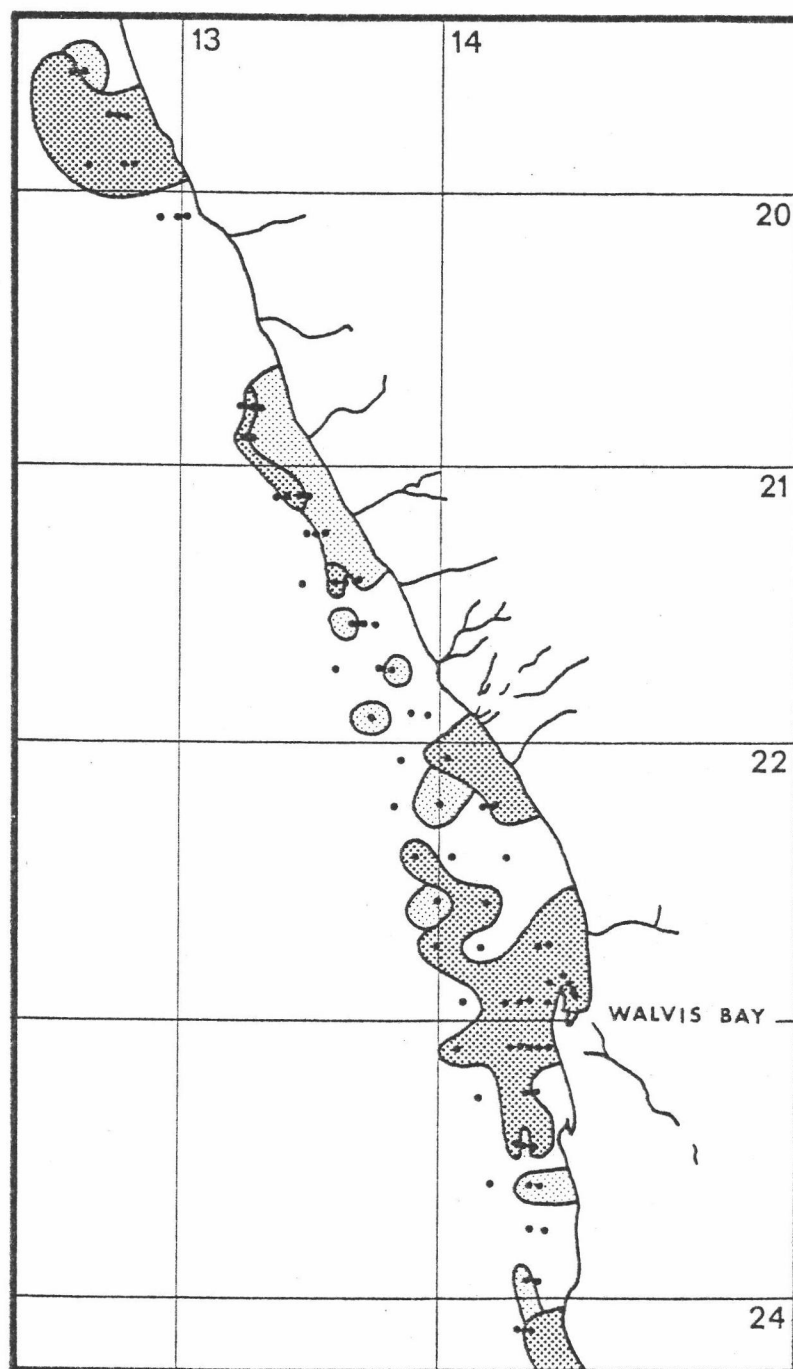
Figure 8:   Distribution of relative abundance of <u>Delphineis karstenii</u>.

Dark shading: ≥15%.   Light shading: 8-14%.   White: <8%.
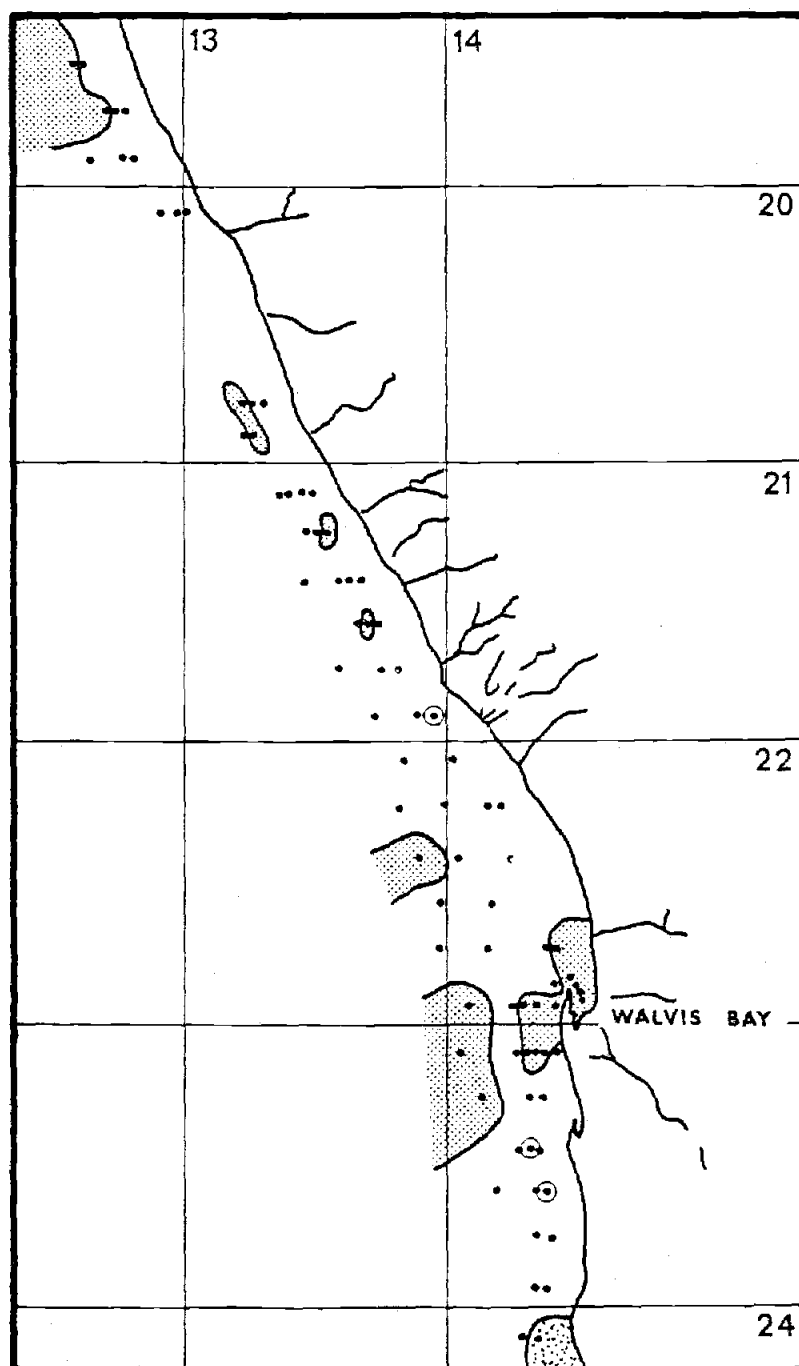
Figure 9: Distribution of relative abundance of <u>Thalassiosira</u>
<u>eccentrica</u> group. Shaded: >8%. Circled samples: absent.
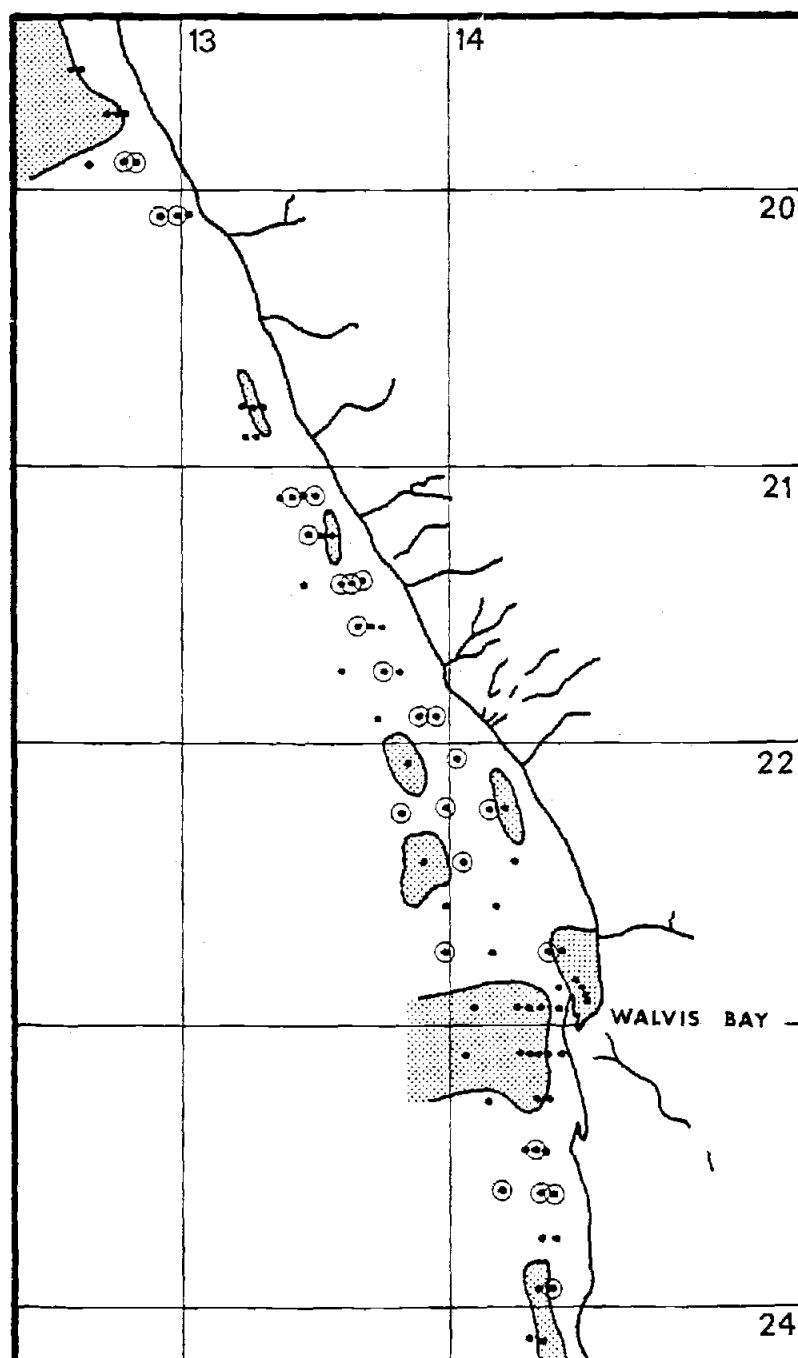
Figure 10: Distribution of relative abundance of Thalassionema
nitzschioides. Shaded areas: ≥5%. Circled samples: absent.
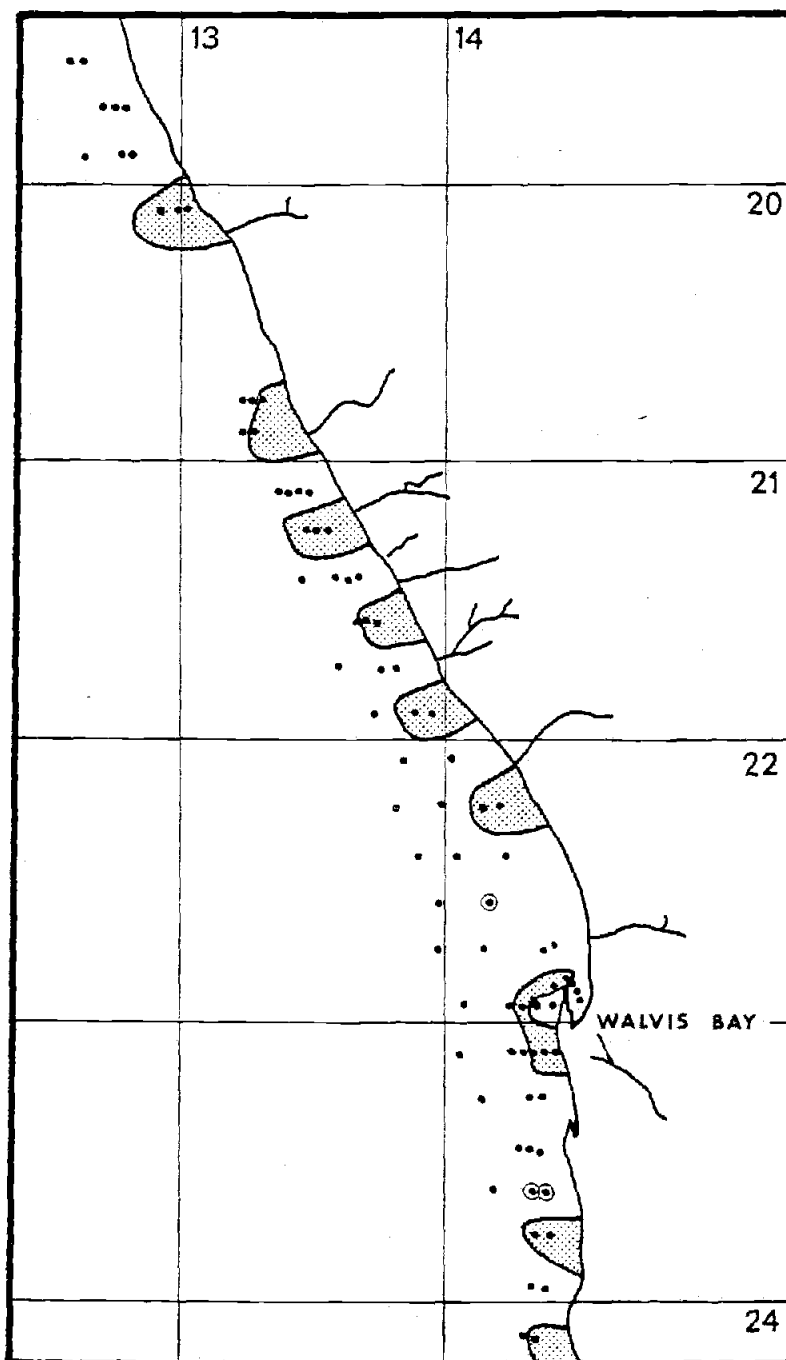
Figure 11: Distribution of relative abundance of <u>Actinocyclus</u>
<u>octonarius</u>. Shaded areas: ≥8%. Circled samples: absent.
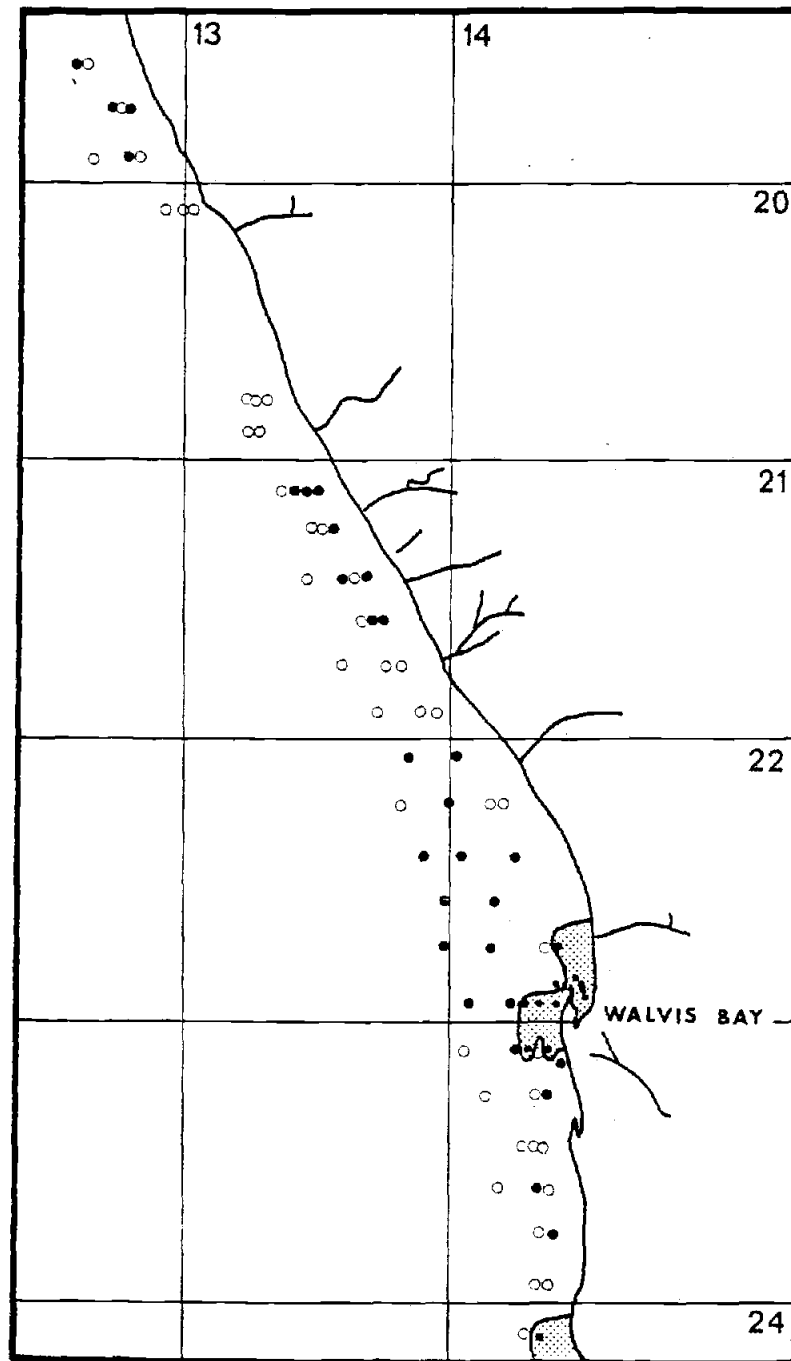
Figure 12: Distribution of relative abundance of Thalassiosira
aestivalis. Shaded areas: ≥2%. Closed circles: present. Open
circles: absent.
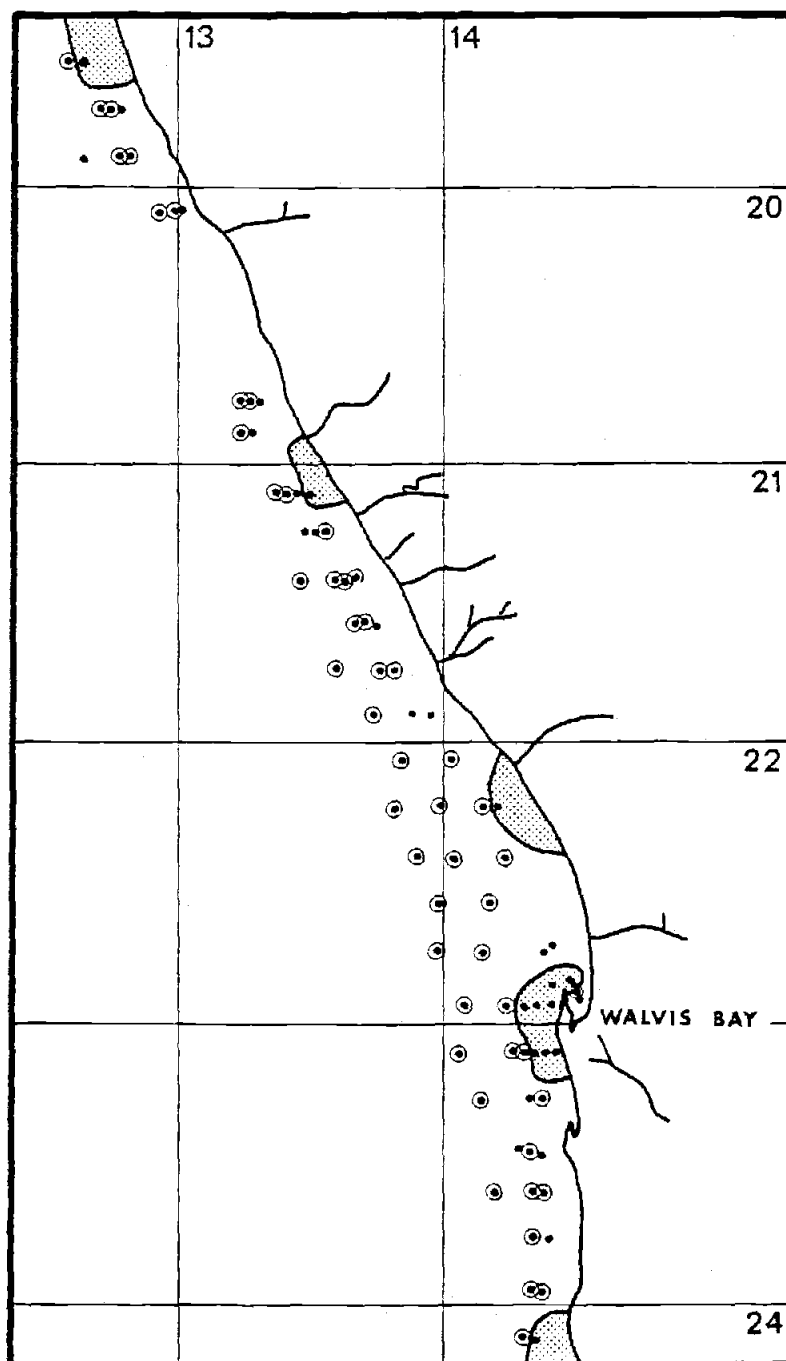
Figure 13:   Distribution of relative abundance of Paralia sulcata.

