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Radiolarian and diatom fluxes in two California borderland basins as indices of climate variability

Weinheimer, Amy Louise, Ph.D.

University of California, Santa Barbara, 1994



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UNIVERSITY OF CALIFORNIA Santa Barbara

Radiolarian and Diatom Fluxes in Two California Borderland Basins as Indices of Climate Variability

A Dissertation submitted in partial satisfaction of the requirements for the degree of

Doctor of Philosophy

in

Biology

by

Amy Louise Weinheimer

Committee in charge:

Professor Robert Holmes, Chairperson

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April 1994

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June 1994

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Lastly, thanks to my husband, Carl, and to my family without whose support I would not have finished.

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ABSTRACT

Radiolarian and Diatom Fluxes in two California Borderland Basins as Indices of Climate Variability

by

Amy Louise Weinheimer

The diversity, wide ranging habitats, and endemism of diatoms and radiolarians make them useful biological indicators of physical oceanography. The unique varved sediment (yearly layers) of the Santa Monica and Santa Barbara Basins (SMB and SBB, respectively) in the Southern California Borderland permits analysis of the diatom and radiolarian record at an annual resolution. In addition to the high resolution record preserved in the sediment, present-day teleconnections suggest that climate variability at SBB is a sensitive indicator of aspects of much broader scale climate variability over the North Pacific/North American sector. The purpose of this study was to determine whether the microfossil fluxes to the Santa Monica and Santa Barbara Basin sediments reflect the physical oceanography of California Current System.

Sediment samples were taken from the two basins with Soutar box cores. These were subcored and X-rayed to aid in delimiting the varves. Sediment from the years 1954-86 was sampled at the varve boundaries and analyzed for their diatom and radiolarian content. Counts of several diatom indicator species and all radiolarian species were made and fluxes calculated (in No.(cm^{-2})(y^{-1})). These data were compared to temperature and salinity data taken off the California coast.

The analyses rendered two important findings. First, the relative proportions of radiolarian species was surprisingly stable through the 33 year record, even during two major El Niños. This suggests some degree of constancy, across a variety of climate regimes, in the water masses circulated in the California Current System. Second, the flux of radiolarians varies on a decadal scale, in correspondence to anomalous, low frequency fluctuations of several environmental parameters. For example, the radiolarian flux is highly correlated to the regional average SST off the California coast. The California coastal environment is affected by large scale atmospheric forcing, therefore it is possible that the radiolarian record will also provide a paleo-index of North Pacific atmospheric circulation variations. The shorter diatom record proved promising as a paleotemperature record, but too brief for more substantial conclusions.

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CHAPTER 1. INTRODUCTION

1.1. GENERAL

The environmental requirements and limited motility of marine plankton constrain them to water masses and currents appropriate for their adaptations. This characteristic of plankton makes them useful as indicators of physical oceanographic parameters, and plankton preserved in the sedimentary record provide the means to decipher paleoceanography. Siliceous microplankton such as diatoms and radiolarians are widely distributed geographically, abundant, and well preserved in oceanic sediments over large areas (Kennett, 1982), making them particularly useful paleoceanographic indicators. The purpose of this study is to determine if radiolarian and diatom tests preserved in the California Borderland basins reflect the circulation of water masses in the California Current System (CCS), with emphasis on the effect of El Niño events on their distribution patterns.

1.2. DIATOM AND RADIOLARIAN BIOLOGY

Diatoms are unicellular, eukaryotic, silica-walled, brown-pigmented algae. The siliceous test, typically ranging in size from 10-200µm, consists of two major units called valves which are joined by a girdle. In the vegetative phase of the diatom life cycle, asexual reproduction involves separation of the two valves, each then forming a second, smaller valve to form a complete test. The average cell size of a population decreases with each generation. Cell size is recovered in the phase of sexual reproduction with the formation of an auxospore by flagellated gametes. This spore forms a new, full-sized test. Resting spores which are morphologically distinct from the vegetative cell may also form, but their role in the life cycle is not clear (Round et al., 1990). High concentrations of marine diatoms are usually associated with high latitude regions, temperate coastal areas and upwelling systems (Garrison, 1984).

Radiolarians are exclusively marine, zooplankton and can be grouped into three categories based on their skeletal composition. The polycystine radiolarians with siliceous tests is the only group used in this study; acantharians with strontium sulfate and phaeodarians with siliceous-organic tests are excluded, since the former are never, and the latter rarely, preserved in sediments. The cell of polycystine radiolarians (referred to as 'radiolarians' in the remaining text) is organized into 1) an inner central capsule containing the nucleus, organelles, and food reserves, and 2) the surrounding extracapsulum with food gathering rhizopodia and cytoplasm containing digestive vacuoles (Anderson, 1984). The skeleton is surrounded by cytoplasm and is usually located in the extracapsulum (Anderson, 1984). The size of most radiolarians is in the range of 20-200µm. Little is known of the radiolarian life cycle due to difficulty in culturing them. However, swarmer cells have been observed in the laboratory and interpreted as asexual reproduction (Anderson, 1983, 1984). Reproduction by fission has been reported (Brandt, 1902; Cienkowski, 1871; Haeckel, 1887). Kling (1971) suggests that some radiolarians may alternate sexual-asexual phases in their life cycles. Their life span has been estimated at 1-3 months (Casey et al., 1971; Berger, 1976; Takahashi, 1983; Caron and Swanberg, 1990). Radiolarians range geographically from low to high latitudes and live throughout the water column.

1.3. DIATOMS AND RADIOLARIANS AS INDICATORS OF THE PHYSICAL ENVIRONMENT

The use of microfossils as indicators of conditions in the geologic past requires understanding their distribution and response to present-day conditions. One of the most direct methods of determining this relationship is comparison of plankton tows and physical oceanographic data taken simultaneously. Radiolarians from plankton tows have been found to correlate best to temperature and depth. Parameters such as salinity, nutrient content, and chlorophyll <u>a</u> concentration correlate less well (Alder and Boltovskoy, 1993; Gowing and Garrison, 1991). Tont (1976, 1981) observed that diatom blooms off southern California coincide with upwelling events, but that the magnitude of the bloom is tempered by the temperature, salinity, and sea level height at the time of the upwelling. The distributional pattern of diatom species from plankton tows in the North Pacific coincides with hydrographically defined domains, with temperature, salinity and density significantly correlated to diatom distributions (Venrick, 1971).

Collection of plankton tows is time consuming and the temporal coverage of the tows is exceedingly limited. The use of sediment traps and bottom sediment greatly increases the temporal coverage of sampling, without concurrent increase in effort. However, some resolution is lost in comparison to the physical environment. Another disadvantage of sediment trap and bottom sediment material is the significant loss of skeletons due to dissolution. Even though part of the plankton is lost, comparisons of plankton compositions in sediment traps and bottom sediment to that in the overlying waters indicate that the diatom and radiolarian assemblages are reflected in the sediment (Renz, 1976; Boltovskoy and Alder, 1992; Sancetta, 1989; Sautter and Sancetta, 1992). As in the water column, microplankton assemblages in bottom sediment correlate well to the distribution of water masses (Kanaya and Koizumi, 1966; Morley, 1989; Pisias, 1978; Molina-Cruz, 1977).

1.4. SEDIMENTARY SETTING

Although sediment traps allow for collecting samples representing discrete time periods, the temporal coverage is too brief for long term physical oceanographic comparisons. Certainly, sea floor sediments represent sufficient time, but are usually time-averaged by bioturbation, making high resolution physical oceanographic comparisons impossible. In very rare sedimentary marine environments, annual accumulation of sediment is preserved in discrete varves. The Southern California Borderland contains at least two such basins, the Santa Barbara Basin (SBB) and Santa Monica Basin (SMB) (Figure 1.1). Both basins are silled, effectively cutting off circulation of oxygenated water leaving the bottom waters disaerobic. The annual deposits of varves are maintained due to low oxygen bottom waters which exclude bioturbating benthos. The light-colored laver of each varve in these basins (Hulsemann and Emery, 1960; Koide et al., 1972; Gorsline 1992) represents the high productivity of spring and summer and the dark-colored layer the terrestrial sediment from winter rains. The SBB is 580m deep with a maximum sill depth of 468m, the SMB reaches a depth of 925m with a maximum sill depth of 725m (Gorsline, 1992).

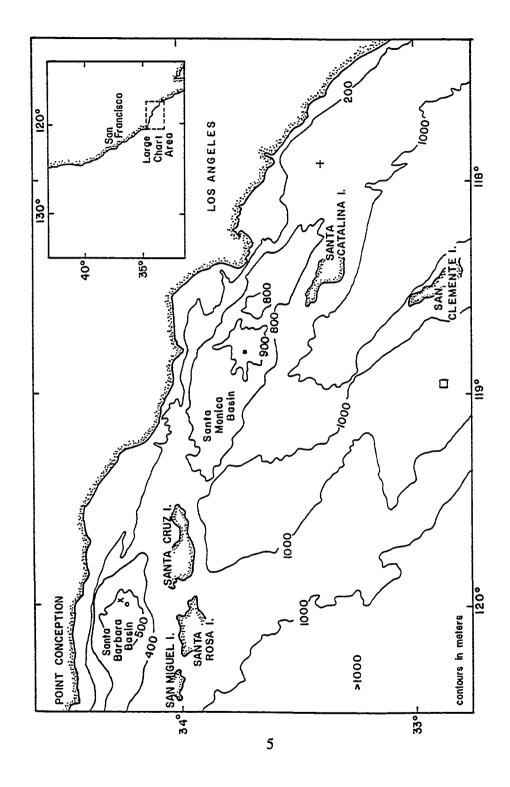
1.5. OCEANOGRAPHIC SETTING

The waters entering the basins in the Southern California Borderland are transported by the CCS. The components of this system (Figure 1.2) can be characterized by their physical parameters as follows: The California Current (CC) transports primarily cool, nutrient-rich and very low-salinity (33.40/00) transition and subarctic waters southward; the California Undercurrent, flowing north below the CC at approximately 200m, carries nutrient-rich, low-salinity (33.80/00) water which is a mixture of subarctic and equatorial waters (Roesler and Chelton, 1987); and cold, nutrient-rich intermediate waters with salinity of 340/00 which upwell landward of the California Current. Warm, high-salinity, low-nutrient water from the North Pacific central gyre enters the CCS from the west (Lynn and Simpson, 1987). South of Point Conception, the CC turns southeast and then counterclockwise over the borderland, merges with warm, highsalinity, low-nutrient tropical water along the coast, forming the California Countercurrent (Hickey, 1992).

The CCS undergoes seasonal and interannual variability. Seasonally, the southward flow of the CC is typically strongest in the spring and summer (Hickey,

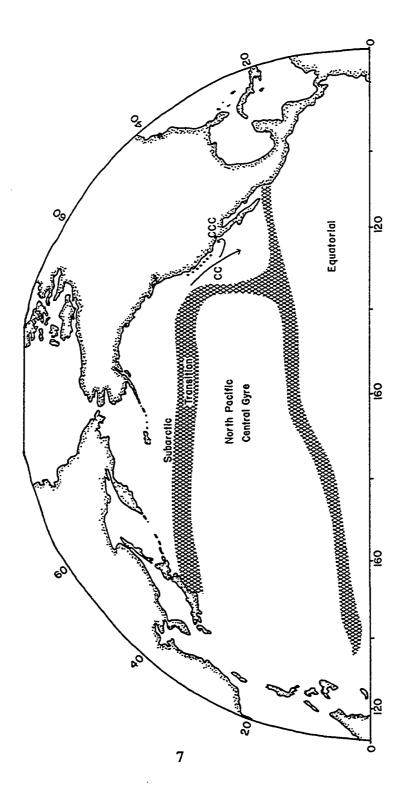
Figure 1.1. Map of the Southern California Borderland showing the core locations in the SBB (O) and SMB (O); and the California Cooperative Fisheries Investigations (CALCOFI) stations 82.46 and 82.47 (X) in the SBB, 90.30 (+) and 90.45 (\square) along line 90.

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Figure 1.2. North Pacific oceanic provinces and general circulation pattern of the California Current System and its main components. Arrows indicate the California Current (CC) and California Countercurrent (CCC); dots indicate upwelled waters. (Modified from Fager and McGowan, 1963.)



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1979) resulting in upwelling, lower sea surface temperatures, and increased production (Chelton, 1982; Tont, 1981). In fall and early winter the CC slows (Hickey, 1992) and moves inshore (Simpson, 1984). Interannual variability in the CCS includes perturbations due to El Niño events every 4-10 years and to longer periods of warm and cool conditions (Lange et al., 1990). Both seasonal and interannual variability in the CCS are due to large-scale atmospheric forcing over the North Pacific basin (Namias and Huang, 1972).

The goal of this study is to determine whether the microfossil record in the sediment reflects the interannual variability, and therefore possibly provide a paleo-index of North Pacific oceanic circulation. The problem is approached in Chapter 3 by analyzing the diatom and radiolarian assemblages to determine the variability in their quantity and quality. This is followed with a comparison of the microfossil fluxes to water masses present, as represented by temperature and salinity, in the Southern California Bight (Chapter 4). Lastly, the microfossil data are compared to data reflecting the circulation of the bight (SST). The appendix contains taxonomic information; Chapter 2 explains the methodology of sample acquisition and preparation and the species lists.