Shaded areas: ≥3%.   Circled samples: absent.

Figure 14: Distribution of Large Centrics Factor and of <u>Chaetoceros</u>-
<u>Delphineis</u> Factor. The Large Centrics Factor is correlated with
<u>Actinocyclus</u> <u>octonarius</u> and several <u>Coscinodiscus</u> species.
1: Positive factor loadings, Large Centrics Factor. The
<u>Chaetoceros</u>-<u>Delphineis</u> Factor is positively correlated with
<u>Delphineis</u> <u>karstenii</u> and <u>Paralia</u> <u>sulcata</u> and negatively with
<u>Chaetoceros</u> resting spores.
2: Positive factor loadings, <u>Chaetoceros</u>-<u>Delphineis</u> Factor.
3: Negative factor loadings, <u>Chaetoceros</u>-<u>Delphineis</u> Factor.
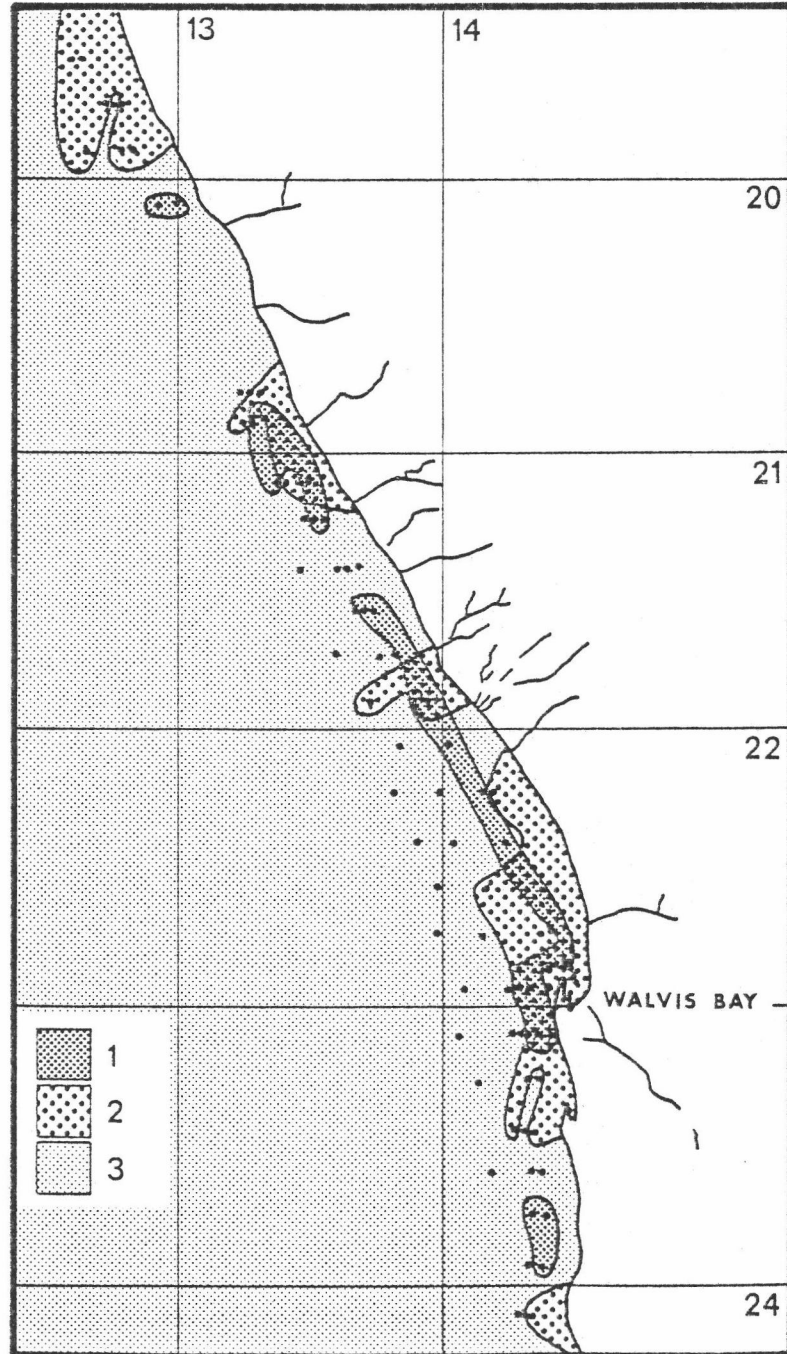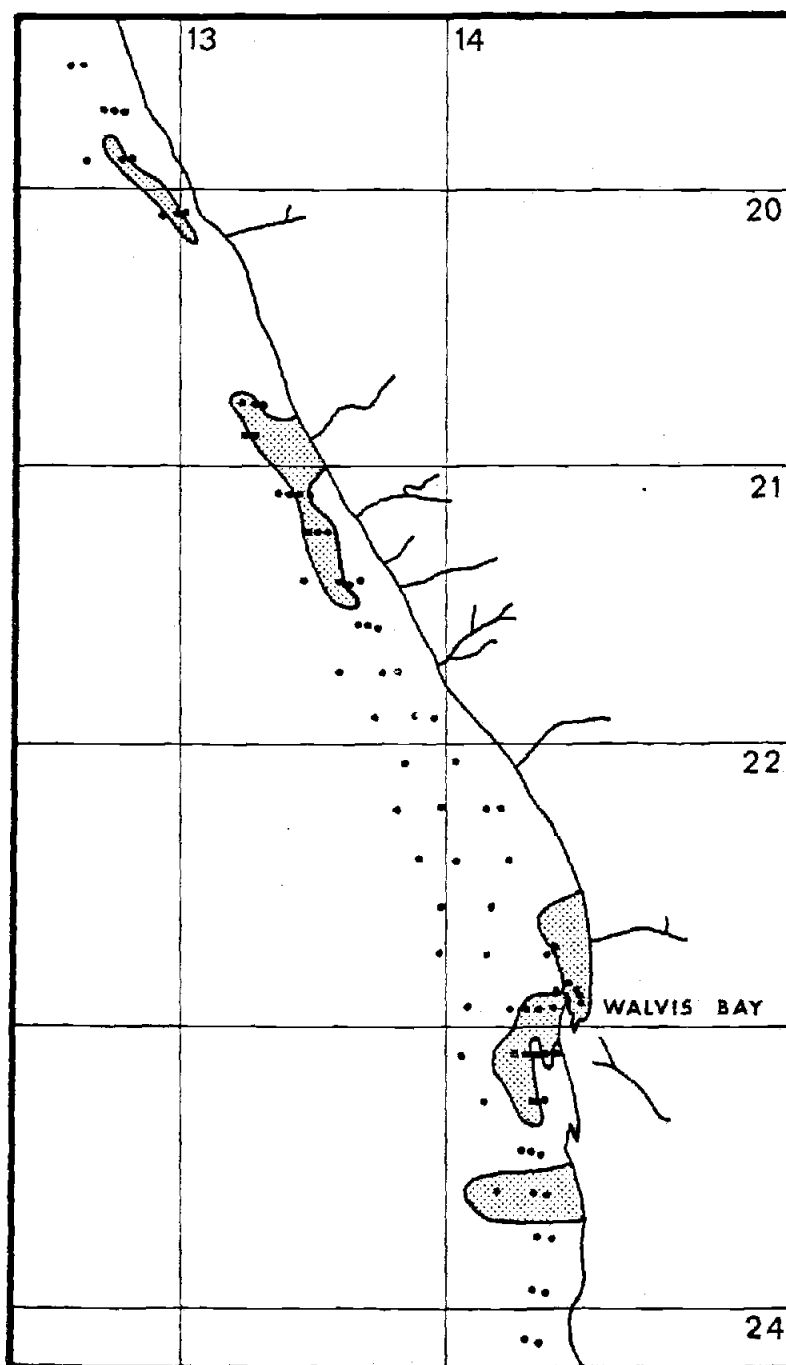
Figure 15:   Distribution of Thalassiosira Factor which is negatively
correlated with Thalassiosira aestivalis, Navicula spp. and
Thalassiosira eccentrica group.   Shaded areas: negative factor
loadings.
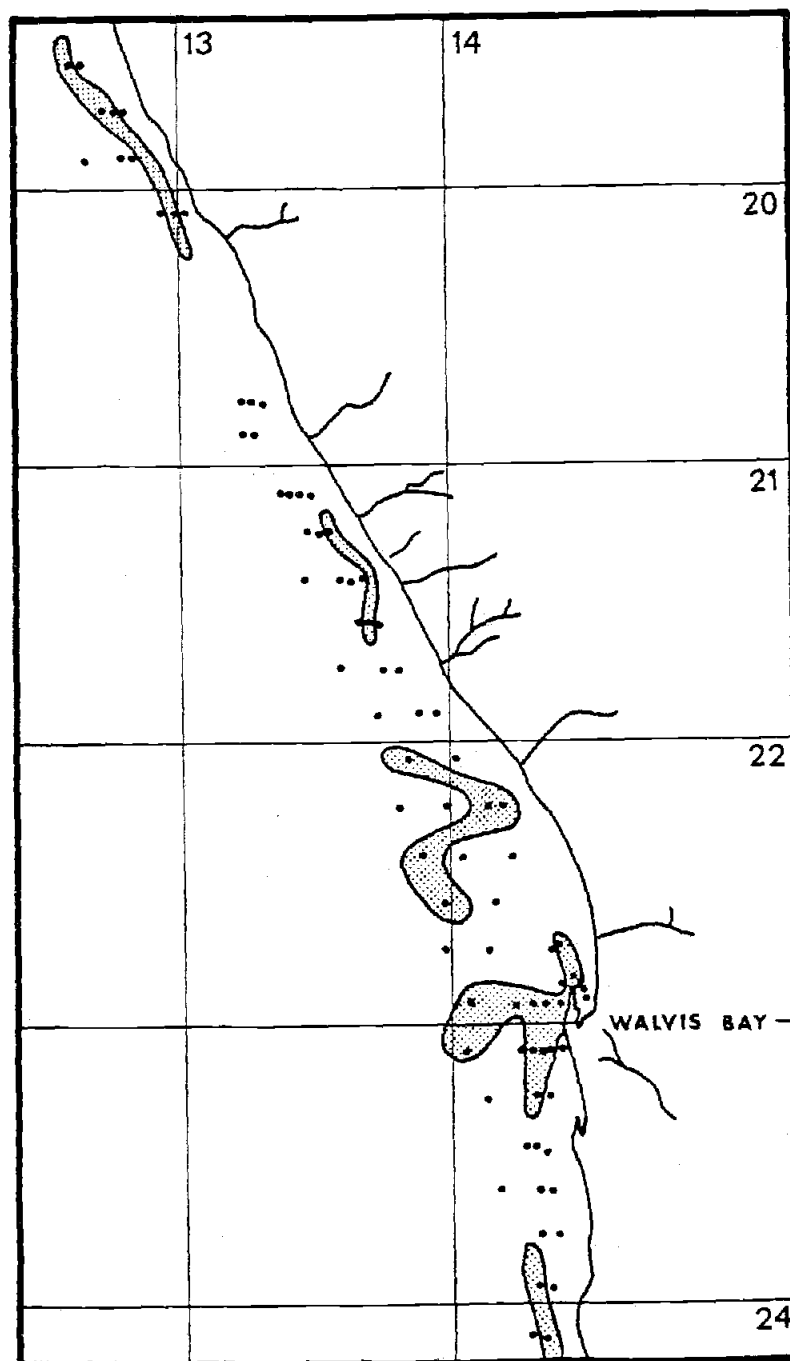
Figure 16: Distribution of Walvis Bay Factor which is positively correlated with Chaetoceros resting spores and negatively with Thalassionema nitzschioides. Shaded areas: negative factor loadings.
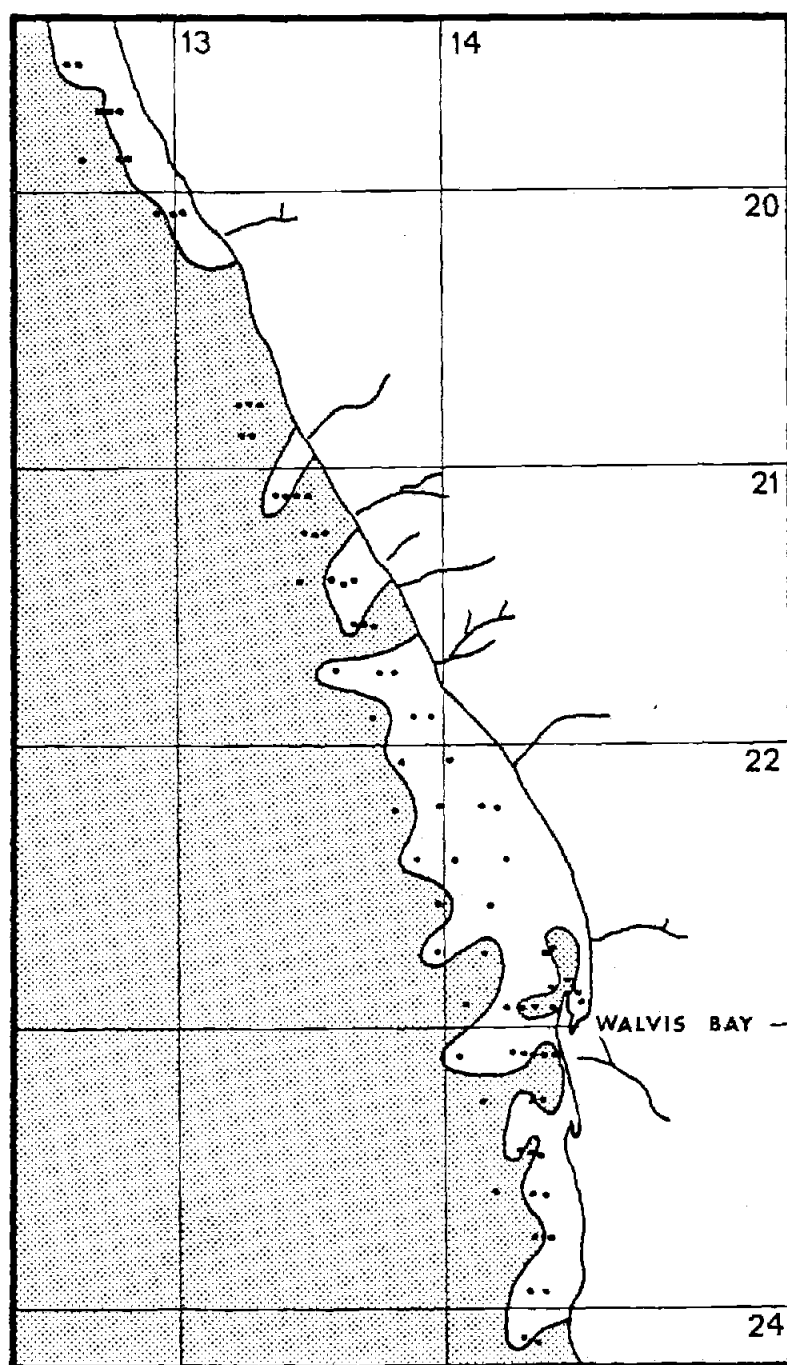
Figure 17: Distribution of C. radiatus Factor which is correlated
with Coscinodiscus radiatus, Actinocyclus curvatulus and
Thalassiosira lineata. Shaded areas: positive factor loadings.

Appendix A: Relative abundance of 41 species in 16 offshore sediment samples.

Sample no.	AOCT	ACUR	AELL	ASEN	ASPL	CHAE	CAFR	CAST	CCUR	CGIG	CNOO	CRAO	CPER	CONE
1	1.31	1.31	.58	.15	0.00	.87	4.07	0.00	2.62	0.00	5.52	0.00	0.00	1.16
5	.61	3.47	0.00	4.29	.41	7.35	.61	0.00	6.33	0.00	11.34	0.00	.82	0.00
6	1.51	3.46	0.00	2.16	2.59	1.51	2.59	0.00	8.21	0.00	14.25	0.00	.86	0.00
7	.88	3.54	0.00	17.70	.88	7.08	0.00	0.00	.88	0.00	49.56	0.00	0.00	0.00
8	2.86	.95	0.00	6.67	2.86	10.48	0.00	0.00	6.67	0.00	34.29	0.00	0.00	0.00
9	1.07	1.78	.36	7.83	9.25	2.85	0.00	0.00	2.85	0.00	42.35	0.00	.36	.71
17	5.88	4.04	0.00	1.47	0.00	2.94	.37	0.00	14.71	0.00	19.49	0.00	0.00	0.00
18	3.19	2.66	.27	2.39	0.00	1.06	1.33	0.00	10.11	.27	7.71	0.00	0.00	0.00
19	3.58	1.57	.67	1.57	.22	0.00	4.70	0.00	3.36	.22	25.95	0.00	0.00	0.00
20	.56	1.12	0.00	1.97	.56	.28	1.97	0.00	1.40	0.00	64.61	0.00	0.00	0.00
21	6.82	.45	1.36	.45	0.00	0.00	3.18	0.00	7.73	.45	22.27	0.00	0.00	0.00
27	3.98	1.33	0.00	3.98	.44	0.00	6.64	.44	1.77	0.00	22.12	0.00	0.00	0.00
30	1.66	.62	0.00	.62	.21	0.00	5.59	0.00	3.11	0.00	9.73	0.00	0.00	0.00
31	2.14	0.00	.53	.53	0.00	0.00	4.28	0.00	.53	0.00	10.16	0.00	0.00	0.00
35	.27	.82	0.00	0.00	0.00	0.00	5.75	0.00	1.37	0.00	0.00	.27	0.00	0.00
37	.66	.33	0.00	0.00	0.00	0.00	7.31	0.00	0.00	0.00	3.65	0.00	0.00	0.00

Sample no.	CTWO	DLPH	PSUL	TNIT	TECC	TDEC	TOES	TLIN	TALT	NAVI	NITZ	PLEU	RHIZ	RTES
1	0.00	0.00	0.00	14.39	14.10	0.00	4.36	.44	0.00	.44	1.74	.58	7.70	4.36
5	0.00	0.00	.41	3.27	29.80	.61	1.02	1.63	0.00	0.00	0.00	0.00	0.00	6.33
6	0.00	0.00	.86	3.02	17.28	0.00	1.30	1.30	.43	0.00	0.00	0.00	.86	8.64
7	0.00	.88	.88	0.00	3.54	0.00	5.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	0.00	2.86	11.43	0.00	2.86	0.00	.95	0.00	0.00	.95	0.00	1.90
9	1.07	.36	2.14	6.05	5.69	0.00	1.42	.36	.36	0.00	0.00	0.00	1.42	3.20
17	0.00	0.00	0.00	16.91	20.22	1.47	1.47	.74	0.00	0.00	0.00	0.00	1.10	3.31
18	0.00	0.00	0.00	13.03	16.22	2.39	1.60	3.19	0.00	0.00	0.00	0.00	1.60	7.98
19	0.00	0.00	0.00	5.59	4.47	.67	0.00	2.01	0.00	0.00	0.00	0.00	.45	12.75
20	0.00	0.00	0.00	.84	5.34	1.97	.28	.56	.28	0.00	0.00	0.00	.56	1.12
21	0.00	.45	0.00	5.45	2.18	2.27	0.00	3.18	0.00	0.00	0.00	0.00	1.36	3.18
27	0.00	0.00	0.00	8.85	10.18	0.00	2.21	3.54	0.00	0.00	0.00	0.00	.88	6.64
30	0.00	0.00	0.00	14.70	6.83	2.48	.21	1.24	0.00	0.00	1.04	0.00	.62	4.97
31	0.00	0.00	0.00	12.30	2.14	4.81	0.00	.53	.53	0.00	0.00	0.00	1.07	9.63
35	0.00	0.00	0.00	1.37	0.00	0.00	.82	0.00	0.00	0.00	0.00	0.00	.27	0.00
37	.33	0.00	0.00	.66	3.65	5.32	.33	2.66	0.00	0.00	.33	0.00	1.99	17.28

Sample no.	PDOL	UNCN	TRIC	ASTE	TNIP	CSTR	HCUN	TRIX	CLEN	TGRA	SCHI	NKER	EUCA
1	18.31	3.34	1.31	.73	5.09	1.74	1.31	2.47	0.00	0.00	0.00	0.00	0.00
5	11.43	3.06	0.00	.82	0.00	0.00	3.27	2.65	0.00	0.00	0.00	0.00	0.00
6	16.85	3.46	0.00	1.30	0.00	0.00	3.89	3.67	0.00	0.00	0.00	0.00	0.00
7	0.00	3.54	0.00	2.65	0.00	0.00	.88	1.77	0.00	0.00	0.00	0.00	0.00
8	6.67	6.67	0.00	0.00	0.00	.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	1.42	1.42	0.00	1.42	0.00	0.00	2.85	1.42	0.00	0.00	0.00	0.00	0.00
17	3.31	.74	0.00	.37	0.00	0.00	0.00	1.47	0.00	0.00	0.00	0.00	0.00
18	14.10	3.72	0.00	1.33	.53	0.00	1.33	3.99	0.00	0.00	0.00	0.00	0.00
19	15.44	8.05	.22	1.79	0.00	0.00	4.03	2.68	0.00	0.00	0.00	0.00	0.00
20	5.06	4.21	.28	1.40	0.00	0.00	3.37	.28	0.00	0.00	0.00	1.97	0.00
21	18.18	2.73	1.36	.45	2.73	0.00	4.55	2.73	0.00	0.00	0.00	.45	0.00
27	11.50	4.87	0.00	1.33	0.00	0.00	7.96	.88	0.00	0.00	0.00	.44	0.00
30	32.92	3.52	.41	.83	1.66	0.00	1.66	4.97	0.00	0.00	0.00	.41	0.00
31	33.69	6.42	1.07	0.00	0.00	0.00	6.42	3.21	0.00	0.00	0.00	0.00	0.00
35	0.00	0.00	0.00	1.10	0.00	0.00	0.00	2.47	16.44	.55	2.19	65.75	.55
37	36.54	5.98	0.00	.33	1.99	0.00	2.99	1.66	0.00	0.00	0.00	5.65	0.33

AOCT = Actinocyclus octonarius
ACUR = Actinocyclus curvatulus
AELL = Actinocyclus ellipticus
ASEN = Actinoptycnus senarius
ASPL = Actinoptychus splendens
ASTE = Asteromphalus spp
CHAE = Chaetoceros resting spores
CAFR = Coscinodiscus africanus + C. tabularis
CAST = Coscinodiscus asteromphalus
CCUR = Coscinodiscus curvatulus
CGIG = Coscinodiscus gigas
CNOD = Coscinodiscus nodulifer
CPER = Coscinodiscus perforatus
CRAD = Coscinodiscus radiatus

CONE = Coscinodiscus #1
CTWO = Coscinodiscus #2
CSTR = Cyclotella striata
DLPH = Delphineis karstenii
HCUN = Hemisdiscus cuneiformis
NAVI = Navicula spp.
NITZ = Nitzschia marina
PSUL = Paralia sulcata
PLEU = Pleurosigma spp.
PDOL = Pseudoeunotia doliolus
TRIC = Pseudotriceratium punctatum
RHIZ = Rhizosolenia bergonii
RTES = Roperia tesselata
TNIT = Thalassionema nitzschioides
TNIP = Thalassionema nitzschioides v. parva

TDEC = Thalassiosira decipiens
TECC = Thalassiosira eccentrica group
TLIN = Thalassiosira lineata
TOES = Thalassiosira oestrupii
TRIX = Thalassiothrix mediterranea/ longissima+frauenfeldii
TALT = Trigonium alternans
UNID = Unidentifiable diatoms
CLEN = Coscinodiscus lentiginosus
TGRA = Thalassiosira gracilis
SCHI = Schimperiella antarctica
NKER = Nitzschia kerguelensis
EUCA = Eucampia balaustium

Appendix 8: Relative abundance of 39 species in 82 inner shelf samples.