CHAPTER 2: METHODS

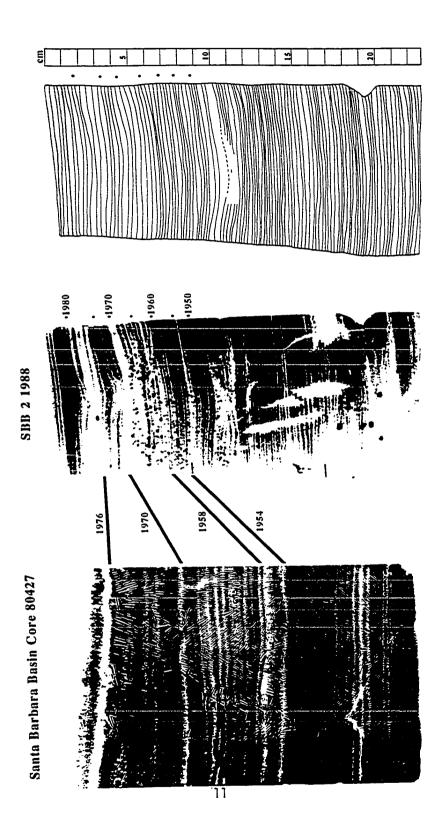
2.1 SAMPLE ACQUISITION AND DATING

Sediment samples taken from three Soutar box cores (Soutar and Crill, 1977) in the SBB and one from the SMB (Figure 1.1) were analyzed for their diatom and radiolarian content. Three different methods were tested in subcoring the box cores. The SMB box core (SMB 85) and one from the SBB (SBB 85) were subcored with a hollow aluminum wedge. The wedge was inserted into the sediment, and filled with alcohol and dry ice which froze the sediment onto the outer surface of the wedge. This sediment was wrapped in plastic and foil, then kept frozen for processing on shore. The second SBB box core (SBB 2 1988) was subsampled with a 10cm x 10cm surface area Plexiglass tube inserted into the box core sediment. The sediment remained refrigerated in the core liner for 3.5 years allowing the sediment to dry to a firm consistency; it also shrank vertically approximately 30%. Increasing the firmness of the sediment makes slabbing of the core possible (see below). The third SBB (SABA 87/1) box core was subsampled with a cylindrical core liner inserted into the sediment. A rectangular plexiglass tube was also taken from the box core for later x-raying.

All cores (except SABA 87/1, see the next paragraph) and the rectangular subcore taken with SABA 87/1 were X-rayed with a 65-75 kv beam for 3-4.5 minutes to aid in delimiting the varves and to provide a permanent record of the cores. The X-radiographs were taken within weeks prior to subsampling to avoid potential problems of core shrinkage due to desiccation and consequently making the X-radiographs inaccurate renditions of the cores. Preparation of the frozen SMB 85 and SBB 85 subcore wedges for X-ray required cutting away the vertical face; only this part of each wedge was used. The dried SBB 2 1988 subcore was cut vertically into seven 1cm thick slabs. The two slabs with the clearest Xradiographs, 2 and 5, were used in this study. Templates of the varves were made from contact photographs of the X-radiographs. Years were assigned to the varves by counting the varves from the top down and by using distinct marker layers of known age from other X-radiographs of dated SBB cores (Soutar, pers. comm.). Plate 2.1 illustrates the core used here (SBB 2 1988) and core 80247 dated by Soutar using ²¹⁰Pb. Lines correlating distinct layers used to aid in dating the SBB 2 1988 core are shown along with the template of the dated varves constructed from a print of the X-radiograph. The years 1976-85 were sampled from the SMB 85 core; 1980-85 from the SBB 85 core; 1979-86 from the SBB 2 1988 slabs; and 1954-86 from the SABA 87/1 core.

Plate 2.1. Contact prints of x-radiographs of Santa Barbara Basin cores 80247 (left) and SBB 2 1988, slab 5 (center). A template of the slab from SBB 2 1988 outlining the varves is shown on the far right. Lines of correlation join distinct marker layers in the two prints.

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The cylindrical SABA 87/1 subcore was sampled on board the ship using distinct color changes in the sediment as boundary markers (Schimmelmann et al, 1990). These samples were subsequently dated using the dates generated from sediment taken with the rectangular plexiglass tube. The frozen SBB 85 and SMB 85 subcores were cut along template lines with a razor blade; a scalpel was used to sample the two SBB 2 1988 subcore slabs. Samples were oven dried and weighed; dry weights were 1-7 grams.

The different methods of sampling the cores (all of which were used in this study) each have advantages and disadvantages. The frozen sediment maintains original varve thickness allowing the possibility of sampling at less than annual intervals. However, the ice crystals reduce the clarity of the X-radiographs and inserting the wedge into the sediment caused some distortion of the varves. The X-radiographs of the dried sediment provided the best rendition of the varves, but drying shrinks varve thickness increasing the difficulty of sampling. Although sampling the subcore on board eases transport of the sediment, it precludes X-raying the material. This method resulted in sample boundaries rarely falling at annual intervals, requiring averaging of the record in order to estimate annual fluxes. Of these three subsampling methods, that of drying the core in the core liner and cutting it into the slabs provides the best material for clear X-radiographs. The high resolution X-radiographs of these slabs improves the age dating of the cores using varve counting and inter-core correlation. However, the vertical shrinkage of the varves increases sampling difficulty.

2.2. SAMPLE PROCESSING AND COUNTING

All samples were disaggregated, sieved over a 25 μ m stainless steel sieve, then treated with dilute hydrochloric acid (approximately 5% HCl). After the acid treatment, the final sieving was through stacked 25 μ m and 45 μ m sieves. The two size fractions were stored in vials of deionized water until slides were made. Diatom slides were made by pipetting 10% of the 25-45 μ m fraction onto no. 1, 40 x 22 mm cover slips and air dried. These were then mounted onto slides with Cumar mounting medium. Radiolarian slides were made with 10-20% of the greater than 45 μ m fraction by pipetting the sample onto slides, air drying and mounting with Permount mounting medium.

On the diatom slides, seven diatom species were identified (see Table 2.1 and Plate I.1 in the appendix) and the total number of valves enumerated. The species were chosen based on their utility as environmental indicators. Approximately 500 diatom valves per sample were counted. All the radiolarians on the slides were counted to the lowest taxonomic unit possible (species, genus,

or group; see Table 2.1 and Plates I.1 and I.2 in the appendix). Ninety-four of these counting groups occurred in all the cores; 22 groups, accounting for 3.5% of the total flux, occurred in less than all the cores. Only those groups present in all cores are used for further analysis. The 22 groups not included are noted in Table 2.1. Approximately 300 specimens per sample were identified. Counts on the diatom and radiolarian slides were done along adjacent transects over the entire slide. Both the diatom and radiolarian fluxes were calculated for each core.

Table 2.1 Species lists of indicator diatom species counted and all radiolarian 'counting groups' (usually species, otherwise, the lowest possible taxonomic unit two which a specimen could be assigned) used. A list of the radiolarian species documented but not included in analysis due to absence in one or more cores succeeds the list of ranked radiolarian species.

Diatom species list: Asteromphalus arachne Azpeitia nodulifer Azpeitia africanus Coscinodiscus marginatus

Radiolarian species list: Actinommid gp. Amphiplecta spp. Amphirhopalum ypsilon Anthocyrtidium ophirense Anthocyrtidium zanguebaricum Arachnocorallium calvata gp. Arachnocorys circumtexta Astrosphaerid gp. Botryocyrtis scutum Botryopyle spp. Botryostrobus auritus/australis Botryostrobus aquilonaris Cannobotryid gp. Carpocanistrum gp. Cladoscenium tricolpium Clathrocanium coarctatum Clathrocyclas bicornis Collosphaerid gp. Cornutella profunda Corocalyptra columba Cypassis irregularis Dictyocoryne profunda Dictyocoryne truncatum Dictyocoryne spp. Dictyophimus spp. Dictyophimus infabricatus Dictyophimus gracilipes Dictyophimus crisiae

Hemidiscus cuneiformis Pseudoeunotia doliolus Roperia tessellata

Dictyophimus hirundo Didymocyrtis tetrathalmus Euchitonia furcata Eucyrtidium acuminatum Eucyrtidium hexagonatum Eucyrtidium anomalum Eucyrtidium spp. Heliodiscus asteriscus Helotholus histricosa Hexacontium gp. Hexapyle spp. Lamprocyclas maritalis Lamprocyrtis nigriniae Lampromitra spp. Lampromitra quadricuspis Larcopyle butschlii Larcospyra quadrangula Lipmanella dictyoceras Litharachnium tentorium Litheliid gp. A Litheliid gp. B Lithelius minor Lithomelissa setosa Lthopera bacca Lithostrobus hexagonalis Lophocorys polyacantha Lophophaena gp. A Lophophaena gp. B

Table 2.1 continiued

Lophospyris pentagona pentagona Lophospyris/Phormospyris spp. Neosemantis distephanus Octopyle stenozona Peridium spinipes longispinum Peridium spinipes Peripyramis circumtexta Peromelissa spp. Phormospyris stabilis stabilis Phormostichoartus corbula Plectacantha spp. Porodiscid gp. Pterocanium praetextum praetextum Pterocanium praetextum eucolpum Pterocanium korotnevi Pterocanium trilobum Pterocorys minythorax Pterocorys spp. Pterocorys zancleus

Excluded Radiolarian Species Acanthocorys macropodia Callimitra carolotae Corocalyptra kruegeri Dictyocephalus papilosus Enneaphormis rotula Eucecryphalus sestrodiscus Euchitonia spp. Euchitonia elegans Lamprocyrtis spp. Lipmanella spp. Lithomitra lineata gp. Lithomitra infundibulum Pseudocubus obeliscus Sethoconus tabulatus Sethophormis aurelia Spongaster cf. S. pentas Spongosphaera streptacantha

Pterocorys hertwigii Pteroscenium pinnatum Pylospyra octopyle Spirocyrtis scalaris Spongaster tetras irregularis Spongocore puella Spongodiscid spp. Spongopyle osculosa Spongotrochus glacialis Spongotrochus (?) venustum Spongurus cf. S. elliptica Stichopilium bicorne Stylosphaerid gp. Tetrapyle octacantha Theocalyptra bicornis Theocalyptra davisiana cornutoides Theocalyptra davisiana davisiana Theocalyptra gegenbauri Theocorythium trachelium

Stichopilium variable Tricolocampe cylindrica Trictenartus elegans Trisulcus triacanthus Zygocircus productus

CHAPTER 3: ANALYSIS OF RADIOLARIAN AND DIATOM FLUX, DIVERSITY, AND SPECIES IMPORTANCE

3.1 INTRODUCTION

The geographic distribution of phyto- and zooplankton species determined from plankton tows and the sedimentary record reflect distinct oceanic provinces (McGowan, 1974; Nigrini, 1970; Renz, 1976; Casey, 1971; Molina-Cruz, 1977). The geographic extent of oceanic provinces coincide with currents and water masses which can be characterized by unique physical conditions such as temperature, salinity, oxygen, and nutrient concentrations (Fager and McGowan, 1963; McGowan, 1974; Kling, 1979; Kanaya and Koizumi, 1966). Within an oceanic province, the species abundances in a taxonomic group have been found to be distributed in a persistent hierarchy, such that a few species are consistently most abundant (dominant) and many are few to very rare (Matrai, 1986; McGowan and Walker, 1985; Venrick, 1990). Copepod species within the North Pacific gyre exhibit a constant dominance structure (McGowan and Walker, 1985). McGowan and Walker's (1985) analysis of copepod species along a transect north from the North Pacific gyre across the Transition Zone and into the Subarctic water mass showed significant shifts in species dominance at the boundaries between these three physical environments.

Paradoxically, when the physical environment of a province is perturbed, species' abundances may change but relative species' abundances are not affected (Colebrook, 1977; Bernal and McGowan, 1981; McGowan and Walker, 1985; Venrick, 1971). In the CC, anomalies in temperature and salinity associated with eastward and northward transport of water during El Niño (Simpson, 1983a and 1983b; Cane, 1986) did not alter the species structure of the dinoflagellate, genus *Ceratium* (Matrai, 1986). The phytoplankton species structures off Peru and in the subarctic Pacific exhibit similar resiliency to environmental fluctuations due to El Niño (Rojas 1981; Takahashi, 1987a). Kling (1977) found a persistent dominance pattern of the 40 most abundant radiolarian species in the SBB and SMB sediment in five year increments from 1890-1970, in spite of the changes in circulation of the CC during this time period. Phytoplankton and zooplankton abundances, however, are affected by variability in the physical environment and typically diminish during El Niño conditions in the CC (Chelton et al., 1982; Takahashi, 1987a).

3.2 PURPOSE

This study extends the work of Kling by including more radiolarian and some diatom species over the period 1954-1986. The radiolarian and diatom tests from the SBB and SMB were analyzed on an annual scale to determine the yearly flux to the sediment, the species dominance pattern, and radiolarian diversity. Additionally, an attempt is made to distinguish anomalously warm years (El Niños) from normal years with radiolarian environmental groups.

3.3 METHODS

The total fluxes of radiolarians and diatoms were extrapolated from the raw counts to generate the No.cm⁻²y⁻¹ for both plankton groups. Radiolarians were observed in the SBB for the years 1954-86 and the SMB for the years 1976-85. The radiolarian record for the SBB was generated from three cores; SABA 87/1 (1954-86), SBB '85 (1980-85), and two replicates, slab 1 and slab 5, from core SBB 2 1988 (1979-86). The radiolarian flux for the years in common is taken as the average over the cores. The diatom record for the SBB and SMB includes the years 1979-86 and 1976-85, respectively. The number of radiolarian counting units (the lowest possible taxonomic unit to which a specimen can be assigned) per year were tallied and used as an index of diversity.

The radiolarian species were assigned to environmental groups according to the water type to which the species are restricted and the flux of cells (No.cm $^{-2}y^{-1}$) per species calculated. References to the species in the literature (see Appendix I) were discriminatingly used to determine their province. The use of 'province' here follows that of McGowan (1974); oceanic provinces are semi-closed ecosystems maintained by circulation patterns and with mixing at their boundaries. Of the 94 species used in this study, 64 were found to be geographically restricted. Appendix I gives the diatom and radiolarian taxonomy and assigned environmental groups. In the CCS, three groups can be defined (see Figure 1.2 for the geographic layout of the provinces). The warm fauna includes species from the North Pacific central gyre and eastern equatorial Pacific, carried by the California Countercurrent; transition fauna transported in the CC from the transition and subarctic waters; and intermediate fauna upwelled in the intermediate waters. Since not all species were placed in an environmental group, the sum of the three is less than the total flux, with the species of unknown environment constituting the balance.

To measure the degree of inter-basin similarity in species composition, the diatom and radiolarian species were ranked by their total abundance in each core and the Spearman rank correlation coefficients calculated. The interannual similarity from 1954-1986 was measured by the coefficients of the annual radiolarian species ranks.

3.4 RESULTS

TOTAL RADIOLARIAN FLUX AND DIVERSITY

The abundance and diversity of radiolarians preserved in the SBB sediment during the years 1954-86 can be divided into three distinct periods. The first spans 1954-72 and has relatively high radiolarian flux (average of $192 \text{cm}^{-2}\text{y}^{-1}$) (Figure 3.1) and low diversity (average of 54 counting groups) (Figure 3.2). This is followed by the period 1973-78 which has low flux (average of $52 \text{cm}^{-2}\text{y}^{-1}$) (Figure 3.1) and low diversity (average of 56 counting groups) (Figure 3.2). The third period, 1979-86 has high radiolarian flux (average of $188 \text{cm}^{-2}\text{y}^{-1}$) (Figure 3.1) and high diversity (average of 89 counting groups) (Figure 3.2).