Sample No.	AOCT	ACUR	AELL	ASEN	ASPL	ABIP	CHAE	CAFR	CAST	CCUR	CGIG	CMAR	CNOO
1	1.69	1.69	.56	.19	0.00	0.00	49.72	0.00	.19	2.07	.19	.19	0.00
2	1.22	.24	0.00	.73	.24	0.00	75.10	0.00	.98	0.00	.24	0.00	1.71
3	2.10	1.26	0.00	.21	0.00	.21	50.00	0.00	0.00	1.05	0.00	0.00	0.00
4	.75	1.50	0.00	.38	0.00	0.00	40.71	0.00	0.00	.75	0.00	0.00	0.00
5	.91	.91	0.00	.30	0.00	-0.00	62.31	0.00	.91	.30	0.00	0.00	.30
6	3.23	.81	0.00	.81	0.00	0.00	59.30	0.00	0.00	.54	0.00	0.00	.27
7	3.07	3.26	0.00	0.00	0.00	0.00	56.22	0.00	.38	.58	0.00	.19	0.00
8	1.27	1.27	0.00	0.00	0.00	0.00	53.81	0.00	0.00	.25	0.00	0.00	0.00
9	9.49	1.28	0.00	0.00	0.00	0.00	68.21	0.00	.77	2.56	0.00	0.00	0.00
10	20.05	.27	0.00	.27	.27	0.00	43.96	0.00	13.19	.82	1.65	0.00	0.00
11	11.63	.33	0.00	.33	0.00	0.00	62.79	0.00	1.00	0.00	0.00	0.00	0.00
12	3.43	3.43	0.00	0.00	0.00	0.00	74.86	0.00	0.00	0.00	.29	0.00	0.00
13	5.19	1.37	0.00	.27	0.00	0.00	60.93	0.00	.27	.92	0.00	0.00	0.00
14	7.79	.56	0.00	.19	0.00	0.00	58.65	.19	1.30	.37	0.00	0.00	0.00
15	5.30	1.96	0.00	0.00	0.00	0.00	62.67	0.00	.20	1.18	0.00	0.00	0.00
16	7.75	1.55	0.00	.34	0.00	.17	59.55	0.00	.34	.34	.17	0.00	0.00
17	4.99	0.00	0.00	0.00	0.00	0.00	85.03	0.00	1.52	1.08	.65	0.00	0.00
18	1.38	1.10	0.00	.28	0.00	0.00	58.32	0.00	0.00	0.00	0.00	0.00	0.00
19	3.96	2.23	0.00	.25	0.00	.25	50.50	0.00	0.00	2.48	0.00	0.00	0.00
20	5.78	1.76	0.00	1.26	0.00	.50	64.57	0.00	1.26	1.01	.25	0.00	0.00
21	7.71	2.14	0.00	0.00	0.00	0.00	70.24	0.00	.64	.43	0.00	.43	0.00
22	12.62	1.55	0.00	.39	0.00	0.00	70.68	0.00	.78	.39	.19	0.00	0.00
23	9.91	.53	0.00	0.00	0.00	.27	44.83	0.00	.53	1.33	.27	0.00	0.00
24	5.16	2.21	0.00	.25	0.00	0.00	31.33	0.00	0.00	1.72	.25	0.00	0.00
25	.75	1.49	0.00	.15	0.00	0.00	69.96	0.00	0.00	1.49	0.00	0.00	0.00
26	4.22	.67	0.00	0.00	0.00	0.00	88.22	0.00	1.11	.44	.22	0.00	0.00
27	2.01	.91	0.00	0.00	0.00	0.00	81.93	0.00	0.00	1.46	0.00	0.00	0.00
28	.83	.28	0.00	.14	0.00	0.00	83.75	0.00	0.00	.41	0.00	0.00	0.00
29	7.56	.57	0.00	.19	0.00	0.00	72.21	0.00	.38	.75	.19	0.00	0.00
30	7.79	1.73	0.00	0.00	0.00	0.00	74.91	0.00	.35	.35	.35	0.00	0.00
31	1.16	.58	0.00	.29	0.00	0.00	80.23	0.00	0.00	1.74	0.00	0.00	0.00
32	1.15	.58	0.00	0.00	0.00	0.00	85.60	0.00	0.00	.38	.19	0.00	0.00
33	6.27	.63	0.00	.63	0.00	0.00	73.98	0.00	.53	.94	.31	0.00	.31
34	1.70	1.22	0.00	0.00	0.00	0.00	75.91	0.00	0.00	.73	0.00	0.00	0.00
35	16.81	.85	0.00	0.00	0.00	0.00	50.58	0.00	7.41	.57	1.71	0.00	0.00
36	27.39	0.00	0.00	0.00	0.00	0.00	51.70	0.00	3.72	.80	0.00	0.00	0.00
37	1.04	.41	0.00	0.00	0.00	0.00	58.80	0.00	0.00	1.56	0.00	0.00	0.00
38	4.64	0.00	0.00	0.00	0.00	0.00	72.39	0.00	2.99	1.16	1.16	0.00	0.00
39	1.52	1.21	0.00	.91	0.00	0.00	86.57	0.00	0.00	0.00	0.00	0.00	0.00
40	1.58	.12	0.00	.35	0.00	0.00	75.21	0.00	.12	.12	0.00	.24	0.00
41	32.00	.33	0.00	1.00	0.00	0.00	39.00	0.00	12.33	.67	3.00	0.00	0.00
42	3.76	1.18	0.00	.39	0.00	0.00	47.93	0.00	0.00	.30	0.00	.39	0.00
43	1.58	.88	0.00	.18	0.00	0.00	49.30	0.00	0.00	1.06	0.00	0.00	.18
44	1.56	.78	0.00	0.00	0.00	0.00	86.23	0.00	0.00	.52	.26	0.00	.26
45	5.03	.75	0.00	0.00	0.00	0.00	82.16	0.00	1.51	1.75	.50	0.00	.75
46	.56	2.92	0.00	.80	0.00	0.00	66.90	0.00	.13	3.32	0.00	0.00	.53
47	.36	.18	0.00	.18	0.00	0.00	50.55	0.00	0.00	1.27	0.00	0.00	0.00
48	.74	.49	0.00	.25	0.00	0.00	74.07	0.00	0.00	.49	0.00	0.00	.25
49	3.33	1.90	0.00	0.00	0.00	0.00	81.71	0.00	.24	.95	.24	0.00	1.19
50	1.01	0.00	0.00	.25	0.00	0.00	44.33	0.00	.25	.25	0.00	0.00	0.00
51	2.59	2.07	0.00	.26	.52	0.00	20.47	0.00	0.00	.78	0.00	0.00	0.00
52	7.91	.59	0.00	.20	0.00	0.00	42.29	0.00	.20	1.38	0.00	.20	.20
53	5.11	1.02	0.00	.25	0.00	0.00	21.12	0.00	.25	1.53	.25	0.00	0.00
54	1.59	.79	0.00	.26	.26	0.00	29.37	0.00	.26	.26	.53	0.00	.26
55	2.65	.53	0.00	0.00	0.00	0.00	32.10	0.00	.53	.27	0.00	0.00	.30
56	1.19	.45	0.00	.15	0.00	0.00	29.02	0.00	.45	.45	0.00	0.00	.89
57	2.32	1.30	0.00	.26	0.00	0.00	33.25	0.00	0.00	.52	0.00	0.00	0.00
58	.61	.81	0.00	0.00	0.00	0.00	56.30	0.00	.20	.61	.20	0.00	.20
59	11.53	1.33	0.00	.57	.22	0.00	25.28	0.00	.39	0.00	.89	0.00	0.00
60	7.36	.65	0.00	0.00	0.00	0.00	20.56	0.00	.87	.43	.22	.22	1.30
61	6.12	.93	0.00	.56	0.00	0.00	33.21	0.00	.74	.19	0.00	.37	.56
62	1.29	0.00	0.00	.22	0.00	0.00	51.08	0.00	0.00	.22	0.00	0.00	0.00
63	.68	.23	0.00	0.00	0.00	0.00	64.86	0.00	0.00	0.00	.23	0.00	0.00
64	.39	.58	0.00	.19	0.00	.19	22.82	0.00	0.00	.77	0.00	0.00	0.00
65	9.28	.32	0.00	.32	0.00	0.00	27.84	0.00	.48	.32	.48	0.00	0.00
66	14.71	1.23	0.00	.49	0.00	0.00	17.89	0.00	.98	.74	.98	0.00	0.00
67	28.65	.52	0.00	.26	0.00	0.00	19.79	0.00	1.30	1.04	.52	0.00	.26
68	1.25	.89	.18	.18	.18	0.00	74.06	0.00	0.00	4.11	0.00	0.00	.18
69	5.05	1.13	0.00	.76	0.00	0.00	47.07	0.00	.19	0.00	0.00	.19	0.00
70	7.02	1.17	0.00	.88	0.00	0.00	82.75	0.00	.29	0.00	.29	0.00	0.00
71	2.27	.68	0.00	0.00	.23	.45	70.68	0.00	0.00	0.00	0.00	0.00	0.00
72	.92	1.90	0.00	0.00	0.00	0.00	82.88	0.00	0.00	0.00	0.00	0.00	0.00
73	2.15	.24	0.00	0.00	0.00	0.00	72.25	0.00	0.00	.48	0.00	0.00	0.00
74	2.27	1.42	0.00	0.00	0.00	0.00	87.22	0.00	.28	0.00	0.00	0.00	.27
75	.48	.24	0.00	0.00	0.00	0.00	85.96	0.00	0.00	0.00	0.00	0.00	0.00
76	.57	.57	0.00	0.00	0.00	0.00	84.14	0.00	0.00	.57	0.00	0.00	0.00
77	7.99	1.48	0.00	0.00	0.00	0.00	30.77	0.00	.59	1.48	.59	0.00	0.00
78	11.14	.68	0.00	0.00	0.00	0.00	70.45	0.00	1.59	.23	.68	0.00	0.00
79	.72	.91	0.00	.18	0.00	0.00	61.23	0.00	0.00	0.00	0.00	0.00	0.00
80	2.36	.52	0.00	0.00	0.00	0.00	81.94	0.00	0.00	1.05	1.31	0.00	0.00
81	4.40	0.00	0.00	0.00	0.00	0.00	88.10	0.00	1.10	.18	.18	0.00	0.00
82	7.97	1.20	0.00	.60	.40	0.00	30.49	0.00	.80	.40	.20	1.59	1.20

AOCT = Actinocyclus octonarius
ACUR = Actinocyclus curvatulus
AELL = Actinocyclus ellipticus
ASEN = Actinoptychus senarius
ASPL = Actinoptychus splendens

ABIP = Actinoptychus bipunctatus
CHAE = Chaetoceros resting spores
CAFR = Coscinodiscus africanus
CAST = Coscinodiscus asteromphalus

CCUR = Coscinodiscus curvatulus
CGIG = Coscinodiscus gigas
CMAR = Coscinodiscus marginatus
CNOO = Coscinodiscus nodulifer

Appendix 8. (continued)