In the years 1954-72, there is especially low radiolarian flux in 1958 and 1959, and high flux in 1954 and 1960-63 (Figure 3.1). In 1964, there is a drop in radiolarian flux which continues through 1972, interrupted by a small rise in 1966.

All years from 1973 to 1978 have very low radiolarian flux with a peak in 1977, but this is still lower than any years in the period before or after. There is a steady increase in flux from 1979 to the peak in 1984. This is followed by a steep drop in 1985 and increase in 1986.

During the short record observed in the SMB, 1976-85 (Figure 3.1), the radiolarian flux from 1976-79 is low, peaks in 1980 and 1982, then falls off. In general, the SMB has a higher flux of radiolarians than the SBB, except in the years 1984 and 1985. In both basins, the flux increases in 1979, but in the SMB, it reaches its peak sooner, remains high for a shorter time and drops to a lower low than in the SBB.

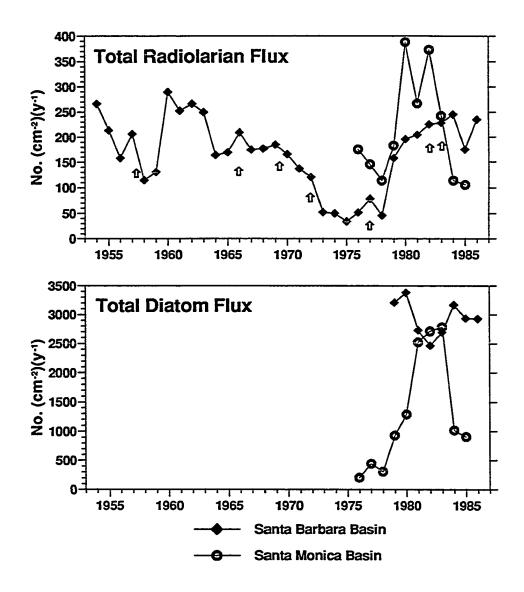
TOTAL DIATOM FLUX

The diatom record from the SBB (1979-86) (Figure 3.1) shows maximum flux in 1979 and 1980, low flux from 1981-83, then peaks in 1984 and falls off slightly in 1985 and 1986. The low in diatom flux (1981-83) occurs when the radiolarians show a steady increase in flux. However, the 1984 peak in diatoms coincides with the 1984 radiolarian peak.

Diatom flux in the SMB (1976-85) (Figure 3.1) steadily increases from 1976 to a maximum in 1983, after which it falls off sharply in 1984 and 1985.

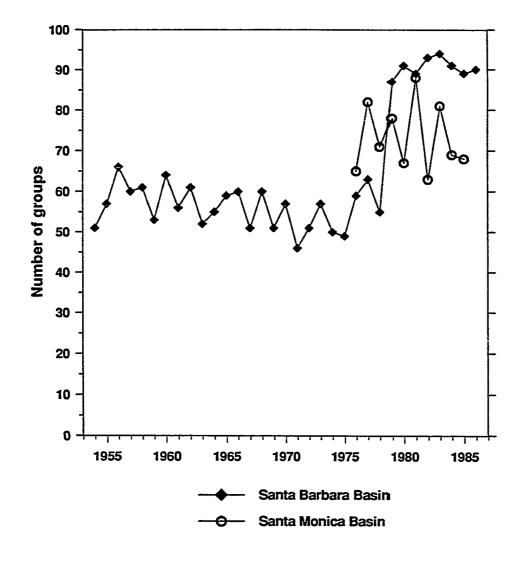
Figure 3.1. Total radiolarian flux in number per square centimeter per year (upper panel) and total diatom flux (lower panel), in number per square centimeter per year for the SBB (diamond) and SMB (circle). Arrows indicate El Niño years.

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Figure 3.2. Number of counting groups per year for SBB (diamond) and SMB (circle).



Annual Number of Counting Groups

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INTERBASIN COMPARISON OF FLUX AND DIVERSITY

The SBB has higher flux of diatoms than SMB, except in 1981-83 when the fluxes in the two are similar. The radiolarian flux in the SBB is slightly higher than that in the SMB. Radiolarians in both basins generally behave the same, with a high flux in the early 1980s bounded by low fluxes. Diatoms in the two basins show an inverse relationship from 1980 to 1984 (when one is high, the other is low).

The annual number of species in the SMB (Figure 3.2) does not suddenly increase in 1979, as it does in the SBB. The number of counting groups ranges from 63 to 81, averaging 73, with no consistent pattern.

MICROFOSSIL FLUX COMPARISON

In the SBB, the radiolarian and diatom fluxes show some dissimilarity. Although both peak in 1984, the radiolarian flux in the years prior steadily increase to the 1984 peak; whereas the diatoms are low in 1981-83. In the SMB, radiolarian flux leads the diatom flux, as it peaks and falls approximately one year sooner.

RADIOLARIAN ENVIRONMENTAL GROUP FLUXES

In the SMB, the warm and transition radiolarian environmental groups are most abundant and essentially make up equal amounts of the total flux (Figure 3.3). The intermediate fauna makes up 25-50% of what either the other two contribute to the total flux. In general, the trend of each group is the same as the total flux.

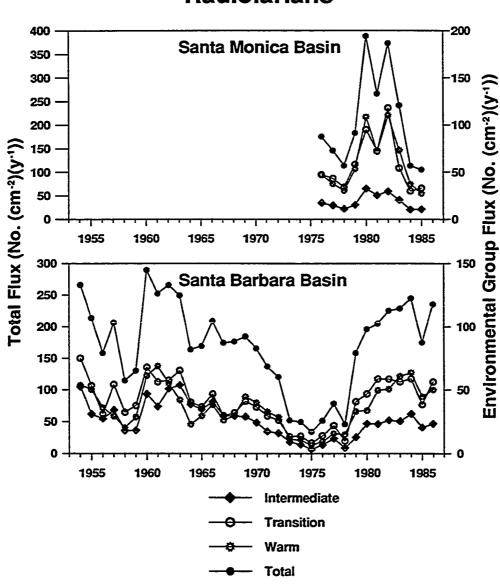
Similarly, the radiolarian environmental groups in the SBB also resemble the total flux. In 1954 through 1978, the three groups have about equal shares of the total flux. From 1979-86, the flux of intermediate group radiolarians is only about half of that of the warm and transition faunas.

In order to determine any possible effect of El Niño on the distribution of environmental groups, the dominance sequence of the groups on an annual scale was assessed. The results are listed in Table 3.1. All peaks in the total flux have transition fauna as the most abundant group, except for 1969 and 1984. Not all years with transition fauna as dominant are peaks and many of these years are lows. In fact, the transition fauna dominates most years (22 out of 33).

Shifts in environmental group dominance do not correspond to the total flux in any predictable pattern. All 9 peaks in radiolarians precede or follow a change in the dominant environmental group and all but four changes in dominant group are associated with a peak (the change from 1955 to 56, 1967 to 68, 1972 to 73, 1978 to 79, and 1982 to 83). The exceptions are associated with lows (except 1982 to 83 and 1978 to 79, which is on a steep increase but not a peak).

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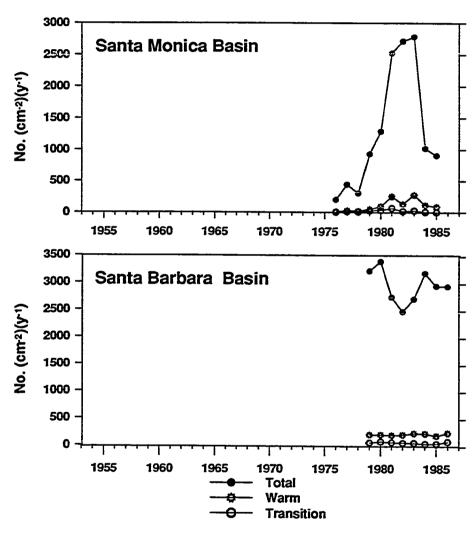
Figure 3.3. Flux of radiolarian environmental groups in the SMB (upper panel) and SBB (lower panel). The total flux (solid circle) is shown for comparison. Intermediate fauna = diamond, Transition = open circle, Warm = star. Note that the sum of the environmental group fluxes is less than the total flux because not all species were found to be environmentally restricted (see Section 3.3).





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Figure 3.4. Diatom environmental group and total flux for the SMB (upper panel) and SBB (lower panel) in number per square centimeter per year. Total = solid circle, Warm = star, Transition = open circle.



Diatoms

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Table 3.1. Order of environmental groups in the SBB by abundance, in descending order left to right, for each year. T = transition fauna, W = warm, I = intermediate. El Niño years are marked with "II"; years of peak radiolarian flux with "*"; years of low radiolarian flux with "-".

54*	Т	W	I	70	W	Т	Ι
55	Т	W	I	71	W	Т	I
56-	W	Т	Ι	1172	W	Т	I
1157*	Т	Ι	W	73	Т	W	I
li58-	Т	W	I	74	Т	W	Ι
59	Т	W	I	75-	Т	W	I
60*	Τ	W	I	1176	Т	W	Ι
61-	W	Т	Ι	ll77*	Т	W	I
62*	Т	W	I	78-	W	Т	I
63	Т	Ι	W	79	Т	W	Ι
64-	Т	Ι	W	80	Т	W	I
1165	Τ	Ι	W	81	Т	W	Ι
66*	Τ	Ι	W	1182	Т	W	I
67-	Ι	Т	W	1183	W	Т	Ι
68	Т	Ι	W	84*	W	Т	Ι
1169*	W	Т	I	85-	W	Т	I
				86*	Т	W	Ι

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However, not every low is associated with a change in environmental group dominance pattern (i.e., 1964, 1975).

The inconsistent abundances of the environmental groups during known climatic events indicate that the isolated highs and lows in flux, as well as the rapid shifts in environmental group dominance, may not be the important signal to study. The lower frequency variability, on the order of 10 years, may be a more useful scale to use when analyzing the fluxes of the environmental groups.

DIATOM ENVIRONMENTAL GROUP FLUXES

The seven species comprising the warm and transition diatom fluxes resemble each other, but, in contrast to the radiolarians, do not closely resemble the total flux (Figure 3.4). The species constituting a major portion of the remaining total flux were *Coscinodiscus* and *Chaetoceros* species. In the SMB, the transition and warm increase with increased diatom flux in 1981 & 1983. The flux of warm and transition diatoms (1979-86) in the SBB shows insignificant variation.

SPECIES RANK AND IMPORTANCE

The Spearman rank correlation coefficients of radiolarian and diatom species ranks for each core over all years show that the cores are highly correlated (Table 3.2). The ranks of radiolarians between the threeperiods of similarity in flux and diversity, 1954-72, 1973-78, and 1979-86, are also highly correlated to each other (coefficients range from .78 to .86).

The Spearman rank correlation coefficients for the annual radiolarian ranks over the entire study period, 1954-86, are all high (Table 3.3). In general, adjacent years are more similar to each other than to years farther removed. The year 1974 is the most unique year and the years 1973-75 have lower coefficients with the years 1976-86 than any other years.

The radiolarian species importance, measured as a percentage of the total, shows a log normal distribution with most of the flux due to relatively few, abundant species and many species occurring very rarely (Figure 3.5). Radiolarian species ranked 1-65 occur regularly all years, species 66-94 occur consistently only after 1978 and are all very rare. Similar treatment of the diatoms is not conclusive due to the small number of species counted. However, the trend in abundances of the seven species counted shows a similar log normal distribution (Figure 3.5).

Table 3.2. Spearman rank correlation coefficients between cores for
radiolarian and diatom species ranks over all years. SBB = SBB '85; SMB =
SMB '85; SABA = SABA 87/1; SLAB1 = SBB 2 1988, slab 1; SLAB5 =
SBB 2 1988, slab 5

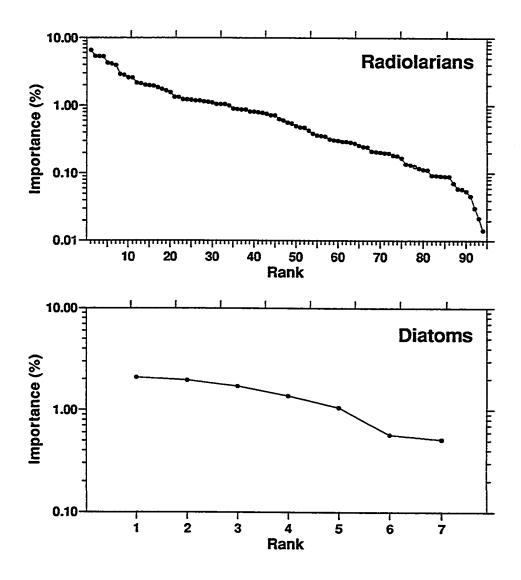
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Radiolarian	IS			
	SMB	SLAB1	SABA	SBB
SLAB5	.80	.88	.74	.85
SMB		.82	.71	.90
SLAB1			.68	.87
SABA				.77
Diatoms				
	SMB	SLAB1	SBB	
SLAB5	.76	.86	.60	
SMB		.79	.83	
SLAB1			.64	

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Figure 3.5. Radiolarian (upper panel) and diatom (lower panel) species importance for SBB and SMB. Species are ranked by total abundance (in flux) over all cores, all years. See Appendix I, Table I.1 for species ranks. Notice the y-axis is a log scale.



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Table 3.3. Spearman rank correlation coefficients between each year for radiolarian species, SBB.

0.77 0.77 0.85 0.85 0.85 0.85 0.85 0.77 0.77 0.83 0.83 0.85 0.85 0.85 0.85 0.74 0.79 0.79 959 0.78 0.81 0.85 0.85 0.78 0.89 1957 956 956 955

3.5 DISCUSSION:

TOTAL RADIOLARIAN AND DIATOM FLUX AND DIVERSITY

El Niños typically result in low zooplankton biomass in the CCS (Chelton et al., 1982) and between 1954 and 1986, several El Niños occurred (Norton et al., 1985). The low radiolarian flux in 1958 and 1959 may be due to the effects of the 1957-58 El Niño. The years 1965 and 1972 were also El Niño years with low radiolarian fluxes. However, during the strongest El Niño, 1982-83, the radiolarian flux was relatively high. Additionally, it was high during the 1969 El Niño. This apparent inconsistency in radiolarian response to El Niño suggests some mechanism other than El Niño has greater influence on flux.

Based on the total radiolarian flux and diversity, there seems to be a switch in circulation regimes in the 1970s. Prior to 1973, the character of radiolarian flux could be considered "normal" for the CCS, being relatively high and in flux and low in diversity. The flux of radiolarians during this time is also fairly variable. After what seems to be a transition period of low flux from 1973-78, the fauna takes on a more tropical character in 1979-86, reflected in its higher diversity and number of warm radiolarian species (see Table I.1 in Appendix I). Diatom data from the SBB also exhibits a change in the 1970s. Lange et al. (1990) document an order of magnitude decrease in productivity from 1973 to 1978, in the SBB, attributing it to an intensified Aleutian Low and associated diminished CC. Intensification of the Aleutian Low in the early 1980s, compared to the late 1960s to early 1970s, has been correlated to increased chlorophyll a in the Central North Pacific (Venrick et al., 1987). During the intervening years, 1974-79, chlorophyll a only increased significantly in the subsurface maximum (Venrick et al., 1987).

The period of lower productivity in the Central North Pacific (1968-73) corresponds to that of strong southerly transport of cool water by the CCS; the period of higher productivity in the Central North Pacific (1980-85) to lower productivity in the CCS, with diminished southerly transport. These two periods approximately coincide with those of distinct radiolarian flux in the SBB; high radiolarian flux, low diversity prior to 1973 and high flux, high diversity, after 1978. The six year transition (1974-79) in chlorophyll a corresponds to the lowest radiolarian flux and low diversity (similar to 1954-73) in the SBB (1973-78). Although the warm and transition fauna have very similar fluxes during the cool 1968-73 period (Figure 3.3), it is not clear why the warm fauna dominates.

Development of a deep Aleutian Low over the Central North Pacific, as in the 1980s, shifts the westerlies south, reducing the cool water entering the CCS (D. Cayan, pers. comm.). Greater influence of gyre or tropical water is indicated in the post-1978 radiolarian record in the higher diversity (Figure 3.2) and greater number of warm species (Appendix I, Table I.1). However, if there is a more tropical influence on the system, one might expect the production, and therefore the flux of radiolarians, to decline. For some reason, this is not the case. Possibly, the radiolarian food source is greater in warmer waters and consequently, the radiolarian density higher. Typically, warmer waters are more oligotrophic with longer food webs and smaller primary producers and consumers. Since radiolarians are small heterotrophs, their prey are most likely small such as exist in oligotrophic water. Alternatively, the high flux in the 1980s may be due to advection of fauna into the basin where the radiolarians die, rather than to high productivity.

The generally higher flux of diatoms in the SBB than SMB suggests higher productivity in the former. The peak in SMB diatoms from 1981-83, when SBB diatoms are relatively low, may indicate a period of anomalous conditions for both basins; the SMB being unusually productive and the SBB unproductive.

RADIOLARIAN AND DIATOM ENVIRONMENTAL GROUP FLUX

The coincidence of peaks in flux having transition radiolarians as the dominant group is probably due to the fact that this group typically dominates. This is not too unexpected since the transition fauna are carried in the CC. The only apparent relationship between flux and dominant environmental group is the association of the flux peaks and lows with the changes in the dominant environmental group (Figure 3.3 and Table 3.1). This suggests that it is perhaps a change in circulation which influences the flux pattern. However, the direction of change in flux (increase or decrease) is not consistent with the change in group dominance pattern. That is, for example, maxima (minima) are not always associated with a change from transition-warm-intermediate (warm-transition-intermediate).

Additionally, there is no consistent pattern in environmental group dominance for El Niño years (1957-58, 1965, 1969, 1972, 1982-83) or for warm, non-El Niño years off California (1967-68, 1976, 1978, 1980-81 years) (Chelton et al., 1982; Norton et al., 1985). Keep in mind that the differences in the fluxes of the environmental groups is very small and statistically insignificant. However, Schimmelmann et al. (1990) conclude that during El Niños, the relative abundance of warm diatoms in the SBB sediment increases.

The lower flux of intermediate relative to the warm and transition radiolarians in the SMB and SBB in the 1980s may be an important feature because it lasts several years and is evident in both basins. Casey et al., (1989) develop a model for 'strong El Niños' in which transition waters move over the borderland and intermediate waters are deeper than normal. The diminished flux of intermediate fauna may be due to this type of mechanism. The depressed intermediated flux in the 1980s occurs when the Aleutian Low deepens (Venrick et al., 1987) and perhaps indicates a deepening of the undercurrent due to diminished geostrophic upwelling and tilting of isopycnals and/or to thickening of the surface layer. Whereas, the "not last" rank of intermediate fauna from 1963-68 suggests upward tilting of the isopycnals perhaps due to stronger southward transport of the CC.

The pattern of low intermediate fauna flux is consistent with a more tropical CCS in 1979-86 and reduced geostrophic upwelling conditions.

In contrast to the radiolarians, the diatom environmental group fluxes do not change with the total diatom flux. This may be due to the inclusion of coastal and oceanic forms in the total flux and only oceanic forms are included in the environmental groups. The different forms respond to different influences so would probably have different fluxes under similar conditions. The radiolarians are all oceanic forms, so this problem is avoided.

SPECIES RANK AND IMPORTANCE

The high correlation of ranks between SMB and SBB radiolarians and diatoms (Table 3.2) indicates no significant difference in environment (i.e., water masses) between the two basins. The high correlation of radiolarians is contrary to the conclusions of Kling (1977) where he shows the two basins contain significantly different species ranks. This discrepancy may be due to the different size fractions used and consequently different species; Kling used the greater than $24\mu m$ while the greater than $45\mu m$ fraction was used here.

The high correlation between cores from the SBB suggests no significant difference between the cores or years since one core covers years 1954-86 (SABA 87/1) and the other cores contain years 1979-86 (SBB 2 1988, slabs 1 and 5) and 1980-85 (SBB '85). It also shows that there is no significant species specific, post-depositional alteration of the assemblage. Through time, the less resistant forms would dissolve more quickly than the more robust forms, reducing their abundance in the older sediment. The reduction in abundance would change the species rank. Although the findings here and those of Kling (1977) indicate stability in ranks on an annual basis, others (Boltovskoy and Riedel, 1987; Welling et al., 1992; Takahashi, 1987a) have found that on a monthly or seasonal scale, relative abundances of species in the CCS varies.

The year to year stability of the species' ranks supports the conclusion that the annual relative proportions of water masses in the CCS have not changed significantly from 1954-86 in spite of the major oceanographic events which have occurred in this time (i.e., 1957-58 and 1982-83 El Niños). However, the very rare species which occur after 1978 (#66-94), indicate incursion of water into the CCS from closer to the core of a water mass (where diversity can be higher than at its periphery (Venrick, 1992)). Twenty one of the species ranked 66-94 are assigned to an environmental group; 18 of these are warm fauna and this supports the conclusion that the CCS was more tropical from 1979-86. The physical oceanography, primarily temperature and salinity, should be useful in determining whether these warm "new" species occur due to incursion of the core of warm water into the CCS. This will be discussed in the next chapter.

In addition to persistent species ranks, the log normal distribution of species abundance is typical of species distributions in other environments (McGowan and Walker, 1985; Hubbell, 1979). Log normal distribution of species within an assemblage (similar to the radiolarian assemblage here) has been attributed to random partitioning of resources (MacArthur, 1957; Cohen, 1968). However, the results of the rank analysis suggest that there is some degree of organization and resilience of the population and that the relative abundances of species are not random. The degree of organization observed is somewhat puzzling since the CCS is a composite of water masses known to undergo fluctuation.

The process(es) responsible for the log normal distribution of radiolarian species and their ranks in the CCS is not clear, but knowledge of the radiolarian distribution is important background information. From a practical standpoint, it allows the analysis of the CCS in the context of being a single environment, where changes in species rank at a location in the CCS would indicate a large scale geographic shift in biotic provinces.

CHAPTER 4: POSSIBLE MECHANISMS AFFECTING RADIOLARIAN FLUX I: WATER MASS

4.1 INTRODUCTION

The lack of any significant change in radiolarian species composition during the study period suggests that the character of the water masses present remained constant. The physical parameters to measure this, temperature and salinity, are unique to each water mass (Sverdrup et al., 1942). The shape of the temperature/salinity (T/S) curve reflects the water masses present. In the CCS, the salinity minimum of Pacific subarctic water (33.40/00) is traceable along the course of the CC from approximately 48°N to 25°N (Lynn and Simpson, 1987). North Pacific central water is also carried by the CC, entering from the south and east, characterized by relatively high temperature and salinity (Lynn and Simpson, 1987). The California Undercurrent (CU) transports a mixture of subarctic, intermediate, and equatorial waters identifiable by low temperature and high salinity (>340/00) (Roesler and Chelton, 1987; Lynn and Simpson, 1987; Pickard and Emery, 1982). South of Point Conception, the CC turns southeast and then counterclockwise over the borderland, merges with warm, high salinity tropical water, forming the California Countercurrent (CCC) (Hickey, 1992). The relative amounts of water masses present can be determined from the water depths along a T/S curve.

Another approach to tracing water masses is to use temperature, or salinity, and depth of density surfaces. An advantage of this method over T/S curves is that water masses can be followed as they mix along a density surface. As the waters mix, their original temperature and salinity are altered, but still traceable along a density surface. In the case of the CCS, a greater influence of northerly (southerly) water is reflected in lower (higher) temperatures and lower (higher) salinities on any given density surface (Lynn, pers. comm.). The core of the CU is characterized by a salinity maximum and dissolved oxygen minimum, both of which lie on the density surface where sigma-t is 26.6 (Lynn and Simpson, 1990). The salinity minimum of the CC is on the sigma-t surface 25.5. This was determined from California Cooperative Oceanic Fisheries Investigations (CalCOFI) data, stations 82.46 and 82.47 in the SBB, by averaging the sigma-t of the salinity minimum over the time period studied.

In addition to indicating the character of the water, the depth of a density surface gives information on the strength of flow. Shoaling of a density surface occurs in areas of upwelling (Simpson and Lynn, 1990). Mackas et al. (1991) found that the zooplankton composition across the CCS shifted at the boundary between the low salinity water of the CC and high salinity, upwelled water. Similar results were obtained from the analysis of phytoplankton (Hood et al., 1991). Both the phyto- and zooplankton biomass in these studies were found to be higher in the upwelled water than in the CC. Radiolaria, however, were observed to increase in flux to sediment traps along a transect from coastal California to CC to North Pacific gyre stations (Gowing and Coale, 1989).

4.2 PURPOSE

From data on T/S curves and sigma-t surfaces, it can be determined whether the physical oceanography supports the radiolarian and diatom data indicating that the CCS water masses have not changed significantly from 1954 through 1986. Variability in the water masses present can be determined from the shape of the T/S curve, while comparisons of depths along the curves will indicate relative amounts of the water masses.

The temperature and salinity of the 25.5 and 26.6 sigma-t surfaces should shed light on whether the water in the CC (25.5) or CU (26.6) has changed in temperature and salinity, indicating northerly or southerly sources. The depth of these surfaces indicates shoaling associated with increased transport and deepening associated with diminished transport, which may correlate to the changes observed in the magnitude of radiolarian flux and/or to the increased diversity apparent in 1979-86.

4.3 METHODS

TEMPERATURE AND SALINITY DIAGRAMS

Temperature and salinity data available from CalCOFI (Scripps Institution of Oceanography, 1954 through 1986) were used in constructing seasonal T/S diagrams for the SBB (CalCOFI stations 82.46 (34° 16.3'N, 119° 56.5'W) and 82.47 (34° 15.0'N, 119° 59.0'W), Figure 1.1). For each season, data from not more than one cruise were used; December, January, and February cruises are considered winter; March, April, and May are spring; June, July, and August are summer; and September, October, and November are fall. Only one cruise per season per year was used so that no season or year were over-represented. In those cases where data from more than one cruise were available for a season, the data taken closest to the middle of the season were used. The average temperature and salinity from 0-300m were calculated for each season over the entire study period and the three time periods of similar flux (1954-72, 1973-78,

Table 4.1

Number of observations (number of years with the season's T/S diagram) for the three time periods of similar radiolarian flux and for the entire study period. The fractions in parentheses are the number of observations per year for the given time period. Excluded fall because there are so few points.

	1954-72	1973-78	1979-86	1954-86
Winter	13(.68)	2 (.33)	3 (.38)	18 (.55)
Spring	8 (.42)	2 (.33)	4 (.50)	14 (.42)
Summer	12(.63)	2 (.33)	4 (.50)	18 (.55)
Fall	4 (.21)	1 (.17)	3 (.38)	8 (.24)
Depth	300m	300m	400-500m	

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and 1979-86). See Table 4.1 for a list of the seasons with data. The seasonal T/S curves were analyzed visually and compared to the average T/S of these three time periods and to the average of the entire period studied. These were then compared to the radiolarian flux and diversity in search of any evidence indicating that changes in flux magnitude and/or diversity coincide with physical changes in the water.

SIGMA-t SURFACES

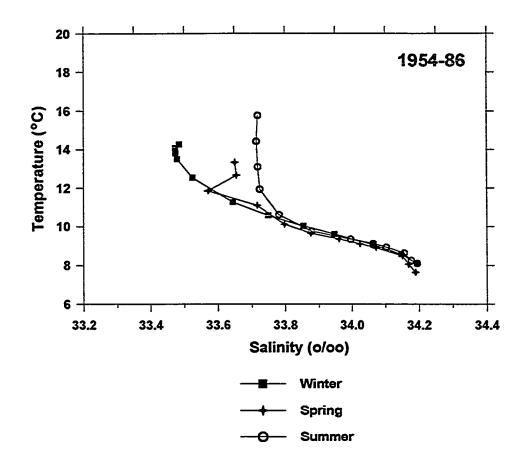
The salinity and depth of the 25.5 sigma-*t* surface, indicating the CC, and of the 26.6 sigma-*t* surface for the CU, were plotted to determine whether water in the currents has remained constant over the study period. Data from CalCOFI stations in the SBB (82.46 and 82.47) are used and augmented with depth data from stations along line 90, stations 30, 32, 33 and 45 (Figure 1.1). Stations 30, 32, and 33 are proximal, so their data were combined and referred to as station '30'. Stations 30 and 45 were chosen so as to monitor the southern California eddy; station 30 lies on the landward side and station 45 at the center of the eddy. Line 90 is included because it is the most frequently occupied line in the CalCOFI grid.