Sample No.	CRAD	CPER	CONE	OLPH	PSUL	TNIT	TECC	TDEC	TOES	TPLI	TAES	TLIN	TALT
1	.38	.56	0.00	25.05	.38	7.16	8.10	.19	0.00	0.00	.38	.56	.19
2	.98	0.00	0.00	3.54	3.90	1.71	2.68	.24	0.00	0.00	0.00	0.00	0.00
3	1.05	.42	0.00	23.74	0.00	8.19	10.50	.21	0.00	0.00	.42	0.00	.63
4	.19	0.00	0.00	25.89	.19	22.33	6.38	.19	0.00	0.00	0.00	0.00	0.00
5	.61	0.00	0.00	25.84	.61	1.82	3.65	0.00	0.00	0.00	.30	.30	0.00
6	1.08	.81	0.00	22.37	2.16	3.23	4.04	.27	0.00	0.00	0.00	0.00	0.00
7	1.73	0.00	0.00	16.31	0.00	.19	5.37	0.00	0.00	.38	.38	.19	.58
8	.51	.51	0.00	39.85	.25	.25	1.78	0.00	0.00	0.00	0.00	0.00	0.00
9	1.54	1.28	0.00	3.08	.26	.26	4.87	1.03	0.00	1.03	0.00	3.85	0.00
10	.27	5.77	0.00	6.04	.27	0.00	6.32	0.00	0.00	0.00	0.00	0.00	0.00
11	.33	1.33	0.00	8.31	1.33	4.32	4.98	1.33	0.00	0.00	0.00	.33	0.00
12	.86	0.00	0.00	.57	.29	1.14	8.29	.29	0.00	0.00	0.00	6.29	0.00
13	.55	.82	0.00	14.75	0.00	5.46	6.83	0.00	0.00	0.00	0.00	0.00	.82
14	1.11	0.00	0.00	11.69	1.67	.74	3.71	.93	.19	0.00	0.00	0.00	0.00
15	.98	.79	0.00	17.29	0.00	1.96	5.70	.20	0.00	.39	0.00	.20	.59
16	.69	2.93	0.00	11.53	1.03	1.33	8.95	0.00	0.00	.17	0.00	.69	.34
17	.22	.43	0.00	.87	.22	2.82	1.52	.22	0.00	0.00	0.00	0.00	0.00
18	.55	1.10	0.00	22.04	0.00	.28	3.03	0.00	0.00	.28	.28	0.00	0.00
19	.74	.99	0.00	28.47	2.23	.74	3.71	0.00	0.00	0.00	1.24	0.00	.50
20	1.76	2.01	0.00	7.54	5.03	0.00	4.02	.25	0.00	.25	.75	.75	.25
21	1.28	.86	0.00	6.21	1.07	.21	6.64	0.00	0.00	.21	0.00	1.28	.21
22	1.17	1.17	0.00	1.36	.97	.97	4.27	0.00	0.00	.39	0.00	.58	.58
23	1.33	0.00	0.00	10.08	.27	14.35	13.00	0.00	0.00	.27	1.33	.53	0.00
24	2.70	0.00	0.00	.25	0.00	1.23	3.69	0.00	.25	.25	0.00	.25	0.00
25	.15	.15	0.00	19.58	.30	.45	4.33	0.00	0.00	0.00	.15	.15	0.00
26	0.00	.67	0.00	1.33	.22	.22	2.44	0.00	0.00	0.00	0.00	0.00	0.00
27	.73	.18	0.00	8.21	.18	0.00	3.10	0.00	0.00	0.00	.36	0.00	.18
28	.28	.41	.14	8.40	.55	0.00	3.17	.55	.14	.14	0.00	0.00	.14
29	1.32	.38	0.00	2.84	.19	1.32	10.21	.19	0.00	.57	.57	0.00	.57
30	1.56	1.38	0.00	0.00	.69	1.56	6.92	.17	0.00	0.00	.35	0.00	1.04
31	0.00	.58	0.00	7.27	0.00	1.16	5.52	.29	.29	0.00	0.00	0.00	0.00
32	.38	0.00	0.00	6.33	.19	.38	4.41	0.00	0.00	.19	0.00	0.00	.19
33	.63	.31	0.00	10.03	.31	1.25	.94	.31	.31	0.00	0.00	.63	0.00
34	.73	.24	0.00	13.87	.49	1.46	3.41	0.00	0.00	0.00	0.00	0.00	0.00
35	.28	3.99	0.00	.85	1.99	.28	3.13	0.00	0.00	0.00	0.00	.85	0.00
36	.80	3.99	0.00	.27	.80	0.00	.53	0.00	0.00	0.00	0.00	0.00	0.00
37	.62	.21	0.00	7.04	.21	22.77	5.38	0.00	0.00	.62	.41	0.00	0.00
38	0.00	.23	0.00	15.55	0.00	.23	1.62	0.00	0.00	0.00	.23	0.00	0.00
39	.30	0.00	0.00	1.52	0.00	0.00	5.45	.91	0.00	0.00	0.00	.91	0.00
40	.12	.73	0.00	11.65	.12	.49	6.80	.61	0.00	0.00	.24	.12	.12
41	.33	9.00	0.00	0.00	.33	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
42	.30	1.78	0.00	17.75	3.25	10.06	4.73	.59	0.00	0.00	0.00	0.00	0.00
43	.18	0.00	0.00	14.61	.18	23.59	7.75	0.00	0.00	0.00	.18	0.00	0.00
44	0.00	1.04	0.00	6.23	.26	0.00	1.82	.26	0.00	0.00	.52	0.00	0.00
45	0.00	1.51	0.00	1.01	.50	1.01	2.01	.25	0.00	0.00	.25	.75	0.00
46	.93	.13	0.00	10.62	.27	4.52	6.37	.66	.27	0.00	.53	.40	.13
47	0.00	.18	0.00	39.45	.18	1.64	5.45	0.00	0.00	0.00	.18	.18	0.00
48	.25	0.00	0.00	18.52	0.00	0.00	1.98	.74	0.00	.25	.49	0.00	0.00
49	.71	.24	0.00	.48	.48	1.19	4.28	0.00	0.00	0.00	.48	0.00	1.43
50	.50	.25	0.00	49.37	.76	.25	2.02	0.00	0.00	0.00	0.00	.30	0.00
51	.52	.25	0.00	30.57	.78	15.28	21.24	1.55	0.00	0.00	1.55	0.00	0.00
52	.79	.99	0.00	32.21	3.75	1.58	4.74	.79	0.00	.40	.29	.20	0.00
53	.51	1.78	0.00	31.04	3.82	3.65	20.36	.25	0.00	0.00	1.78	0.00	0.00
54	.26	.26	0.00	37.57	.79	6.08	15.08	.53	.26	0.00	2.38	0.00	0.00
55	0.00	.27	0.00	24.14	.53	7.16	15.92	.30	.53	0.00	10.34	.27	0.00
56	.15	.45	0.00	42.71	1.04	5.80	9.82	.15	.15	0.00	2.83	.30	.30
57	.25	.52	0.00	9.79	.26	29.38	18.30	.77	.26	.26	1.03	.26	0.00
58	0.00	0.00	0.00	18.70	.20	13.62	7.11	0.00	0.00	0.00	.41	0.00	0.00
59	3.33	2.66	0.00	17.52	2.88	5.54	23.29	.44	0.00	0.00	2.44	0.00	0.00
60	.22	.87	0.00	20.56	5.41	10.61	21.00	.22	0.00	0.00	7.14	0.00	0.00
61	1.11	.93	0.00	31.54	3.90	3.90	11.69	.93	0.00	0.00	1.86	0.00	0.00
62	.66	.22	0.00	17.46	0.00	20.04	7.76	0.00	0.00	0.00	0.00	0.00	0.00
63	.23	0.00	0.00	22.97	.23	4.05	4.95	0.00	0.00	0.00	.68	0.00	0.00
64	.19	0.00	0.00	23.79	.39	11.41	30.75	.19	0.00	0.00	6.96	0.00	0.00
65	1.12	1.28	0.00	33.44	3.04	13.44	8.00	.32	0.00	0.00	0.00	0.00	0.00
66	.98	4.17	0.00	21.81	2.70	7.60	19.85	1.23	0.00	0.00	2.21	.25	0.00
67	.62	4.69	0.00	23.70	10.94	2.34	3.91	.26	0.00	0.00	.26	0.00	0.00
68	1.25	0.00	0.00	.89	0.00	1.61	10.91	.36	0.00	.89	0.00	2.68	.18
69	.19	.76	0.00	21.17	.75	15.69	4.91	.19	0.00	0.00	0.00	0.00	0.00
70	.58	0.00	.29	.88	.29	1.17	3.51	0.00	.29	0.00	.29	0.00	0.00
71	0.00	.23	0.00	15.45	1.82	1.36	4.09	1.82	0.00	.45	0.00	0.00	0.00
72	.27	.27	0.00	12.50	.27	0.00	0.00	.27	0.00	0.00	0.00	0.00	0.00
73	0.00	0.00	0.00	20.81	.72	.72	1.67	0.00	.24	.24	0.00	0.00	0.00
74	1.14	0.00	0.00	.28	0.00	.57	2.56	.28	.28	.28	0.00	2.84	0.00
75	0.00	0.00	0.00	10.41	.24	0.00	.97	.24	0.00	0.00	.24	0.00	0.00
76	0.00	.28	0.00	11.90	0.00	.28	.28	0.00	0.00	0.00	0.00	0.00	0.00
77	.59	1.18	0.00	.89	.59	1.48	2.07	0.00	0.00	.30	0.00	0.00	0.00
78	.45	1.36	0.00	4.32	.91	2.95	3.18	1.14	0.00	0.00	.45	0.00	0.00
79	.36	0.00	0.00	8.88	.18	20.47	5.62	.36	.36	0.00	0.00	0.00	0.00
80	.26	1.57	0.00	4.71	.26	.52	4.97	.26	0.00	0.00	0.00	0.00	0.00
81	0.00	.92	0.00	1.47	.18	1.47	1.28	.37	0.00	0.00	0.00	0.00	0.00
82	1.20	1.00	0.00	21.91	5.78	6.57	11.75	1.39	1.00	.20	1.59	.40	0.00

CRAD = Coscinodiscus radiatus   TNIT = Thalassionema nitzschioides   TPLI = Thalassiosira plicata
CPER = Coscinodiscus perforatus   TECC = Thalassiosira eccentrica group   TAES = Thalassiosira aestivalis
CONE = Coscinodiscus #1   TDEC = Thalassiosira decipiens   TLIN = Thalassiosira lineata
OLPH = Delphineis karstenii   TOES = Thalassiosira oestrupii   TALT = Trigonium alternans
PSUL = Paralia sulcata

Appendix 8. (continued)

Sample No.	NAVI	NITZ	PLEU	RHIZ	PSOL	TIRA	TRIX	HCUN	ASTE	POOL	RTES	TRAC	STEP
1	.19	0.00	.19	.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	.24	0.00	.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5	0.00	.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	.27	0.00	0.00	0.00	.54	.27	0.00	0.00	0.00	0.00	0.00
7	.77	0.00	.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	0.00	0.00	.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	0.00	0.00	.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	0.00	0.00	0.00	.33	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
12	0.00	0.00	.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
13	1.37	.27	.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
14	.37	0.00	.19	.19	.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
15	.20	0.00	.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16	.69	0.00	1.55	0.00	.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17	0.00	0.00	.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
18	0.00	0.00	.83	0.00	0.00	0.00	.28	0.00	0.00	0.00	0.00	.28	0.00
19	1.24	0.00	.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
20	.25	0.00	.25	0.00	0.00	0.00	0.00	0.00	.50	0.00	0.00	0.00	0.00
21	.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22	.73	0.00	1.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
23	.53	0.00	.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.25	0.00	0.00	0.00	.25
25	.45	.15	0.00	0.00	0.00	0.00	.15	0.00	.25	0.00	0.00	0.00	0.00
26	0.00	0.00	.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27	.36	0.00	0.00	0.00	0.00	0.00	.18	0.00	0.00	.18	0.00	0.00	0.00
28	.55	0.00	.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	.35	0.00	.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
31	.29	0.00	.29	0.00	0.00	.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00
32	0.00	0.00	.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
33	.31	0.00	.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.53	0.00	.31
34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
35	0.00	0.00	.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
37	0.00	.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
38	0.00	0.00	.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
39	0.00	.30	0.00	0.00	.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
40	0.00	0.00	.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.12	0.00	0.00
41	0.00	0.00	.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.33	0.00	0.00
42	.30	0.00	0.00	0.00	.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
43	.18	0.00	.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.26	0.00	0.00	0.00	0.00
45	.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
47	.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
48	1.23	0.00	.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
49	.48	0.00	.48	0.00	0.00	0.00	0.00	0.00	.24	0.00	0.00	0.00	0.00
50	0.00	.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
51	.78	.52	.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
52	.20	0.00	.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
53	.51	0.00	.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
54	2.65	.25	.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
55	2.39	0.00	.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
56	2.38	.50	.15	0.00	.15	0.00	0.00	0.00	.15	0.00	0.00	0.00	.30
57	0.00	.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
58	.51	.20	.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
59	.22	.22	.44	.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
60	.55	.22	1.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
61	.37	.56	.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
62	.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.43	0.00	0.00	0.00
63	.45	0.00	.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
64	.77	0.00	.39	0.00	.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
65	0.00	0.00	.16	0.00	.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
66	.25	0.00	1.23	0.00	.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
67	.52	0.00	.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.18	0.00	0.00	0.00	0.00
69	.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
70	0.00	0.00	.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
71	.23	0.00	.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
72	.27	0.00	.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
73	0.00	0.00	.24	0.00	.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
74	.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
75	.97	0.00	.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
76	1.13	0.00	0.00	0.00	.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
78	.23	0.00	.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
79	.54	.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
80	0.00	0.00	.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
81	0.00	0.00	.18	.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
82	.20	0.00	1.00	.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.20	0.00

NAVI = Navicula spp.
NITZ = Nitzschia bicapitata
PLEU = Pleurosigma normanii
RHIZ = Rhizosolenia styliformis
PSOL = Planktoniella sol

TIRA = Thalassiosira #1
TRIX = Thalassiothrix longissima
HCUN = Hemidiscus cuneiformis
ASTE = Asteromphalus heptactis

POOL = Pseudoeunotia doliolus
RTES = Roperia tesselata
TRAC = Trachyneis aspera
STEP = Stephanopyxis turris

CHAPTER III

DIATOM TAPHOCOENOSES: THE REFLECTION OF COASTAL UPWELLING

by

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Abstract

Recent sediment diatom assemblages influenced by overlying strong coastal upwelling processes off Peru, off South West Africa and within the central Gulf of California can be differentiated from adjacent oceanic regimes by: 1) abundant remains of well-preserved diatoms, 2) occurrence of very weakly silicified species, 3) high percentages of meroplanktic species and species groups, and 4) coherent distribution patterns for distinct diatom assemblages.

Diatom floral analysis of sediment surface samples from off South West
Africa was undertaken in order to identify in the sediments the in-
fluence of coastal upwelling. A previous study off Peru (Schuette
and Schrader, 1979) provided a distinction between upwelling and
non-upwelling-influenced diatom taphocoenoses and an identification
of several locations off Peru where the diatom sediment signal was
interpreted as recording intense recurrent coastal upwelling. The
analysis of the remains of primary producers (opal phytoplankters)
in sediment samples underlying these regions provides a summary record
of primary productivity during the period of deposition of each sample.
The data, abundance of diatom valves and diatom species composition,
form an incomplete record of the surface water biota (because of
dissolution during sedimentation or because of mechanical destruction
of valves by predation). Where preservation is good, however, the
data do complement because of their time-averaged nature, surface
water hydrographic measurements and biological counts, which even in
the most labor and instrument intensive studies must be spot checked
on an every changing process. The South West Africa study thus was
undertaken to continue the documentation of opaline floral composition
in sediments of upwelling areas and to contribute to the general under-
standing of upwelling ecosystems. An additional aim was to provide
further characterization of recent (surface) upwelling-influenced
sediments to assist recognition of recurrent coastal upwelling in
ancient diatomaceous sediments (such as those found in the Monterey
and Calvert Formations, for example). A pilot study of cores collected
in the Central Gulf of California (DSDP Leg 64 Site 480 and cores from

the 1979 cruise of the LAMAS project (OSU)) was undertaken simul-
taneously with the South West Africa study. The purpose of the pilot
study was to verify the usefulness of the characterization of
upwelling-influenced sediments in deposits where the results of
alternating upwelling and nonupwelling seasons are recorded in lami-
nated sediments.

The influence of coastal upwelling is reflected in sediment opal
phytoplankton assemblages off both Peru and South West Africa by:
1) abundant remains of well-preserved diatoms, 2) high percentages
of diatom species and species groups that we suggest are characteristic
of coastal upwelling, and 3) coherent distribution patterns for
distinct diatom assemblages. The sediment signals off Peru and off
South West Africa do differ however, and reflect differences in the
hydrographic regimes of the two areas.

The samples from off South West Africa consisted of two sets:
1) 82 diatom-rich inner shelf samples, and 2) 39 offshore South East
Atlantic samples, 16 of which had sufficient preservation of opal
phytoplankton to allow counts of species abundance. The inner shelf
samples were provided by J.M. Bremner, Marine Geology Unit, Department
of Geology, University of Cape Town. The South East Atlantic samples
were provided by N. Kipp or were collected from the core repositories
of Lamont-Doherty and the School of Oceanography, Oregon State
University.

Slide preparation followed the procedure outlined in Schrader
(1974) and Schrader and Gersonde (1978). Counting procedures followed

the recommendations of Schrader and Gersonde (1978). More than 300
valves were counted per slide. The locations of the offshore sites
and the complete data results of these studies can be found in the
previous Chapter (II).

Abundance of Well Preserved Diatom Valves in Sediments

The coastal upwelling phenomenon results in both regions in the
intense production of diatoms throughout much of the year (Hart and
Currie, 1960, Rojas de Mendiola, 1980 and pers. comm.). This
recurring or quasi-constant production of diatoms results in high
supply of diatom valves to the sea floor. In coastal areas lacking
strong quasi-constant upwelling, diatoms are usually completely
dissolved; whereas, they are extremely abundant in continental slope
and shelf sediments underlying strong coastal upwelling (Diester-
Haass and Schrader, 1979). High supply, perhaps supplemented by
preservational transfer of valves to deeper sites by fecal pellets,
and the high sedimentation rates of these fertile areas, favor
sediments rich in well preserved diatom valves (Berger, 1976).

Off South West Africa the horizontal distributions of temperature
and salinity, especially in winter and spring, show strong temperature
gradients and the presence of a conspicuous belt of cold upwelled water
adjacent to the coast from about 26°S to Walvis Bay (Stander, 1964).
Phytoplankton surveys have characterized the outstanding biological
feature of the South West African region as a contrast in densities
between "coastal" and "oceanic" populations of phytoplankton, with
densities differing by 3-4 orders of magnitude (Hart and Currie, 1960).
Primary productivity values show the same contrast, with values of up

to 1600 mg $C/m^2/$ day along the coast. In regions further removed from the coast, values were less than 200 mg $C/m^2/$ day (Mukhina, 1974). In their analysis of a characteristically active period of upwelling, Hart and Currie (1960) reported the greatest quantity of phytoplankton close to the coast between 24 and 26°S. On this survey the rich coastal floral was confined to nearshore stations, with an abrupt drop in numbers before the shelf edge. Hart and Currie also collected within the coastal region isolated samples which were relatively poor in phytoplankton. Hydrological observations showed that these poor catches were due to tongue-like intrusions of more oceanic surface-water with inherently poorer plankton content. Kollmer (1962, 1963) from data collected in and near Walvis Bay documents the high concentrations of diatoms in the formation of blooms which have a patchy appearance. He also describes the average annual phytoplankton stock of 1959 as having a regular distribution around a center 40 miles north of Walvis Bay. In recent surveys by the Sea Fisheries Branch of South Africa the richest phytoplankton concentrations have been found in a "so-called belt (although patchy) parallel to the coast" (Cram, 1978).