4.4 RESULTS

T/S DIAGRAMS

The water masses in the CCS can be seen in the T/S curve average of the years 1954-1986 (Figure 4.1). Subarctic water in the CC is defined primarily by its low salinity, which can be subsurface at 20-75m (Lynn and Simpson, 1990). The other major surface current, the CCC is warmer and more saline than the CC. The water in the countercurrent is a mixture of Subarctic water and warm, saline North Pacific Central water. At depths of greater than 200m lies the CU which transports a mixture of equatorial, subarctic, and intermediate waters indicated by >340/00 salinity. The faunal groups corresponding to these currents are: Transition fauna in the CC, Warm fauna in the CCC or in the CC (due to mixing with the North Pacific Central water), and Intermediate fauna in the CU.

Analysis of all the curves (each year, each season) indicates that they vary but do not show any obvious interannual trends. However, the seasonal averages for the entire period studied, 1954-1986, are as expected (Figure 4.1). The average winter sea surface temperature (SST) is 14.2°C, sea surface salinity (SAL) is 33.470/00, which corresponds to subarctic type water carried in the CC. Upwelling in spring results in lower SST and higher SAL, 13.8°C and 33.70/00, respectively. By summer, development of the Southern California eddy and associated CCC, is apparent in the higher SST and SAL. The temperature and Figure 4.1. Seasonal average T/S curves for winter, spring, and summer of the study period, 1954-86. Depths of observation are: 0, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250, and 300m. Winter = sauare, Spring = star, and summer = circle.

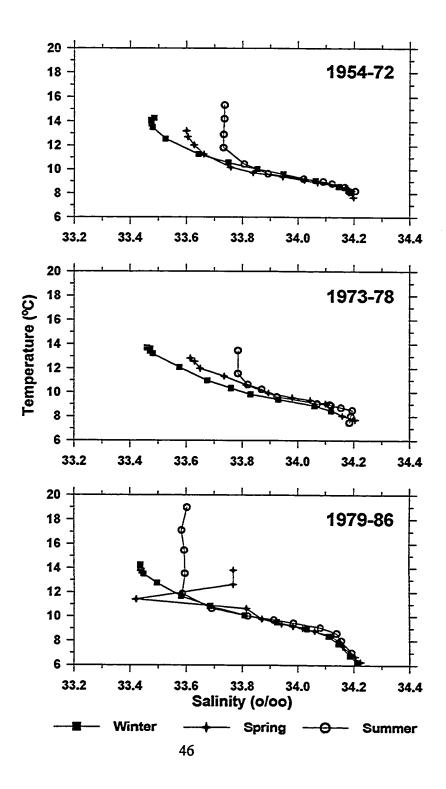


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Figure 4.2. Seasonal average T/S curves for winter (square), spring (star), and summer (open circle) of 1954-72 (upper panel), 1973-78 (middle panel), and 1979-86 (lower panel).

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salinity of water below 10°C and 33.80/00 does not change seasonally. It shoals, as the southerly transport of the CC increases (Hickey, 1979), from a depth of 125m in winter to approximately 60m in summer.

By averaging the T/S curves for each season, over the years in each of three time periods (1954-72, 1973-78, and 1979-86), some trends appear. The winter T/S averages are similar to each other, with surface temperatures of approximately 14°C and salinities of 33.45°/oo (Figure 4.2).

Comparison of winter and spring within each time period

The spring averages of each time period show some differences when compared to the winter curves. Compared to winter, 1954-72, the spring, 1954-72, average is cooler and more saline at the surface (average SST is 13.2°C and SAL is 33.60/00) down to 30m (Figure 4.2). Below 30m, winter and spring curves are the same, but the depths of the points of similar T/S in spring are shallower than winter. In spring, the T/S from 30m to 300m is the same as the winter T/S from 75m to 300m. This shallowing of the T/S is probably due to spring upwelling.

The 1973-78 spring average temperature is lower and salinity is slightly higher at all depths (Figure 4.2). The surface temperature is 12.8°C which compares to the winter temperature at about 38m; surface salinity is 33.60/00 compared to 33.50/00.

The spring average for 1979-86 shows surface temperature about the same as in winter, 14°C, but much higher salinity of 33.80/00, compared to 33.40/00 in winter (Figure 4.2). There is a large excursion at 20m to a salinity minimum of only 33.40/00. Below this, beginning at 30m, the T/S curve is the same as winter at 125m.

Comparison of winter, spring, and summer within each time period

For 1954-72, the summer average surface salinity nearly reaches 33.80/00 and stays constant through 30m. Surface temperature increases from spring's low of 13.2°C to 15.5°C in summer. At 50m and below, the T/S curve is the same as spring at 50m and winter at approximately 110m. The increase in temperature and salinity at the surface indicates development of the CCC. The shallow depths of the curve, as in spring, suggests continued strong southerly flow of the CC.

As in 1954-72, the summer of 1973-78 is warmer and saltier at the surface than in winter and spring, 13.8°C and 33.750/00. Below 20m, the curve is the same as for spring at 50m; and below 50m the same as winter at 150m.

In 1979-86, summer has a very warm and very thick surface layer with SST of 19°C. Its salinity, 33.70/00, is between winter's and spring's. Below 50m, the curve is the same as winter at 75m and below 75m the same as spring at 25m.

Generalized pattern for each time period

1954-72: Surface temperature is lowest in spring, increases to a maximum in summer. Salinity increases in the surface water from winter through summer and the increase in salinity reaches greatest depths in the summer. At depth, the T/S curves are the same. This seasonal pattern is similar to the 1954-86 average.

1973-78: The shape of the winter T/S curve is the same as spring's, but for any given temperature, the salinity is marginally higher in spring (by approximately .050/00). Also, the curve shallows in spring from winter, so the surface conditions are cooler and more saline. In summer, the surface becomes warmer and saltier to a depth of about 30m. T/S at depth does not change through the seasons.

1979-86: Surface water cools and gets saltier in spring, and at 30m an incursion of cool, low salinity water is evident. In summer the surface water gets much warmer and less saline. The water at depth does not change from season to season.

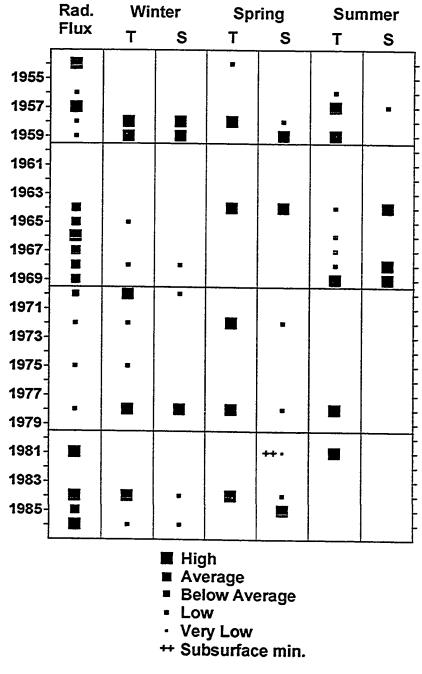
Comparisons of the three time periods to each other

General description of the seasonality of the CC (Hickey, 1979) with cool, low salinity surface conditions in winter, lowering of temperature and increase in salinity in spring due to upwelling, and warmer and more saline surface waters in summer resembles the average seasonality of the years 1954-72. The other two time periods show some departure from this general pattern. The period 1973-78 is cooler at the surface and warmer below the surface in spring than the other two time periods; 1979-86 spring and summer seem reversed compared to the other two periods because the surface salinity in spring, 1979-86, is higher than summer, 1979-86. This is the opposite to spring and summer, 1954-78.

In 1954-72, the summer and spring curves indicate an upwelling of 60m from winter (there is a difference of 60m between waters of equal T/S); 1973-78 shows upwelling of 30m from winter to spring and 45m from spring to summer; 1979-86 shows upwelling of 70m from winter to spring, and downwelling of 50m from spring to summer. On the other hand, the shifting of depths along the T/S curves could be due, in part, to horizontal advection of cool, saline water upwelled.

Table 4.2 Comparison of seasonal T/S curves to the time period averages and to the radiolarian flux. T = temperature, S = salinity.

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A warm, salty cap steadily forms from winter through summer in 1954-72 and forms only in summer during 1973-78. During 1979-86, the cap forms in both spring and summer, however, the summer cap is anomalously thick, warm and low in salinity.

Comparison of T/S to radiolarian flux

Seasons with higher or lower than average temperatures or salinities only occasionally show trends that correlate to the radiolarian flux (Table 4.2). The radiolarian fluxes in 1958 (an El Niño year), 1959, and 1978 (a warm, non el-Niño year) were all below average and were the only years with higher than average winter surface temperatures and salinities. Other lower than average flux years with T/S data, 1972 and 1975, do not exhibit this.

The spring temperature and salinity in 1958, 1972, and 1978 are higher and lower, respectively, than the average of their time period (1954-72 for 1958 and 1972, and 1973-78 for 1978). These three years were El Niño years and all have lower than average radiolarian fluxes. However, 1984, with high radiolarian flux has these same features in its T/S.

SIGMA-t SURFACES

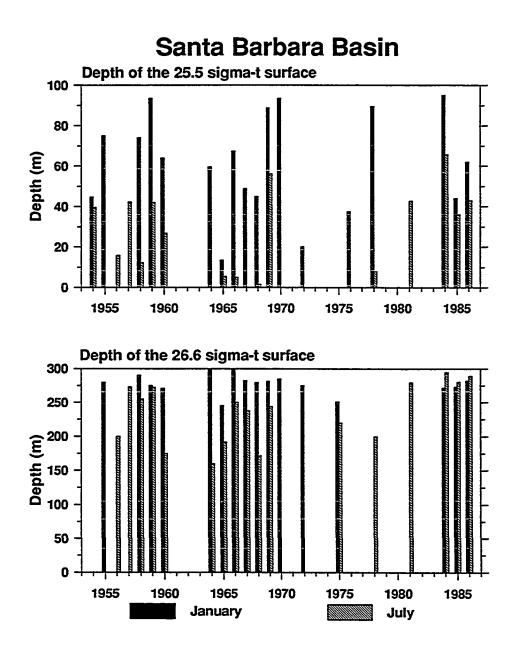
Santa Barbara Basin

The CalCOFI stations in SBB (82.46 and 82.47) were most frequently observed in January and July, therefore only these months will be discussed. The trend of the surfaces from 1954-86 is difficult to assess due to the sparse coverage. However, the depths of the 25.5 and 26.6 surfaces in January are almost always deeper than July (Figure 4.3) and the two surfaces tend to shoal and deepen simultaneously. Occasionally the July depths are similar to the January depths; for the 25.5 surface the years 1954, 1965, 1985; for 26.6, they are 1959, 1985, 1986.

Salinity (and therefore temperature) of the 25.5 surface exhibits seasonality, with higher salinities in July than January (Figure 4.4). The few exceptions to this are the years 1954, 1985, and 1986 when the July salinity is similar to the lower January salinity. The salinity of the 26.6 surface generally does not change seasonally (Figure 4.4). In the few years it does, 1959, 1960, 1985, and 1986, the July salinity is slightly higher than the January salinity. Excepting 1960, these years with higher salinity are the same years with a deeper 26.6 surface.

Figure 4.3. Depth of the 25.5 (upper panel) and 26.6 (lower panel) sigma-*t* surfaces at the CalCOFI Santa Barbara Basin station (82.46 and 82.47) in January and July. Years of observation of the 25.5 surface are: January 1954, 1958-60, 1964-69, 1972, 1978, 1985, and 1986; July 1953, 1954, 1956-60, 1965-69, 1975, 1978, 1981, and 1984-86. Years of observation of the 26.6 surface are: January 1955, 1958-60, 1964-70, 1972, 1975, 1984-86; July 1956-60, 1964-69, 1975, 1978, 1981, 1984-86.

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Figure 4.4. Salinity of the 25.5 (upper panel) and 26.6 (lower panel) sigma-t surfaces at the CalCOFI Santa Barbara Basin station in January and July. See figure 4.3 caption for years of observation.

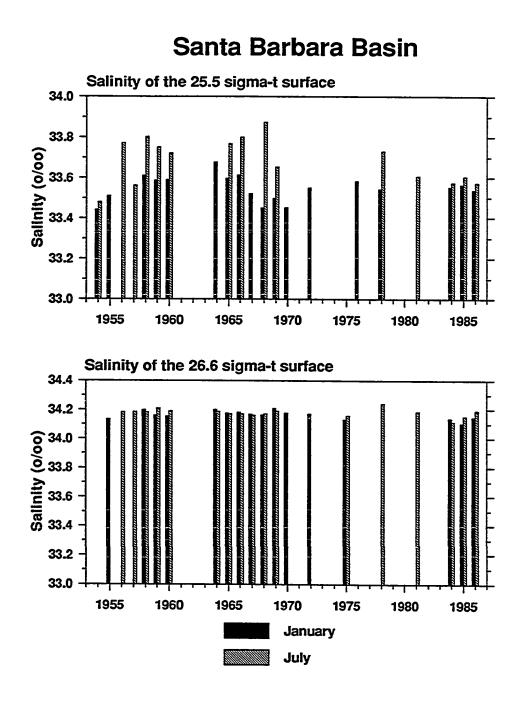
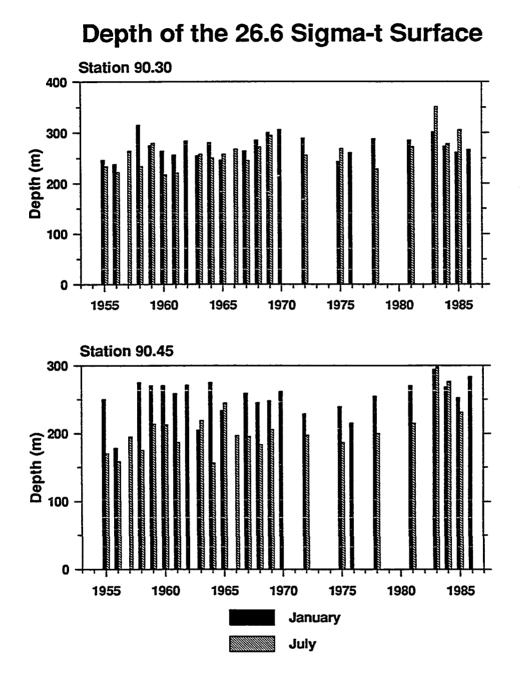


Figure 4.5. Depth of the 26.6 sigma-*t* surface at CalCOFI stations 90.30 (upper panel) and 90.45 (lower panel) in January and July. Years of observation at station 90.30: January: 1955, 1956, 1958-65, 1967-70, 1972, 1975, 1976, 1978, 1981, and 1983-86 (23 out of 34 years); July: 1955-61, 1963-69, 1972, 1975, 1978, 1981, and 1983-85 (21 out of 34 years). Years of observation at station 90.45: January: 1955-56, 1958-65, 1967-70, 1972, 1975-76, 1978, 1981, 1983-86; July 1955-61, 1963-69, 1972, 1975, 1978, 1981, 1983-85.