Sediments rich in diatom remains constitute a record of this nearshore zone of recurrent high primary productivity. Marchand (1928), Hart and Currie (1960), Calvert and Price (1970, 1971) and Mukhina (1974) have reported an area of diatomaceous mud extending principally from 21°30' to about 25°S, and extending, patchily at least, north to 17°30'. The seaward edge of the diatomaceous silts may not

go beyond the 150 m isobath (Hart and Currie, 1960; Mukhina, 1974).
Maximum concentrations of diatoms, 300-820 million valves/g dry
sediment are in sediments of a narrow band, embracing in depths 70-120 m
(Mukhina, 1974). Sediments lying closer to the shore and further to
the side of the open sea of the rich zone contain significantly fewer
diatoms (from 100-300 million valves/g dry sediment). Samples with
less than 100 million valves/g lie out of the zone of high opal accumu-
lation: to the north of 18°S, in a narrow coastal strip, and in a few
isolated stations (Mukhina, 1974). Abundance values calculated for
our samples (Richert, 1976) also show three main distribution zones
(Figure 1): 1) the very nearshore (water depths below 80 m) with less
than 50×10^6 diatom valves/mg sediment, 2) a zone of highest abun-
dance of diatom remains (water depths from 90-130 m) with $50-150 \times 10^6$
diatom valves/mg sediment and, 3) an "offshore" zone (water depths about
140 m) with less than 50×10^6 valves/mg sediment. This sediment
surface distribution with highest values occurring in samples from
Walvis Bay and in a band north to about 21°30'S and south past 24°S
is thus well correlated with the reports of phytoplankton distribution
in the surface waters.

The relatively small quantity of diatoms in sediments closest to
shore may be due to dissolution of the thinly silicified frustules of
a number of meroplanktic diatoms. Dilution of diatoms by terrigenous
material is probably negligible since the continental shelf is bordered
by the almost rainless Namib desert, and the rivers draining the desert
are small and flow intermittently (Calvert and Price, 1971). Although
selective dissolution may account for the lower values nearshore,

alternatively, the total annual production may indeed be lower at sites close to shore where "unconditioned" or "not yet seeded" waters recurrently upwell. The relatively higher values between about 70-130 m water depth may also be related to high percentages of large and solution resistant species in the phytoplankton of this region (see discussion of characteristic species below).

The features noted off South West Africa with regard to phytoplankton concentrations, primary productivity values, and the sediment reflection of high productivity are also observed off Peru (Schuette and Schrader, 1979) (Figure 2). Firstly, there is again a contrast in densities of phytoplankton, in primary productivity (Guillen and Calienes, 1976), and in abundances of diatom remains in sediments, between the "coastal" and "oceanic" settings. Secondly, there is variability in the surface waters within the region of generally high productivity (Guillen, Rojas de Mendiola, and Izaguirre de Rondan, 1971, 1973; Zuta, Rivera and Bustamante, 1978) and correspondingly, there is, at least off Peru, a sinuous seaward boundary for the abundance values in sediment surface samples. Finally, there is some localization of highest values, sites of recurrent high diatom concentrations and/or productivity (Rojas de Mendiola, 1980; Zuta et al., 1978), and, in the sediments influenced by this pattern, zones or centers of highest abundance of valves. Off Peru highest values occur in more or less discrete regions laterally offset from the coast (in addition to a nearshore area at 12°S). The offshore centers of upwelling influence (water depths 2000-3600 m) occur at about 8°S,

13-14°S and 17°S and perhaps bear a relationship both to the areas of major concentrations of phytoplankton where upwelling takes place within 60 miles of the coast (Rojas de Mendiola, 1980), and to observations of tongues of upwelled water extending 70-130 miles offshore (Zuta et al., 1978).

Some similarities in the sediment signals for coastal upwelling off Peru and off South West Africa have been suggested. Differences in the offshore boundaries of the sediment records correspond with reported surface water limits of cold nutrient rich waters in the respective regions. Both regions are characterized by the eddy-like structures of surface isotherms, but a striking feature of the Peru Current region which distinguishes it from the Benguela Current region is the very large apparent extent of the eddies (Hart and Currie, 1960). The small absolute (and relative to the mean) variance in the wind off Peru, where local winds are weak and of short duration (Smith, 1978), contrasts with the wind regime over innershelf waters off South West Africa. Nearshore waters are subject here to the effects of coastal winds superimposed upon the processes induced by the trade winds (Hart and Currie, 1960; Stander, 1963). The local winds because of their variability may either augment or suppress upwelling (Stander, 1963). The resulting intermittent process may contribute to the high primary productivity of the region by frequent reinitiation of bloom conditions. The narrow shelf and steep slope off Peru contrasts with the broad shelf off South West Africa. The observed differences in the extent, intensity and variability of the upwelling influence on the

sediment record may also be related to this contrast. Doubtless the shallow depositional environment off South West Africa enhances diatom preservation. The initial patch or tongue-like structure of upwelled waters may be preserved in the species composition of sediments off South West Africa (see discussion of distribution patterns below) as it is off Peru. But the limited offshore extension of the diatom rich surface waters (and the shallow depositional environment) may restrict the signal of accumulated remains in the sediments into a band-like distribution. This is in contrast to the extended lobes represented off Peru.

Cores collected near Guaymas by DSDP Leg 64, and collected from the circum-central basin by the 1979 cruise of the LAMAS project (OSU), contain laminated sediments, some of which are nearly pure diatom ooze (Schrader et al., 1980; Schrader, 1979). Preliminary examination of box core material suggests that the areas of intense seasonal upwelling and phytoplankton concentration provide an associated record to sediments. In addition, the abundance of diatoms may vary from 70-80% in one lamina to 15-45% in an adjacent lamina presumably recording a seasonal cycle of primary productivity (Schrader et al., 1980). The preservation in laminae with a coastal upwelling flora of weakly silicified diatoms and even of the delicate bristles of _Chaetoceros radicans_ is extraordinary and must bear a relationship to extremely high primary productivity (and to rapid and preservational burial) at these sites in the central Gulf. The known sediment record for the genus _Chaetoceros_ is predominantly in the form of the robust resting spores.

Dissolution may selectively destroy valves of some species more readily than others, as mentioned above, and thus increase the relative abundance in sediments of solution resistant forms. Also, partial dissolution of fine structures may render species identifications tentative, primarily, e.g., within the genus Chaetoceros and the genus Bacteriastrum. The preservation of dissolution sensitive forms, or, in other words, a high correspondence between surface water assemblages and sediment assemblages is characteristic of the coastal upwelling areas (Diester Haass and Schrader, 1979).

Well preserved diatom frustules dominate the siliceous fraction of nearshore samples off South West Africa. Preservation of those species which dominate the surface waters indicates little transformation of biocoenoses to taphocoenoses in these shallow waters. Dissolution of less strongly silicified forms undoubtedly is responsible for differences between the composition of bottom deposits and the average composition of the plankton (Hart and Currie, 1960), but enrichment in large species in some samples may also reflect surface water proliferation of these forms (see discussion below on characteristic species). A high correspondence in composition and relative abundance patterns for diatoms in plankton samples and in stomachs and guts of anchovy and pilchard has been reported (King and Macleod, 1976), and our sediment samples from in and near Walvis Bay preserve a similar relative abundance pattern for the two species which dominate the sediment samples as they do the surface waters above (Table I).

Further offshore, in the low productivity, non-upwelling, oceanic regime, low supply results in many samples barren in opal phytoplankton

(as was also the case off Peru (Schuette and Schrader, 1979). In
addition, there are samples with a high percentage (sometimes 3-4%)
of unidentifiable forms, and all samples are strongly enriched in
robust forms that may be rare in surface waters (e.g., Coscinodiscus
nodulifer).

Off Peru, diverse assemblages are preserved at thousands of
meters of water depth. There is however an enrichment in the sediment
assemblages of species which have not been reported as dominant in
phytoplankton assemblages. Heavy silicification of the valves of
these diatoms accounts for the presence and abundance in sediments of
these robust species. The preservation at deep sites of Skeletonema
costatum, a dissolution sensitive species, is additional testimony of
abundant supply in certain locations. Although a very common pelagic
diatom, frequently associated with a coastal flora (Hendey, 1964),
and previously reported as a dominant species off Peru (Calienes and
Guillen, 1976; Rojas de Mendiola, 1980), Skeletonema costatum is rare
in our sediment samples. But the presence of specimens below 3000
meters of water is remarkable and must be due to enhanced preservation
in these locations.

Characteristic Species and Species Groups

The criteria for adjudging a species or species group as charac-
teristic of coastal upwelling are several. Of course, species with
known abundance in the sediments are candidates. But, species with
high relative abundance in the sediments were considered characteristic
also because their distribution in the sediments shows a relationship

either to the dynamics of coastal upwelling (in so far as they are understood by lapsed biologists-quasi-geologists) or to theories or observations of the biological response to nutrient enrichment. Secondly, the data matrix of the relative abundance of species (16 select species categories off South West Africa) at the sample sites (82 sites off South West Africa) was examined and correlations of species calculated. Principal components analysis of the correlation matrix was performed in order to further examine interrelationships among the species. Varimax rotation and production of the factor loadings associated with the varimax factors was accomplished in order to reveal the distribution of the sediment "associations" which account for variance in the data set. (For details of statistical approach, see Chapter II). And finally, one species (Delphineis karstenii) was considered diagnostic because of its association with highly pro-ductive coastal waters of the present and with deposits representing highly productive ancient environments. Chaetoceros spp. and a set of meroplanktic species characterize coastal upwelling-influenced sediments and the occurrence of Delphineis karstenii may also be indicative of coastal upwelling deposits.

Chaetoceros species have been recorded as dominant in the total phytoplankton off Peru from 4°-18°30'S (Guillen et al., 1971, 1973). Representatives of the genus are among the dominant species that are present all year (Guillen et al., 1971, 1973; Rojas de Mendiola, 1980). Chaetoceros resting spores contribute abundantly to the sediments off Peru (Zhuze, 1972; Schuette and Schrader, 1979), as they contributed

in the past to the sedimentation process forming the diatomites of the Pisco formation (Mertz, 1966).

Off South West Africa, Hart and Currie (1960) noted the outstanding importance of the <u>Chaetoceros</u> group in the rich coastal waters during both seasons studied (autumn and spring). In spring, the season of characteristically active upwelling, the rich coastal flora consisted mainly of <u>Chaetoceros</u> spp. associated with <u>Asterionella</u> and <u>Delphineis</u> <u>karstenii</u> (ex-<u>Fragilaria</u> <u>karstenii</u>, Fryxell and Miller, 1978). In Kollmer's studies (1962, 1963) the nearshore community was represented mainly by <u>Chaetoceros</u> spp., <u>Delphineis</u> <u>karstenii</u> and <u>Thalassiosira</u> spp. <u>Chaetoceros</u> spp. are marked as constituting together with <u>Delphineis</u> <u>karstanii</u> 96% and 87% of the total cell counts during winter and spring months of 1971 and 1972, respectively (Rep. Div. Sea Fish. S. Af. 40, 1972). Again the following year, important diatoms were <u>Delphineis</u> <u>karstenii</u> and species of the genus <u>Chaetoceros</u> (Rep. Div. Sea Fish. S. Af. 41, 1973). In the study by King and Macleod (1976) of the diets of pilchard and anchovy, and of the species composition of ambient waters, <u>Delphineis</u> <u>karstenii</u> and <u>Chaetoceros</u> again dominate the total cell counts. Apparently the richest concentrations of phytoplankton off South West Africa consist mainly of <u>Delphineis</u> <u>karstenii</u> and <u>Chaetoceros</u> spp. (Cram, 1978).

<u>Chaetoceros</u> spores occur in all of our sediment samples from the inner shelf off South West Africa and their relative abundance ranges from 18-80%. <u>Chaetoceros</u> resting spores may be produced during a <u>Chaetoceros</u> dominated stage of species succession when nutrients are nearly

exhausted in the euphotic zone (Guillard and Kilham, 1977; Margalef, Estrada and Blasco, 1979). The offshore distribution pattern for these species off Peru thus was interpreted to reflect the seaward edge of nutrient-replete surface waters. Off South West Africa as well, the _Chaetoceros_ pattern of relative abundance may be related to species succession.

The importance of _Delphineis karstenii_ in the phytoplankton off South West Africa has already been suggested above. Off Peru it is rare in our samples, but the occurrence is still noteworthy because this species may be a specific indicator of productive coastal waters. The genus was defined by Andrews (1976) and the species he assigned to the genus seem to have flourished in Miocene shallow shelf environments of the eastern U.S. _Delphineis karstenii_ (Fryxell and Miller, 1978) is the only recognized living taxon in the genus so far and was described from a phytoplankton sample taken off South West Africa. Simonsen (1974) reported _Delphineis karstenii_ (cited as _Raphoneis surirelloides_) in the Indian Ocean. _Delphineis_ has not been found in sediments from the Gulf of California.

Off South West Africa three morphotypes occur in the sediments each with characteristics of the _Delphineis_ genus. This complex occurs in all but one sample and ranges from <1 to 49% relative abundance. (Mukhina (1974) reported _Delphineis_ (her _Raphoneis_ complex) with relative abundance of <1 to 32% in sediment samples.) _Delphineis karstenii_ is characterized as a "pioneer coastal species" (Rep. Div. Sea Fish. S. Af. 39, 1971) and, by Hart and Currie (1960), as the most strictly coastal species of diatoms encountered in the plankton off South West

Africa. Its occurrence in sediments off this coast seems to be related to those characteristics.

The final group of species characteristic of these two areas is represented in sediments off Peru by Cyclotella striata/stylorum, Actinocyclus octonarius and Actinoptychus senarius. These are mero-planktic species, i.e. organisms which either produce a resting spore or possess a sedentary stage or dormant phase in their life cycle (Smayda, 1958) and which prefer turbulent nearshore waters. None of these species are known to dominate living phytoplankton assemblages off Peru, but each of these centric forms is relatively large and heavily silicified, accounting apparently, or at least in part, for their preservation in the deep sediments off Peru.

Off South West Africa, Actinocyclus octonarius also contributes importantly to sediments. Mukhina (1974) records the occurrence of A. octonarius in suspension samples, but attributes the accumulation of this species in sediments to the coarse silicification of its valves. Hart and Currie (1960) also suggest that the greater proportion of strongly silicified centrics found in sediment samples compared to plankton samples was due to rapid solution of less silicified forms. Round (1967), however, in discussing the phytoplankton and sediments of the Gulf of California attributes the abundance of large centrics in sediments to the recurrence of blooms of these species in surface waters, and cites the frequent records from neritic regions of a phytoplankton dominated by large centric diatom species. This flora may be determined by active mixing which can transport such forms off the sediments and even maintain them in suspension.

Off South West Africa the distribution in the sediments of
Actinocyclus octonarius is correlated with that of _Coscinodiscus per-
foratus_ (correlation, 0.87), with _Coscinodiscus asteromphalus_
(correlation, 0.69), and _Coscinodiscus gigas_ (correlation, 0.62).
The principal components analysis collected these species in a factor
accounting for 22% of the variance in the data. _Coscinodiscus per-
foratus_ occurs also in sediments off Peru (Zhuze, 1972; Schuette and
Schrader, 1979), and in our study from that area its distribution is
correlated with the abundant meroplanktic species _Cyclotella striata/
stylorum_. _Coscinodiscus asteromphalus_ and _C. gigas_ are amongst the
largest species present in the sediments off South West Africa. _C.
asteromphalus_ forms immense blooms in the Gulf of California and
contributes to the sediment there (Round, 1967, 1968). It forms almost
monospecific assemblages in some samples from laminated sediments
collected off Guaymas (Schrader et al., 1979).

Smayda (1975) in a study of phytoplankton of the upwelling waters
off Baja California made note of blooms of large species of the genus
Coscinodiscus which is not generally expected to flourish in unmodified
pelagic waters. Walsh (1967) implicates larger phytoplankton cells in
the more efficient yields of the food chain in coastal upwelling areas,
while remarking on the controversy over the relationship of cell size
to nutrient concentration (Hecky and Kilham, 1974; Parsons and Takahashi,
1974; Malone, 1975). He cites evidence that larger phytoplankton cells
are usually found in the eastern boundary currents than in other areas
(Ryther, 1969; Parsons and Takahashi, 1973; Margalef, 1974). Without

taking a stand on the cell size/nutrient concentration controversy, we speculate that the adaptability to changing conditions of the mero-planktic species accounts for their episodic flourishing in surface waters and thus for their presence in the sediments of upwelling areas. Of course, their large size does act to enhance the preservation of this reflection of the biocoenoses.

Distinct Distribution Patterns of Coastal Upwelling Diatom Assemblages.

The coherent distribution of sediment assemblages which are distinct from adjacent "oceanic" regimes or which have features reflecting biological or hydrological observations in the upwelling areas provides evidence for the spatial and, in the Gulf of California, temporal limits of the strong influence of coastal upwelling.

Off South West Africa, Hart and Currie (1960) distinguished between a coastal and an oceanic flora. Kollmer (1963) uses the terms "neritic" and "oceanic" to indicate main areas of distribution of two associations distinguished by his monthly records of phytoplankton species in the area off Walvis Bay during 1959-1960. Of those species which are preserved in the inner shelf sediment assemblages, the "neritic" association includes Chaetoceros species, Delphineis karstenii, Thalassiosira spp. and Thalassionema spp. The richest phytoplankton concentrations off S.W. Africa, as stated above, are dominated by Delphineis karstenii and Chaetoceros spp., and our nearshore sediment samples are also dominated by Chaetoceros, a complex which includes Delphineis karstenii, Thalassiosira eccentrica, Actinocyclus octonarius, and Thalassionema nitzschioides, among others. Kollmer's

"oceanic" association is comprised mainly of species which are not preserved in abundance in the offshore South East Atlantic samples. In these samples, very different assemblages are formed with _Coscinodiscus nodulifer_, _Pseudoeunotia doliolus_, _Thalassiosira eccentrica_, _Thalassionema nitzschiodes_ and _Roperia tesselata_, the most abundant species.

Two main complexes of diatoms are evident off Peru as well, one associated with cold coastal waters and one with offshore oceanic waters. Sediment assemblages also allow for a distinction between oceanic and coastal taphocoenoses (Schuette and Schrader, 1979). Almost all stations on the continental margin off Peru have greater than 25% relative abundance of _Chaetoceros_ resting spores, whereas sediment assemblages offshore are dominated by _Coscinodiscus nodulifer_, _Nitzschia marina_, _Pseudoeunotia doliolus_, and species of _Asteromphalus_. (These oceanic assemblages may "intrude" nearshore where _Chaetoceros_ spores are in less abundance.) In addition, a high abundance of meroplanktic species distinguishes the productive coastal region from incursions of "oceanic" assemblages.

Rythmites indicative of upwelling in the Central Gulf of California contain abundant vegetative cell remains of such delicate species as _Synedra indica_, _Skeletonema costatum_ and _Chaetoceros radicans_, among others; whereas adjacent laminae formed under less nutrient rich "oceanic" conditions contain in abundance _Coscinodiscus nodulifer_, _Pseudoeunotia doliolus_, _Coscinodiscus asteromphalus_, among others. In general, the response to upwelling and non-upwelling seasons can be

defined in the laminated sediments by the abundance of weakly silicified species versus the abundance of heavily silicified "robust" frustules.

Within the highly productive areas of both the Peru and South West Africa regions, there are sediment patterns presumably associated with the dynamics of coastal upwelling in the two regions. Off Peru the distribution of the abundant meroplanktic species reflects the sinuous seaward boundary of the upwelled coastal waters. In addition, the highest relative abundance of this component is in relatively nearshore waters (between ∿25-75 miles from shore and in water depths less than 2500 m) (Figure 3). Chaetoceros resting spores have their peak in abundance further offshore and thus at greater water depths. Off South West Africa there is a similar distribution of Chaetoceros with respect to other dominant groups.

Surveys by the Division of Sea Fisheries report the "pioneer" coastal species Delphineis karstenii occurring up to 40 miles from the shore between Walvis Bay (23°S) and Rocky Point (∿19°S), while various Chaetoceros spp. were mainly offshore (Rep. Div. Sea Fish. S. Af. 38, 1970; Rep. Div. Sea Fish. S. Af. 39, 1971). Hart and Currie (1960) recorded nearshore restriction of Delphineis karstenii to about 30 miles from land and a general importance of the Chaetoceros group in the rich upwelled waters. The most extensive coastal production during their surveys occurred in what they characterized as a "quiescent" stage of upwelling. The plankton included numerous resting spores of Chaetoceros spp. and they considered the flora as representing a late successional stage of waters earlier enriched by upwelling. This effect, they suggest, may occur intermittently throughout the year.

In the sediments off South West Africa there is a negative
correlation between the Chaetoceros complex and the Delphineis complex
(-0.66). Our sediment samples provide a record of overlapping but
distinct distribution patterns for these two dominant species.
Principal components analysis of the correlation matrix and rotation
of the resulting components provides a factor (accounting for about
11% of the variance in the data) whose pattern illustrates the near-
shore distribution of the Delphineis complex (Figure 4). Positive
loadings are associated with that complex and with Paralia sulcata;
negative loadings with the Chaetoceros group. Another factor accounting
for about 22% of the variance in the data shows a distributional
association for the set of large centric diatoms (Actinocyclus
octonarius, Coscinodiscus perforatus, C. gigas, C. asteromphalus)
(Figure 5). The joint occurrence of these two factors in several
nearshore areas, especially those off Ambrose Bay, Cape Cross and
Walvis Bay, suggests the recurrence at these sites of a sequence
of dominating diatom assemblages. As productive waters spread from
"point" sources at the coast, the biocoenoses to which these sediment
assemblages correspond may include the following elements: initial
blooms of the pioneer Delphineis complex, proliferation of large
centric forms, and finally widespread formation of Chaetoceros resting
spores. In other words, there is a recurring biological response to
intermittent coastal upwelling and this response is recorded in distinct
distribution patterns of diatom taphocoenoses. Off Peru the last two
elements of such a response may be recorded in the "meroplanktic" and

Chaetoceros group distributions. The initial bloom portion of the
record was either not sampled, is not preserved in deep waters, or
does not deliver a large signal to the sediments under the more
constant upwelling conditions off Peru.

In summary, comparison of the South West Africa data with the
analogous data from the Peru upwelling area suggests that similar
features occur in both regions. The large-scale patchiness of coastal
upwelling off Peru is preserved in areas of high abundance of diatom
valves per gram of sediment, in the distribution of large meroplanktic
species, and -- still abundant further offshore -- in the distribution
of Chaetoceros spores. Strong, quasi-constant winds may be implicated
in the offshore distribution of diatom taphocoenoses off Peru.
Intermittent winds and a shallow depositional environment off South
West Africa confine the sediment record near shore and impose a band-
like structure on the pattern of abundance of diatom valves in sediment
samples. Here, the pioneer flora -- dominated by Delphineis karstenii
-- is preserved in abundance in discrete nearshore areas. This
distribution reflects the patch or bloom structure of the initial
response to nutrient enrichment. An association of large centrics
occurs at these sites, and Chaetoceros spores, representing a final
stage of species succession, occur in highest abundance on the outskirts
of these sediment patches. The opportunity residing in the laminated
sediments of the Gulf of California is to document the variability in
the seasonal, interannual, and longer term record of these patterns of
abundance and distribution which characterize the influence of coastal
upwelling.

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References

Andrews, G.W., Morphology and stratigraphic significance of Delphineis, a new marine diatom genus, Nova Hedwigia, Beiheft 54, 243-260, 1977.

Berger, W.H., Biogenous deep sea sediments: Production, preservation and interpretation, in Chem. Oceanogr., 5, edited by J.P. Riley and R. Chester, pp. 265-388, Academic Press, London, 1976.

Calienes, R. and O. Guillen, The seasonal cycle of phytoplankton and its relation to upwelling in Peruvian coastal waters (abstract), CUEA Newsletter, 5(1), 8,1976.

Calvert, S.E., and N.B. Price, Minor metal contents of recent organic-rich sediments off South West Africa, Nature, 227, 593-595, 1970.

Calvert, S.E., and N.B. Price, Recent sediments of the South West African shelf, in The Geology of the East Atlantic Continental Margin, edited by F.M. Delaney, pp. 171-185, Institute of Geological Sciences, London, Report 70/16, 1971.

Cram, D.L., A role for the Nimbus-G coastal-zone colour scanner in the management of a pelagic fishery, Fisheries Bulletin South Africa, 11, 1-9, 1978.

Diester-Haass, L., and H.-J. Schrader, Neogene coastal upwelling off northwest and southwest Africa, Marine Geology, 29, 39-53, 1979.

Fryxell, G.A., and W.J. Miller III, Chain-forming diatoms: Three araphid species, Bacillaria, 1, 113-136, 1978.

Guillard, R.L., and P. Kilham, The ecology of marine planktic diatoms, in The Biology of Diatoms, edited by D. Werner, pp. 372-469, University of California Press, Botanical Monographs, 13, Berkeley, 1977.

Guillen, O., and R. Calienes, Seasonal variation of productivity and its relation to upwelling in Peruvian coastal waters (abstract), CUEA Newsletter, 5(1), 9, 1976.

Guillen, O., B. Rojas de Mendiola and R. Izaguirre de Rondán, Primary productivity and phytoplankton in the coastal Peruvian waters, in Fertility of the Sea, 1, edited by J.D. Castlow, pp. 157-185, Gordon and Breach, New York, 1971.

Guillen, O., B. Rojas de Mendiola and R. Izaguirre de Rondan, Primary productivity and phytoplankton in the coastal Peruvian waters, in Oceanography of the South Pacific 1972, compiled by R. Fraser, pp. 405-418, New Zealand National Commission for UNESCO, Wellington, 1973.

Hart, T.J., and R.J. Currie, The Benguela Current, Discovery Report 31, pp. 123-298, University Press, Cambridge, 1960

Hecky, R.E., and P. Kilham, Environmental control of phytoplankton cell size, Limnology and Oceanography, 19, 361-365, 1974.

Hendey, N.I., An Introductory Account of the Smaller Algae of British Coastal Waters, Part V: Bacillariophyceae, Her Majesty's Stationary Office, London, 317 pp., 45 plates, 1964.

King, D.P.F., and P.R. Macleod, Comparison of the food and the filtering mechanism of pilchard Sardinops ocellata and anchovy Engraulis capensis of South West Africa, 1971-1972, Investigational Report

Sea Fisheries Branch South Africa, 111, 1-29, 1976.

Kollmer, W.E., The pilchard of South West Africa (Sardenops ocellata Pappe): The annual cycle of phytoplankton in the waters off Walvis Bay 1958, South West Africa Administration Marine Research Laboratory, Investigational Report, 4, 1-44, Verenigde Pers, Beperk Windhoek, 1962.

Kollmer, W.E., The pilchard of South West Africa (Sardinops ocellata Pappé): Notes on zooplankton and phytoplankton collections made off Walvis Bay, South West Africa Administration Marine Research Laboratory, Investigational Report, 8, 1-78, John Meinert (Pty.) Ltd., Windhoek, 1963.

Malone, T.C., Environmental control of phytoplankton cell size, Limnology and Oceanography, 20, 490, 1975.

Marchand, J.M., The nature of sea-floor deposits in certain regions of the west coast, Fish and Marine Biology Survey, Union of South Africa, Rep. No. 6, pp. 1-11, Pretoria, 1928.

Margalef, R., Distribution de seston dans la region d'affleurement du Nort-ouest de l'Afrique en mars de 1973, Tethys, 6 (1-2), 77-88, 1974.

Margalef, R., M. Estrada, and D. Blasco, Functional morphology of organisms involved in red tides, as adapted to decaying turbulence, in Toxic Dinoflagellate Blooms, edited by D. Taylor and H. Seliger, pp. 89-94, Elsevier, North Holland, Inc., New York, Amsterdam, Oxford, 1979.

Mertz, D., Mikropaläontologische und sedimentologische Untersuchung der Pisco-Formation Südperus, Paleontolographica Abt. B., 118 (1-3), 1-51, 1966.

Mukhina, V., Diatoms in the suspension and surface sedimentary layer of the shelf of South Western Africa, in The Micropaleontology of Oceans and Seas, edited by A.P. Zhuse, pp. 94-105, Nauka, Moscow, (in Russian), 1974.

Parsons, T.R., and M. Takahashi, Environmental control of phytoplankton cell size, Limnology and Oceanography, 18, 511-515, 1973.

Parsons, T.R., and M. Takahashi, A rebuttal to the comment by Hecky and Kilham, Limnology and Oceanography , 19, 366-368, 1974.

Report of the Division of Sea Fisheries South Africa 38, 12, Sea Fisheries Branch, Cape Town, 1970.

Report of the Division of Sea Fisheries South Africa 39, 24, Sea Fisheries Branch, Cape Town, 1971.

Report of the Division of Sea Fisheries South Africa 40, 26, Sea Fisheries Branch, Cape Town, 1972.

Report of the Division of Sea Fisheries South Africa 41, 23, Sea Fisheries Branch, Cape Town, 1973.

Richert, P., Relationship between diatom biocoenoses and taphocoenoses in upwelling areas off West Africa (abstract), 4th Symposium on Recent and Fossil Diatoms, Oslo, 1976.

Rojas de Mendiola, B., Variations of phytoplankton along the Peruvian Coast, Poster session at IDOE International Symposium on Coastal Upwelling, Co-sponsors: American Geophysical Union, American

Meteorological Society, American Society of Limnology and Ocean-
ography, National Science Foundation, Los Angeles, February, 1980.

Round, F.E., The phytoplankton of the Gulf of California. Part I. Its
composition, distribution and contribution to the sediments, Jour-
nal of Experimental Marine Biology and Ecology, 1, 76-97, 1967.

Round, F.E., The phytoplankton of the Gulf of California. Part II.
The distribution of phytoplanktonic diatoms in cores, Journal of
Experimental Marine Biology and Ecology, 2, 64-86, 1968.