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CalCOFI Line 90, Stations 30 and 45

As in the SBB, the 26.6 surface is usually deeper in January than July. At station 90.30, in seven of the 19 years with both January and July data, the depth of the 26.6 level was deeper in July than January (Figure 4.5). The years in which the July depth is greater (1959, 1963, 1965, 1975, 1983-85) have no apparent underlying physical oceanographic similarity, that is, they are not all El Niño years, etc. The average January depth is 273m, average July depth is 260m. At station 90.45, the 26.6 level was deeper in January than July, except in 1963, 1965, 1983, and 1984 (Figure 4.5). The average January depth is 252m and the average depth in July is 205m.

The January depth of the 26.6 surface at station 90.30 is nearly always greater than at 90.45. This upward tilt of the isopycnals at station 90.45 is evidence of the cyclonic Southern California eddy. Exceptions include 1955, 1960, 1961, and 1986. The July depths at station 90.30 is greater than 90.45 for all years observed.

4.5 CONCLUSIONS:

T/S DIAGRAMS

Seasonal coastal upwelling off California results in lower SST and increased SAL, whereas advection of CC water lowers salinity. Advection of CCC water increase temperature and salinity. The seasonal pattern of spring upwelling and summer formation of the CCC is evident in the T/S curves for 1954-72 and 1973-79. The seasonal averages for 1979-86 deviate slightly from this pattern in that low salinity surface water was present in summer rather than spring, and high SAL water existed in spring rather than summer. This probably represents the effects of the 1982-83 El Niño which resulted in an onshore movement of the CC and increase advection of tropical and gyre water.

The similarity of the shapes of the T/S curves on all scales, seasonal, annual, and interannual, suggests there is no significant change in the water masses entering the SBB, and by extrapolation, the Southern California Bight. This is consistent with the high correlation of both diatom and radiolarian species ranks for the two basins studied. This being the case, the changes in flux may be due more to the dynamics of the system rather than to changes in water mass. The relative and absolute amounts of vertical to horizontal advection could be the dominant force on the flux of diatoms and radiolarians.

The high fluxes, and presumably high productivity in the 80s might be due to the springtime subsurface, and within the mixed layer, incursion of California type water which is typically high in nutrients. Although the surface temperature in the summer was relatively high, its low salinity indicates that the water is from a northerly source and typical of the water in the CC. Since this water is usually high in nutrients, the high radiolarian flux might be reflecting this source of nutrients. On the other hand, the increased temperature indicates the water has been at the surface for some period, over which the nutrients may have been stripped from the water and not replaced. Data available on nutrient concentrations (i.e., CalCOFI) is insufficient to provide a basis for any conclusions.

SIGMA-t SURFACES

The changes in salinity on the density surfaces sigma-t 25.5 and 26.6 are within the range of seasonal variability, so it seems unlikely that the water masses in the CCS have changed in the period studied.

The depths of the 25.5 and 26.6 sigma-t levels, both in SBB and on line 90 (sigma-t = 26.6 only), are greater in 1983-1986, especially in July. The July depth of these years is more similar to January's. The only trend that appears is the more winter-like summers in the 1980s. Otherwise, the changes in depth are within the range of seasonal variability.

The years in which the July depth and salinity of the 26.6 surface are as great as in January (1959, 1985, and 1986) may indicate a higher proportion of southerly waters mixing in the CU. However, neither the total flux of radiolarians (Figure 3.1) nor the Spearman rank correlation coefficients (Table 3.3) indicate any peculiarities in these three years. Additionally, those years without evidence of the Southern California eddy in January, 1955, 1960, 1961, and 1986, show no distinction in the radiolarian flux or correlation coefficients.

Variability in the T/S curves and sigma-t surfaces for the three time periods are within the range of seasonal change indicating that the water masses in the CCS are fundamentally unchanged over the time period studied. This supports the radiolarian data which also indicate a consistency in water masses of the CCS. Although the temporal coverage of the CalCOFI data set is sporadic, lack of significant change in the water masses in the CCS suggests that the pattern of radiolarian flux from 1954 to 1986 is due more to the dynamics of the system rather than a change in water mass character. Dynamic heights across the CC can be used to determine the rate and direction of flow (and potential upwelling); low heights and southerly flow are conducive to upwelling and should correspond to high fluxes. The following chapter addresses the question of flow and its relationship to radiolarian and diatom flux.

CHAPTER 5: POSSIBLE MECHANISMS AFFECTING RADIOLARIAN FLUX II: CIRCULATION

5.1 INTRODUCTION

The radiolarian and diatom data analyzed in the previous chapters suggest that plankton accurately reflect the character of waters in the CCS. That is, over the time period studied, there is no indication from the plankton of a shift in the physical character of the water masses in the CCS greater than interannual variability and this is supported by the T/S curves and sigma-*t* data. However, the low frequency variability in the magnitude of flux and the coincidence in 1979 of increased flux and diversity suggest a nonrandom, biological response to a fluctuating environmental parameter(s).

The strength of the CC fluctuates on time scales of five to ten years (Huang, 1972), which is the same frequency of change seen in the diatom (Lange et al, 1990) and radiolarian abundances from the SBB sediment. Flow of the CC has been mapped with dynamic height data from CalCOFI (Lynn et al, 1982) and is probably one of the best measures of southerly flow. However, the form of the data (maps) and the temporally incomplete record make direct comparison to the plankton flux data difficult. Chelton et al. (1982) have demonstrated that in the CCS, SST is inversely correlated to southerly transport. Therefore, the record of SST off the California coast can be used as an index of southerly flow in the CCS.

Chelton et al. (1982) also show that zooplankton biomass in the CCS is lower when southerly flow is diminished and SST high. In comparing SST, dynamic height, and chlorophyll \underline{a} across a thermal front in the CCS, Hood et al. (1990) found higher concentrations of chlorophyll \underline{a} on the cooler and geopotentially lower side of the front. The higher production of the cooler periods and of geographic locations is attributed to upwelling (Chelton et al. 1982; Hood et al., 1990) or enhanced southward advection of subarctic water (Chelton et al., 1982), both of which result in lower SST.

The species distribution of zooplankton across the thermal front in the CCS off Northern California exhibit a distinct pattern, with oceanic species only abundant on the seaward side of the front (Mackas et al., 1991), in the low salinity and relatively warmer water (Hood et al., 1991). The distribution of radiolarians in the CCS was found to increase in abundance offshore (Gowing and Coale, 1989) and Alder and Boltovskoy (1993) found that radiolarian abundance

in the Weddell-Scotia confluence area increased with increased temperature. Therefore, the flux of radiolarians to the SBB should correlate positively to sea surface temperatures.

5.2 PURPOSE

The flux of radiolarians and diatoms to the SBB appears to be sensitive to some large scale environmental parameter. One possibility is the southern transport of the CCS which varies at a similar frequency as the flux. However, for reasons mentioned in the previous section, a complete and usable direct measure of flow is not obtainable. By using an indirect measure of flow, e.g. SST, a year-to-year comparison of CC strength to plankton flux for the study period can be made.

5.3 METHODS

Sea surface temperature data sets from a coastal station in the SBB (34°24.2'N, 119°41.6'W) (Walker et al., 1993) and the Namias (Namias et al., 1988) data set from six 5° squares near the California coast (see Figure 5.1 caption for locations) are used. The SBB record is the annual average of monthly SST from multiple measurements beginning in 1955. The 6-point SST record from offshore California is ship-board data and is generated from the mean of six 5° squares. The fairly broad area covered by the 6-point data set represents the overall SST of the CCS, whereas the SBB record is more influenced by effects of coastal upwelling at Point Conception and within the basin.

The relatively high frequency variability in SST was smoothed by taking a three year running average of the SST (the SST for 1956 is the average of SST for 1955, 56, and 57; 1955 is the average of 1955 and 56). The plankton data were also averaged over three years to reduce the effect of the estimated 1+/- year error in sampling the varves. Relationships between SST anomalies (6-point and Santa Barbara) and the radiolarian and diatom flux anomalies were assessed by linear regression. The SST data were lagged at 0, 1, 2, and 3 years relative to the microplankton data to find the best correlation. The Santa Barbara SST data set begins in 1955, so the radiolarian record from 1958-86 is used for the regressions. These same years are used in the regressions with the 6-point California SST to allow comparison between the two SST data sets.

Sea surface salinity data from Scripps Institution of Oceanography in La Jolla, California, in conjunction with the 6-point SST data, provide a continuous measure of the character of the water for the time period studied. The

temperature and salinity are used to evaluate the correlation of radiolarian flux to SST and whether the lags are due to problems in dating the core or due to a fundamental change in the radiolarian response to environmental perturbation.

5.4 RESULTS:

SANTA MONICA BASIN DIATOMS

The flux of diatoms in the SMB shows some correlation to the Santa Barbara SST (Figure 5.1 and Table 5.1). The total flux, as well as the flux warm and transition groups, all correlate best to the Santa Barbara SST with a three year lag of SST. The warm diatoms have the highest correlation (r=.57), followed by the total (r=.52) and transition (r=.46) diatoms.

The six-point California SST shows the highest correlation to the transition and total diatom flux with no lag in the SST (r=.33 and .78, respectively, Table 5.1). The warm diatoms have a high correlation to the SST at zero lag (r=.82), but is highest at a three year lag (r=.84).

Flux of the total and warm diatoms to the SMB exhibits a higher correlation to the 6-point California SST than to the Santa Barbara SST. The flux of transition diatoms, on the other hand, correlates better to the Santa Barbara SST in every case. Additionally, the transition fauna shows a negative correlation to Santa Barbara SST at 0 (r=-.44) and 1 (r=-.39) year lags.

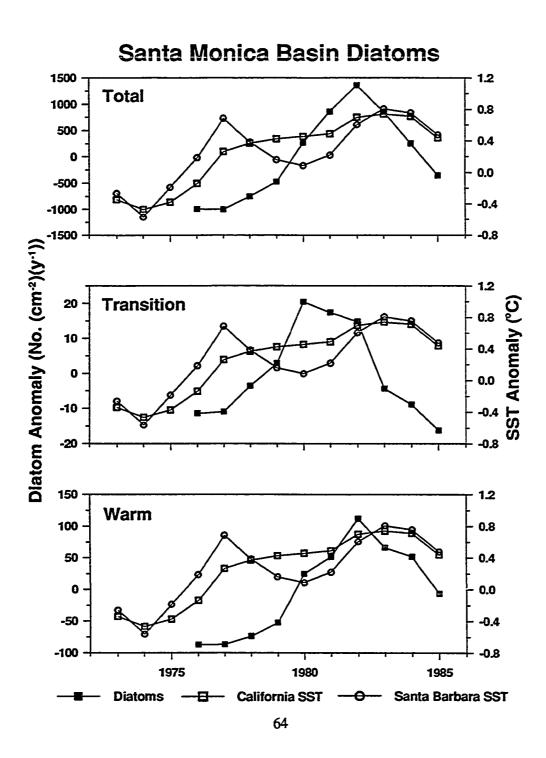
SANTA BARBARA BASIN DIATOMS

Diatoms in the SBB also correlate to SST (Figure 5.2 and Table 5.1). Compared to the Santa Barbara SST, the transition and warm diatoms fit best at zero, the total at two year lags (Table 5.1). The fit of the SBB diatoms to Santa Barbara SST is much better than for the SMB diatoms with the highest r ranging from .65 to -.88. The transition fauna correlate negatively to the Santa Barbara SST.

Relative to the 6-point California SST, the transition and warm diatoms correlate best at a one year lag in SST (r=-.93 and .82 respectively); the total at zero lag, r=-.63 (Table 5.1). These correlations are higher than with the Santa Barbara SST for the transition diatoms, slightly lower for the warm and total. In contrast to the SMB record, the SBB diatom record best fits the SSTs

Figure 5.1. Total (upper panel), transition (middle panel), and warm (lower panel) diatom flux anomalies from the SMB (solid square) and the Santa Barbara SST (open circle) and the six-point California SST (open square) anomalies. The six 5 degree squares are centered at: 40°N, 125°W; 35°N, 125°W; 30°N, 125°W; 30°N, 120°W; and 30°N, 115°W.

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Table 5.1. Results of linear regressions (at the 95% level) of the two SST data sets on the SMB (upper panel) and SBB (lower panel) diatom flux data. The lag is the number of years lag in SST (0-3 years) relative to flux; highest correlation for each temperature and group is bold. Also listed are the y-intercept and slope. All data used were three year running averages of annual values.

TABLE 5.1					
SMB DIATOMS	LAG (yrs)		r	y intercept	slope
A. TOTAL	SBB SST	0	0.25	976	784
		1	0.07	1258	166
		2	0.22	-107	450
ł		3	0.52	1171	1126
	6-PT CA	0	0.53	-1133	2540
		1	0.66	767	1515
		2	0.69	-335	1359
		3	0.74	1117	1465
B. TRANSITION	SBB SST	0	-0.44	10	-22
		1	-0.39	6	-16
		2	0.05	24	2
		3	0.46	23	16
	6-PT CA	0	0.33	17	17
		1	0.2	22	7
		2	0.24	23	7
		3	0.21	24	6
C. WARM	SBB SST	0	0.34	70	91
		1	0.19	95	40
		2	0.31	97	55
		3	0.57	96	106
	6-PT CA	0	0.82	8	227
		1	0.74	57	144
		2	0.78	78	131
		3	0.84	90	141

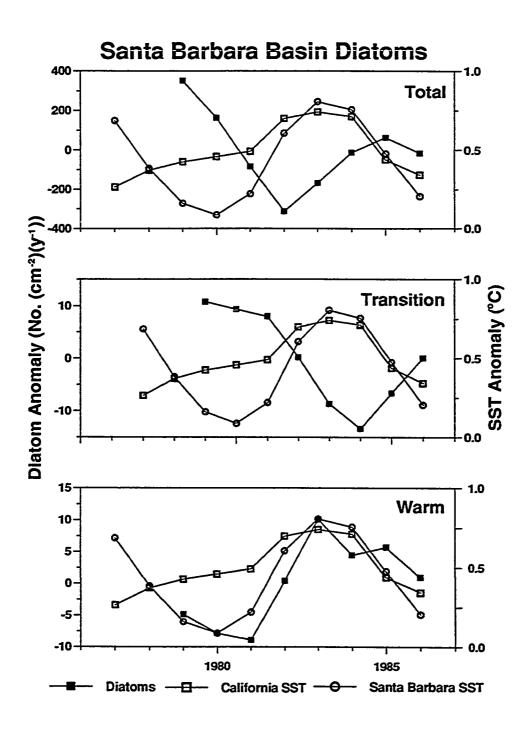
SBB DIATOMS	1	LAG (yrs)	r	y intercept	slope
A. TOTAL	SBB SST	0	-0.62	3127	-441
	r	1	0.05	2927	39
		2	0.65	2730	463
		3	0.28	2862	210
	6-PT CA	0	-0.63	3391	-830
	1	1	-0.34	3196	-464
	1	2	-0.29	3118	-334
		3	0.55	3113	-407
B. TRANSITION	SBB SST	0	-0.88	62	-28
		1	-0.85	63	-28
		2	-0.16	53	-5
		3	0.23	48	8
	6-PT CA	0	-0.59	69	-34
		1	-0.93	81	-56
		2	-0.76	71	-39
		3	-0.64	59	-21
C. WARM	SBB SST	0	0.84	194	20
		1	0.83	194	21
		2	0.19	201	4
		3	-0.27	205	-7
	6-PT CA	0	0.51	191	22
		1	0.82	182	37
		2	0.62	190	24
		3	_ 0.54	197	13

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Figure 5.2. Total (upper panel), transition (middle panel), and warm (lower panel) diatom flux anomalies from the SBB (solid square) and the Santa Barbara SST (open circle) and the six-point California SST (open square) anomalies. All data were averaged over three years. See figure 5.1 caption for the location of the six 5° squares.

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at zero or 1 year lags and, at any given lag, there is no apparent consistency to which SST correlates best. The total is negatively correlated to the 6-point California SST and the transition correlates negatively to both SSTs.

RADIOLARIANS

Upon visual comparison of the SST to total radiolarian flux, there appears to be a positive correlation between the two, with approximately a two to three year lag in the radiolarian flux behind the SST (Figures 5.3 and 5.4). As described below, the correlations between radiolarian flux and the Santa Barbara SST are significant but not as high as with the oceanic, 6-point California SST.

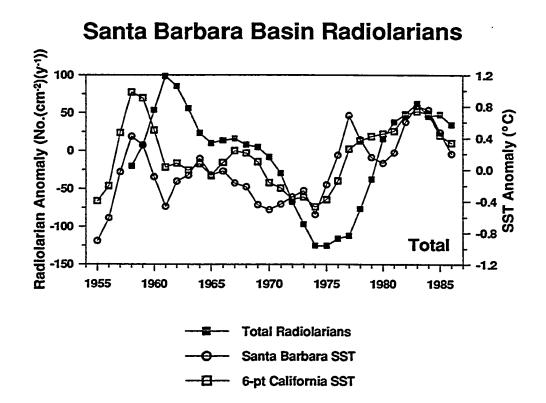
The best correlation of flux to Santa Barbara SST is obtained with a three year lag in the SST (Table 5.2). The total, warm, and transition, correlate at r=.60, .65, and .55, respectively. The intermediate fauna does not correlate to the SST (r=.28).

Six-point California SST has the highest correlation to radiolarian flux at a two year lag (Table 5.2), except for the intermediate fauna which fits best with a 3 year lag in the SST. The fit of the 6-point California SST to the radiolarian flux is better after approximately 1965 than it is prior to 1965. This is measured statistically by linear regression (Table 5.3). The data set is split in 1970, rather than at 1965, in order to have enough data points for a regression and to equalize the number of data points in the two periods (1958-70 and 1971-86).

SAL and the 6-POINT CALIFORNIA SST

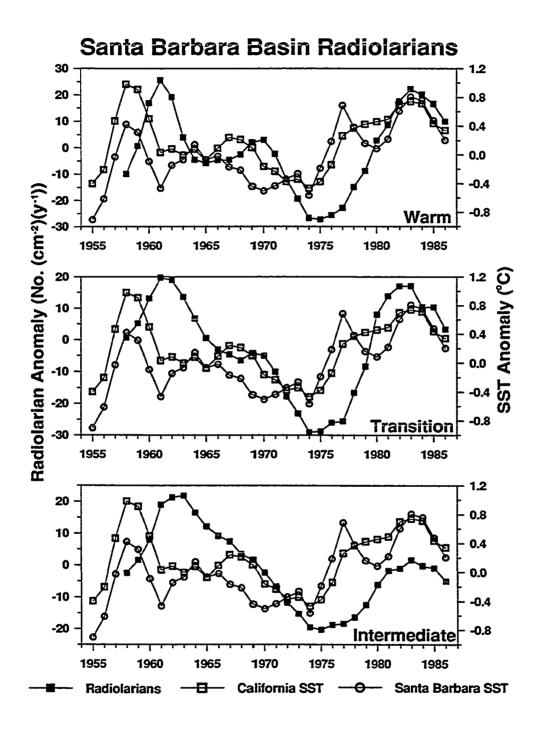
The surface salinity and 6-point SST exhibit an inverse relationship to each other (Figure 5.5) from 1954-86. Periods with lower temperatures and higher salinities indicate the influence of coastally upwelled waters; higher temperatures and lower salinities reflect the shoreward displacement of the CC during periods of low southerly transport.

Figure 5.3. Total radiolarian flux anomaly (solid square) and the Santa Barbara SST (open circle) and the six-point California SST (open square) anomalies. All are three year running averages. See figure 5.1 caption for the location of the six 5° squares.



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Figure 5.4. Warm (upper panel), transition (middle panel), and intermediate (lower panel) radiolarian flux anomalies and the Santa Barbara SST (open circle) and the six-point California SST (open square) anomalies. All are three year running averages. See figure 5.1 caption for the location of the six 5° squares.



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Table 5.2 Results of linear regressions (at the 95% level) of the two SST data sets on the SBB radiolarian data set. The lag is the number of years lag in SST (0-3 years) relative to the flux; highest correlation for each temperature and group is bold. Also listed are the y-intercept and slope. All data used are three year running averages of annual values.

TABLE 5.2					
RADIOLARIANS		LAG (yrs)	r	y intercept	slope
A. TOTAL	SBB SST	0	0.16	-6	26
	1	1	0.32	-7	53
		2	0.5	5	81
		3	0.6	-0.01	96
	6-PT CA	0	0.49	-22	80
		1	0.69	-29	113
		2	0.84	-30	135
		3	0.84	-25	134
B. WARM	SBB SST	0	0.23	-1	9
		1	0.4	-2	16
		2	0.59	1	23
		3	0.65	0.4	25
	6-PT CA	0	0.51	-5	20
		1	0.75	-7	29
		2	0.92	-8	36
		3	0.89	-6	34
C. TRANSITION	SBB SST	0	0.28	-2	11
		1	0.38	-2	15
		2	0.49	-2	19
		3	0.55	-0.7	21
	6-PT CA	0	0.59	-6	23
		1	0.75	-8	29
		2	0.83	-8	32
		3	0.8	6	30
D. INTERMEDIATE	SBB SST	0	-0.1	-1	-3
		1	0.001	-1	0.2
	ł	2	0.14	-1	4
		3	0.28	-1	8
	6-PT CA	0	0.19	-3	6
		1	0.36	-4	11
		2	0.52	-4	16
		3	0.63	-4	20

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Table 5.3. Results of the linear regression (at the 95% level) of the 6-point California SST at 0, 1, 2, and 3 year lags in SST on total radiolarian flux, 1958-70 and 1971-86. All data were averaged over three years.

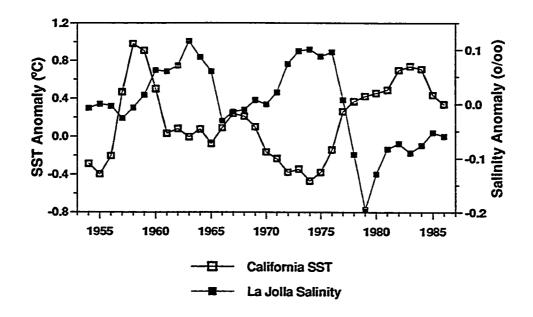
Table	5.3

	LAG (yrs)	Г	y intercept	slope
1958-70 Calif. SST	0	-0.3	0.31	-0.003
	1	0.06	0.26	0.0006
	2	0.69	0.07	0.007
	3	0.93	-0.08	0.01
1971-86 Calif. SST	0	0.81	0.34	0.005
	1	0.92	0.33	0.006
	2	0.96	0.31	0.006
	3	0.92	0.26	0.005

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Figure 5.5. Anomalies of the three year running averages of the six-point California SST (open square) and La Jolla sea surface salinity (solid square).

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5.5 CONCLUSIONS:

Both plankton groups generally correlate well to the 6-point California SST, indicating that the diatom and radiolarian record reflects the broader CCS SST and the strength of the CC. The lag in SST required for best fit is greater for the radiolarians than the diatoms which may be due to the higher trophic level of the radiolarians. The lag could be due to a lag in the response time of the plankton and/or a problem in dating the core. The diatom and radiolarian fluxes are discussed separately in the following paragraphs.

DIATOMS

The brief diatom records for the SMB and SBB indicate a positive correlation between diatom flux and SST. However, most of the correlations to the SMB diatoms generally are low and, considering the short diatom life span, at a rather long lag in SST. The positive correlation to SST is difficult to explain for the transition and total diatom flux, since diatom abundance has been found to be higher in the cooler waters of the CCS (Tont, 1981). The very high positive correlation of the warm flora to the SST indicates the species enumerated are indeed warm water indicators. The transition flora in the SMB correlate better to the Santa Barbara SST suggesting that their distribution is related to a local mechanism affecting the SST in the SBB.

The higher correlation of SBB than SMB diatoms to SST, suggests the flux to the SBB may be a more useful indicator of SST and southerly flow. The significantly high correlations of the warm and transition flora, at zero to one year lags, further supports the conclusion that these groups reflect the SST. The variability in lag and the SST of best correlation does not show any persistent pattern and eludes conclusions. Again, the positive correlation of diatoms to SST is contrary to some studies (Takahashi, 1987b) and is addressed below.

RADIOLARIANS

The three year running average of radiolarian flux is highly correlated to the three year running average of sea surface temperature. All groups are better correlated to the open ocean SST (6-point California SST) than to the coastal SST, regardless of the amount of lag in SST. This is not unexpected because of the pelagic nature of radiolarians (Gowing and Coale, 1989). All groups have higher correlations to the SST when it is lagged by two to three years. This seems long considering the short life span of radiolarians, estimated at 1-3 months (Casey et al., 1971; Berger, 1976; Takahashi, 1983; Caron and Swanberg, 1990). Perhaps part of the lag reflects the population's resistance to environmental variability.

The SST and radiolarian flux show higher correlations after 1970 than

before (Table 5.3). This could be due to either a fundamental change in the radiolarian response to SST or other physical parameter not reflected in the SST, or to an error in dating the core. Since temperature together with salinity are used to define water masses and the source of waters (Huang, 1972; Hood et al., 1991), a change in the relationship between temperature and salinity in the study area could indicate cause for change in the relationship between radiolarian flux and SST. As illustrated in figure 5.4, the SST and SAL are inversely related in the years 1954-86. This does not support the conclusion that the poor fit of radiolarian flux to SST is due to a change in radiolarian response to the environment. Additionally, both periods before and after 1970 contain years with high and low temperature and salinity making it unlikely that the break in 1970 is due to either high or low temperature or salinity. On the other hand, the improved fit of the 1958-70 flux to SST with increased lag in SST (Table 5.3), suggests there could be some error in the dating of the core and this is the source of poor fit prior to 1970.

The positive correlation of the radiolarian flux to SST is somewhat unexpected because, typically higher biomass is associated with lower water temperatures and stronger southerly flow of the CCS (Chelton et al., 1982). However, in the case of radiolarians, positive correlations between temperature and abundance have been documented in the Antarctic (Alder and Boltovskoy, 1993; Gowing and Garrison, 1991; and Morley and Stepien, 1984). Alternatively, the warmer temperature may result in a die-off of radiolarians, producing the higher flux under warmer conditions. The increase in diversity in 1978-86 (Figure 3.2) corresponds to persistently high SST and radiolarian flux during this time, suggesting that water of southerly or gyre origin (which is warmer and has high radiolarian abundance) may also have higher radiolarian diversity.

In the CCS, SST is lower when winds are northerly and more subarctic water enters the CC (Lange et al., 1990; Cayan, pers. comm.). These northerly winds also generate jets of cool, coastal water (Kosro et al., 1991) which are incorporated into the CC. Conceivably, periods of persistent northerly winds would have more jets, resulting in lower temperatures, than periods of more southerly winds. In addition to possibly lowering the CCS SST, the jets add coastal water with lower radiolarian density (Gowing and Coale, 1989). This is one possible explanation for the positive correlation between radiolarian flux and SST, but it does not necessarily explain the positive correlation to the diatom fluxes.