Ryther, J.H., Photosynthesis and fish production in the sea, Science,
166, 72-76, 1969.

Schrader, H.-J., Proposal for a standardized method of cleaning diatom
bearing deep-sea and land-exposed marine sediments, Nova Hedwigia,
Beiheft 45, 403-409, 1974.

Schrader, H., Cruise Report: Baja Vamonos 79, Sept. 7 - Sept. 30, 1979,
Oregon State University Data Report 78, Reference 79-15, 1979.

Schrader, H.-J. and R. Gersonde, Diatoms and silicoflagellates, Utrecht
Micropaleontological Bulletin, 17, 129-176, 1978.

Schrader, H., K. Kelts, J. Curray, D. Moore, et al., Laminated diatom-
aceous sediments from the Guaymas basin slope (central Gulf of
California):250,000 year climate record, Science 207, 1207-1209,
1980.

Schuette, G., and H. Schrader, Diatom taphocoenoses in the coastal up-
welling area off western South America, Nova Hedwigia, Beiheft 64,
359-378, 1979.

Smayda, T.J., Biogeographical studies of marine phytoplankton, Oikos,
9, 158-191, 1958.

Smayda, T.J., Net phytoplankton and the greater than 20-micron phyto-
plankton size fraction in upwelling waters off Baja California,
Fishery Bulletin, 73(1), 38-50, 1975.

Smith, R.L., Physical oceanography of coastal upwelling regions. A com-
parison: Northwest Africa, Oregon, and Peru, Paper presented at
the Symposium on the Canary Current: Upwelling and Living Resour-
ces, International Council for the Exploration of the Sea, Las
Palmas, Canary Islands, 1978.

Simonsen, R., The diatom plankton of the Indian Ocean Expedition of RV
"Meteor" 1964-1965, "Meteor" Forschungsergebnisse, Reihe D, 19,
1-107, 1974.

Stander, G.H., The pilchard of South West Africa (Sardinops ocellata):
Temperature: Its annual cycle and relation to wind and spawning,
South West Africa Administration Marine Research Laboratory, In-
vestigational Report, 9, 1-57, Verenigde Pers, Beperk, Windhoek,
1963.

Stander, G.H., The pilchard of South West Africa (Sardinops ocellata):
The Benguela current off South West Africa, South West Africa
Administration Marine Research Laboratory, Investigational Report,
12, 1-122, Windhoek, 1964.

Walsh, J.J., Herbivory as a factor in patterns of nutrient utilization
in the sea, Limnology and Oceanography, 22(1), 1-13, 1976.

Zhuse, A.P., Diatoms in the surface layer of sediments in the vicinity
of Chile and Peru, Oceanology, 12(5), 697-705, 1972.

Zuta, S., T. Rivera, and A. Bustamante, Hydrologic aspects of the main
upwelling areas off Peru, in Upwelling Ecosystems, edited by R.
Boje and M. Tomczak, pp. 235-257, 1978.

Table I

Relative Abundance of Dominant Species in Phytoplankton and Sediment Samples (percentage of total cell counts).

	Phyto-plankton*	Stomach Contents*	Composition of Sediment Samples Station # 52 53 54 55 56 57 58 66 67 68 69
Delphineis karstenii	37	30	49 30 32 31 38 24 43 24 33 22 24
Chaetoceros spp.	24	15	44 20 42 21 29 32 29 23 28 18 20

*data from *King and Macleod*, 1976.

Figure Captions

Figure 1: Numbers of diatom valves per mg of sediment off South West Africa [after Richert, 1976].

Figure 2: Numbers of diatom valves per g of dry sediment off Peru.

Figure 3: Relative abundance of meroplanktic species group in sediment samples off Peru.

Figure 4: Distribution off South West Africa of a factor associated with the Chaetoceros resting spore group (negative loadings), the Delphineis complex and Paralia sulcata (positive loadings).

Figure 5: Distribution off South West Africa of a factor correlated with several large centric diatoms: Actinocyclus octonarius, Coscinodiscus perforatus, C. gigas, and C. asteromphalus.

Figure 1

Figure 2
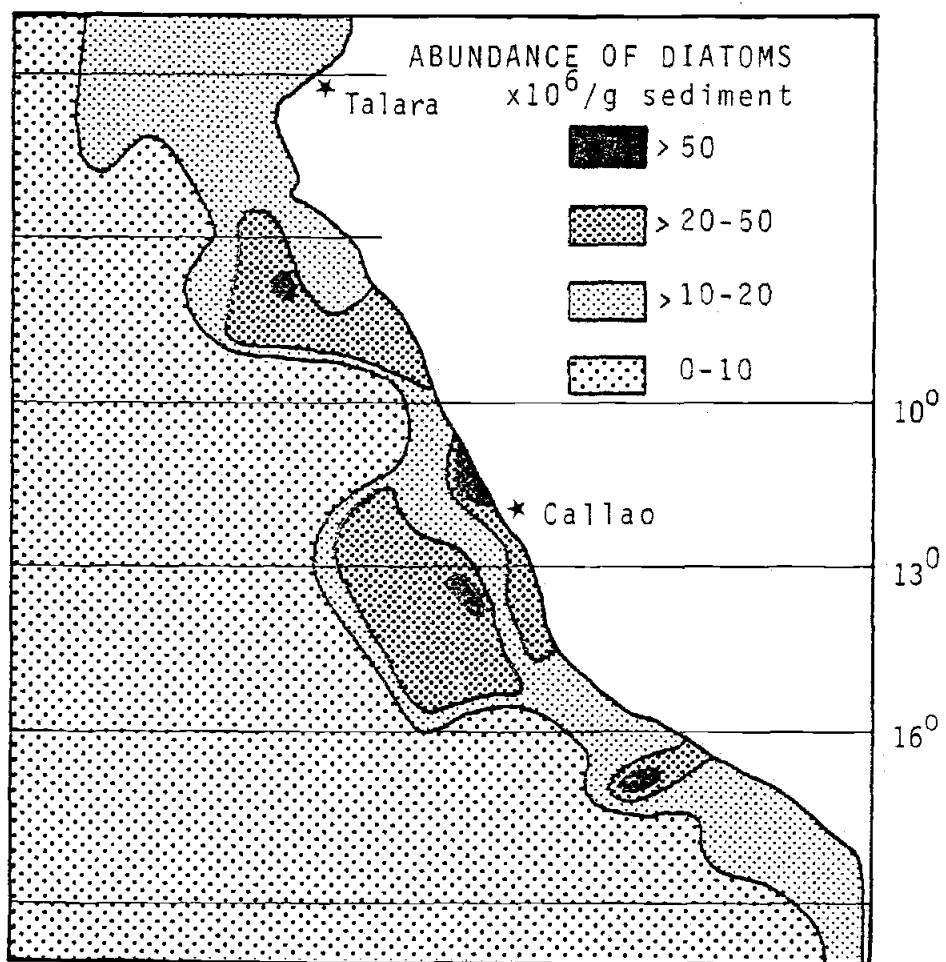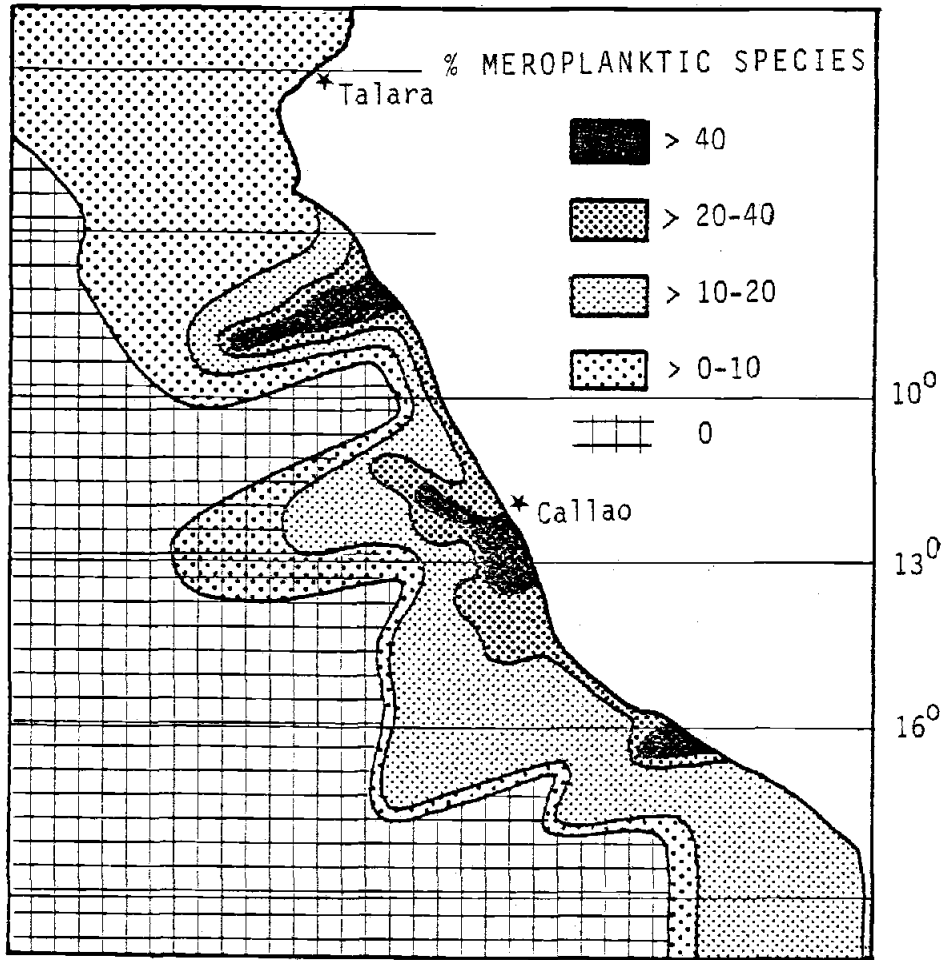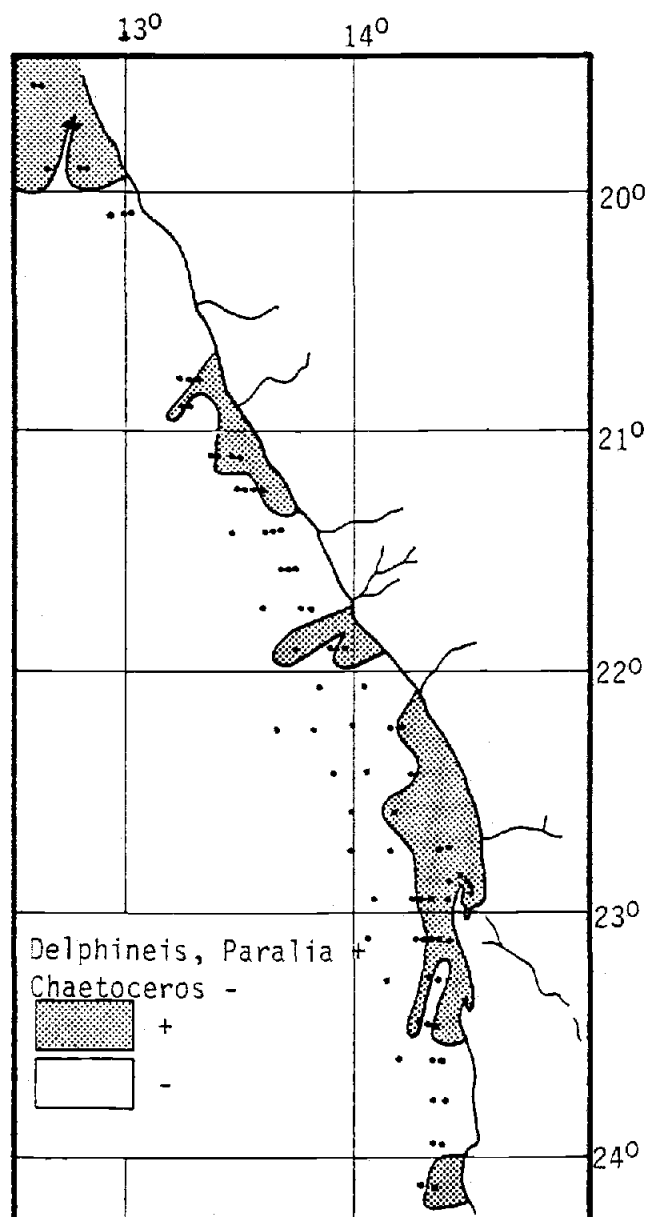
% MEROPLANKTIC SPECIES
> 40
> 20-40
> 10-20
> 0-10
0

Talara

Callao

10°
13°
16°
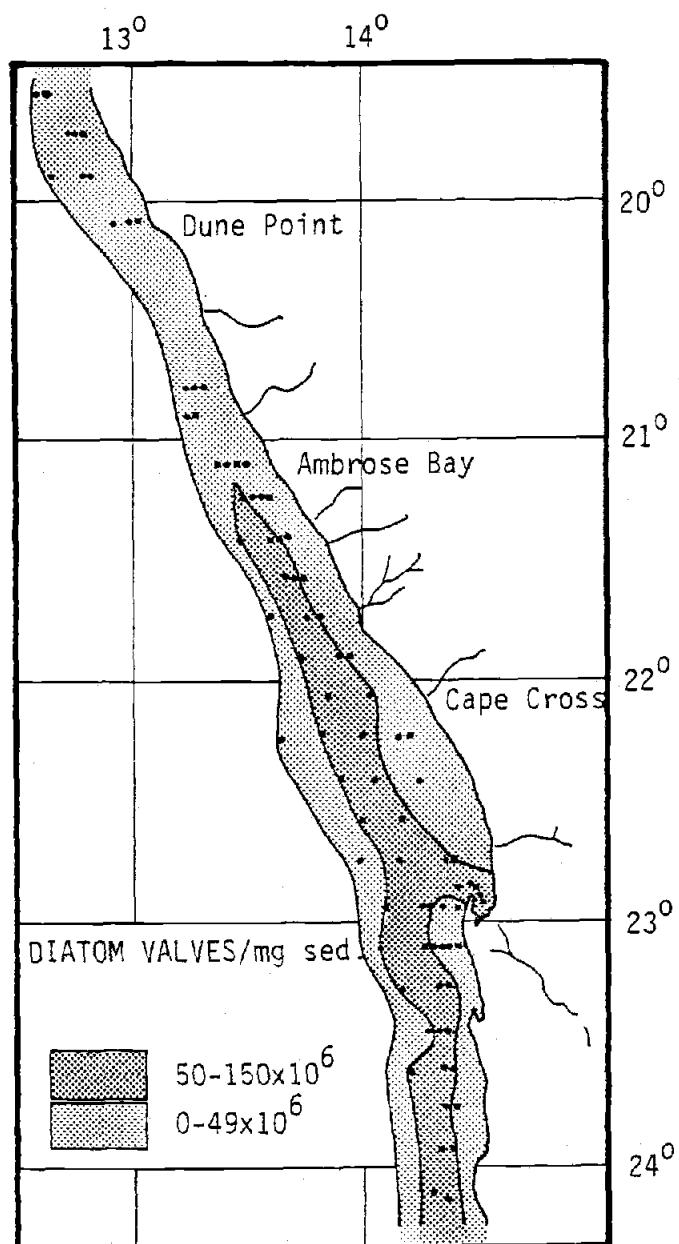
Figure 3

Figure 4

Figure 5