Hood et al. (1991) describe the coastal jet water as being high in chlorophyll \underline{a} with large, chain-forming diatoms (40-50µm), whereas on the low

salinity side of the jet, lower chlorophyll and small, single-celled diatoms were noted. The diatom flux in this study includes the greater than 25µm fraction, which may contain smaller cells abundant in the low salinity water. In periods of warm SST in the CCS, the low salinity water of the CC is displaced shoreward (Huang, 1972; Simpson, 1983b). This could account for the higher abundance of diatoms, as well as radiolarians, in the SBB during warm periods. The high negative correlation of the transition flora in the SBB to SST at 0 and 1 year lags suggests they may serve as a proxy for SST, but more of the record must be analyzed.

CHAPTER 6: CONCLUSIONS

The diversity, wide ranging habitats and endemism of radiolarians and diatoms make these groups useful biological indicators of physical oceanography. However, these same characteristics also make interpretation of radiolarian data difficult due to our lack of knowledge. Understanding the distribution of radiolarian abundance and species is necessary in order to use them as oceanographic tools. In the case of the CCS, whose circulation is closely tied to atmospheric circulation and climate, the potential of radiolarians and diatoms as indicators necessitates a thorough understanding of the plankton distribution. The unique sedimentary conditions of the SBB preserve the microplankton record at an annual resolution. Analysis of this sedimentary record, together with available physical oceanographic data, can improve the utility of radiolarians and diatoms as indicators of the CCS physical oceanography. Unfortunately, the limited scope of the diatom record analysis here may preclude interannual comparison of diatom distribution and annual physical oceanographic data.

Two significant conclusions from the data presented here contribute to the utility of radiolarians as indicators of the CCS. First, the log normal distribution in abundance of radiolarian species suggests that the population in the SBB represents a single environment. The consequence of this on radiolarian abundance is that, in general, all species increase and decrease simultaneously. The relative abundances of the species are sufficiently resilient to withstand perturbations due to El Niño. However, the very small changes in abundance between the environmental groups may contain information on the nuances of CCS circulation not yet evident, but which may become so with further study.

The second important finding is that the SBB radiolarian flux is significantly correlated to the regional SST of the CCS, suggesting that the flux is a response to the prevailing circulatory conditions and not solely anomalous events (i.e. El Niño). This could prove an invaluable tool in reconstructing the recent paleoclimate since climatologists are currently hindered by lack of reliable prehistoric SST values. However, the reliability of the radiolarian record needs further investigation to determine the source of lag which occurs prior to approximately 1965 in the core analyzed here. The problem may lie in the dating of the core. Some resolution was lost by subsampling the SABA 87/1 core prior to X-raying. Additionally, there is no evidence indicating a change in the relationship between radiolarian flux and SST. Such evidence could be a change in the relationship between SST and sea surface salinity, but the two are inversely proportional throughout the study period.

The correlation of radiolarian flux to SST and the consistent species ranks during El Niño and non-El Niño periods indicates that the radiolarian record is controlled by a mechanism other than El Niño. The coincidence of the three periods of similar flux with the periods of productivity in the North Pacific gyre characterized by Venrick et al. (1987) suggests that the flux reflects the coupling of the two systems and the large scale atmospheric circulation over the North Pacific which drives them. Furthermore, the composite winter sea level pressure anomaly over the Northern hemisphere for the 12 years of highest radiolarian flux during 1954-86 (Figure 6.1) is similar to the Pacific North American circulation mode with a deep Aleutian Low over the North Pacific and a high pressure center over the Pacific Northwest.

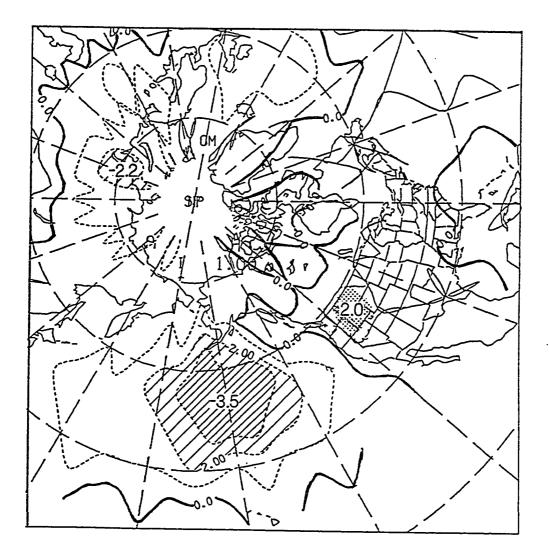
One possible mechanism which can account for the interannualinterdecadal patterns of radiolarian flux and oceanographic data is that they are driven by the atmospheric circulation. First, consider the conditions leading to low SST in the CCS. Upwelling along the West Coast incorporates cold, high salinity water into the southerly flowing CC in the form of 'filaments'. Mixing these filaments into the CCS reduces its SST. Radiolarian densities in the waters of the CCS are lowest along the coast in upwelled waters and increase offshore in the California Current water. Conceivably, with more upwelling, more filaments form and are mixed into the CC, lowering its temperature and incorporating into it waters with low radiolarian density. This would result in lower radiolarian flux with lower SST. It also explains the high salinity which characterizes the very low temperature water in the CCS. The atmospheric condition conducive to upwelling along the West coast is a northerly and westerly positioned weak Aleutian Low producing winds which lie farther north and move more westerly.

When the Aleutian Low is deeper, it shifts south and east forcing the westerly winds to the south, producing southwesterly winds. Winds with this direction are not conducive to upwelling along the West coast, resulting in less cold, high salinity, low radiolarian density water entering the CC. The southerly source of the winds might lead to more gyre-like water entering the CCS and these waters have high radiolarian density. Consequently, with a deep Aleutian Low the SST is higher (because of less upwelled water) as also is radiolarian flux (due to less dilution by upwelled and perhaps more water with high radiolarian density water entering the system). Without conditions conducive to upwelling, the intermediate waters with the endemic fauna do not reach as shallow depths as is the case without deep Aleutian Lows, so there is depressed flux of intermediate fauna.

Figure 6.1. Composite winter sea level pressure anomaly over the Northern Hemisphere for the 12 years of highest radiolarian flux, 1954-86.

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Possibly, during periods of persistent deep Aleutian Lows, such as after the mid-1970s, more water from the Eastern Tropical Pacific and North Pacific central gyre moves along the west coast bringing high radiolarian density and diversity water into the Bight area.

The nearly constant relative proportions of radiolarian groups suggests a degree of constancy in the circulation of the CCS. However, two features of the radiolarian flux after 1978 suggests a shift to slower circulation and a greater influence of tropical and/or subtropical waters. First, the depressed flux of intermediate fauna and second, the persistent occurrence of warm species, ranked between #66 and 94. The constancy in circulation indicated by the radiolarian flux is confirmed by the physical oceanography. The sigmat and T/S curves show no interannual variability greater than that of the seasonal variability for the time period studied. The influence of warm waters after 1978, as indicated by the radiolarian data, is equivocally indicated by the increased depths of the sigma-t surfaces and the warmer surface waters on the T/S curves from 1979-86. The sporadic temporal coverage prohibits a more definitive conclusion.

The extensive temporal and spatial coverage of the SST data sets, on the other hand, provides the basis for a more conclusive comparison of the microplankton data to the physical oceanography. The higher correlation of radiolarian flux to 6-point SST suggests that the flux to the SBB reflects the conditions of the broader CCS; whereas the diatoms correlate better to the Santa Barbara SST indicating the flux of diatoms is influenced more by the coastal environment.

Determining the environmental factors to which plankton respond and the nature of the responses is critical to the development of models of paleocirculation, -productivity, and -climate. The radiolarian and diatom data from the SBB could prove to be a useful tool in this modeling. The unique varved sediment in the SBB and the relatively long SST data set available (1900 to present) provide the opportunity to investigate the relationship between the microplankton and SST beyond 1954. This record may be sufficient to test the correlation between SST and microplankton flux. If the relationship is shown to persist, the varves could be analyzed back thousands of years and the SST reconstructed. By combining this record with other high resolution records such as tree rings, coral bands, and glacial ice layers, the history of interannual paleo-climate change should be attainable.

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APPENDIX I: BRIEF DIATOM AND RADIOLARIAN TAXONOMIES AND SPECIES LISTS BY RANK (TABLE I.1)

TABLE I.1

Ranked diatom and radiolarian species and environmental province as determined from the literature (for references, see the taxonomy following this Table). (For flora and fauna of known province, W=warm, T=transition, and I=intermediate fauna, otherwise the province is not known.)

DIATOM SPECIES

RANK	SPECIES	ENVIRONMENT
1	Roperia tessellata	W
2	Hemidiscus cuneiformis	W
3	Coscinodiscus marginatus	Т
4	Azpeitia nodulifer	W
5	Azpeitia africanus	W
6	Asteromphalus arachne	W
7	Fragilariopsis (Pseudoeunotia) doliolus	W

RADIOLARIAN SPECIES

RANK	SPECIES	ENVIRONMENT
1	Hexacontium gp.	
2	Lophophaena gp. B	
3	Arachnocorallium calvata gp.	Т
4	Larcopyle buetschlii	Т
5	Spongodiscid spp.	Т
6	Lophospyris/Phormospyris spp.	
7	Botryostrobus auritus/australis	
8	Lithomelissa setosa	I
9	Litheliid gp. A	
10	Dictyophimus gracilipes	Т
11	Lophophaena gp. A	
12	Peromelissa spp.	
13	Tetrapyle octacantha	W
14	Pterocorys minythorax	W
15	Litheliid gp. B	
16	Botryostrobus aquilonaris	Ι
17	Phormostichoartus corbula	W

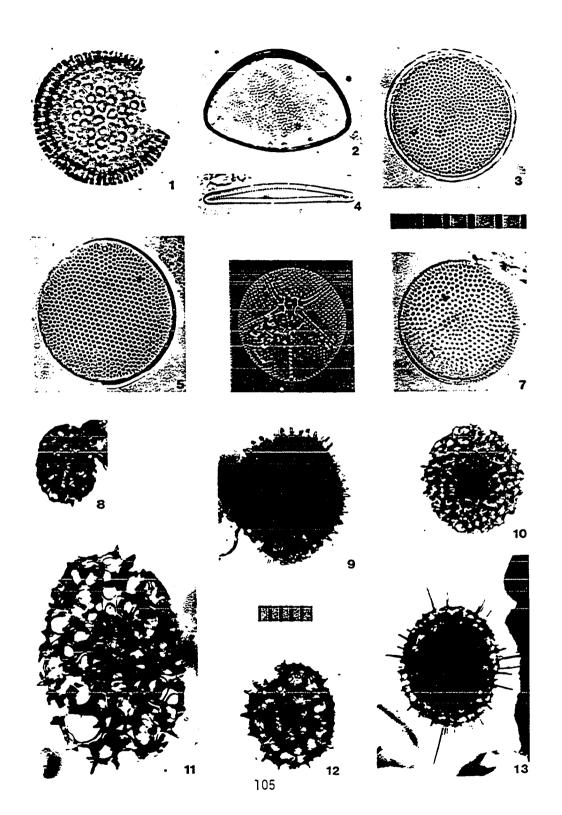
18	Plectacantha spp.	
19	Porodiscid gp.	
20	Actinommid gp.	
21	Peridium spinipes	
22	Pterocorys zancleus	W
23	Spongotrochus glacialis	I
24	Theocalyptra bicornis	I
25	Lithelius minor	T
26	Spongurus cf. S. elliptica	w
27	Spongopyle osculosa	I
28	Spongotrochus (?) venustum	Т
29	Theocalyptra gegenbauri	I
30	Lampromitra quadricuspis	
31	Octopyle stenozona	W
32	Theocalyptra davisiana cornutoides	Т
33	Eucyrtidium acuminatum	W
34	Astrosphaerid gp.	
35	Helotholus histricosa	Т
36	Carpocanistrum gp.	W
37	Cornutella profunda	I
38	Dictyophimus infabricatus	Т
39	Theocalyptra davisiana davisiana	I
40	Pterocanium korotnevi	Т
41	Eucyrtidium hexagonatum	W
42	Hexapyle spp.	W
43	Dictyophimus spp.	
44	Lophospyris pentagona pentagona	W
45	Pylospyra octopyle	W
46	Pterocorys spp.	
47	Lamprocyrtis nigriniae	I
48	Corocalyptra columba	
49	Botryopyle spp.	
50	Arachnocorys circumtexta	Ŵ
51	Eucyrtidium spp.	
52	Didymocyrtis tetrathalmus	W
53	Clathrocyclas bicornis	Т
54	Spongocore puella	Т
55	Dictyophimus hirundo	W
57	Cypassis irregularis	W
58	Cladoscenium tricolpium	
59	Spirocyrtis scalaris	W

60	Anthocyrtidium zanguebaricum	W
61	Dictyocoryne truncatum	w
62	Collosphaerid gp.	
63	Cannobotryid gp.	
64	Peripyramis circumtexta	I
65	Dictyophimus crisiae	-
66	Larcospyra quadrangula	W
67	Stichopilium bicorne	w
68	Neosemantis distephanus	w
69	Pterocanium trilobum	
70	Pterocorys hertwigii	w
71	Eucyrtidium anomalum	w
72	Phormospyris stabilis stabilis	W
73	Pterocanium praetextum praetextum	W
74	Botryocyrtis scutum	w
75	Stylosphaerid gp.	
76	Lampromitra spp.	
77	Litharachnium tentorium	W
78	Lophocorys polyacantha	W
79	Dictyocoryne spp.	W
80	Heliodiscus asteriscus	W
81	Pterocanium praetextum eucolpum	Т
82	Spongaster tetras irregularis	Т
83	Peridium spinipes longispinum	
84	Theocorythium trachelium	W
85	Dictyocoryne profunda	W
86	Lithostrobus hexagonalis	w
87	Pteroscenium pinnatum	
88	Anthocyrtidium ophirense	W
89	Lamprocyclas maritalis	I
90	Lithopera bacca	w
91	Clathrocanium coarctatum	
92	Euchitonia furcata	W
93	Amphiplecta spp.	
94	Amphirhopalum ypsilon	W

Plate I.1.

Figures 1-7 x 400 (large scale bar, each division = 10 um) Figures 8-13 x 250 (small scale bar, each division = 10 um)

- 1. Coscinodiscus marginatus
- 2. Hemidiscus cuneiformis
- 3. Azpeitia africana
- 4. Fragilariopsis (Pseudoeunotia) doliolus
- 5. Roperia tessellata
- 6. Azpeitia arachne
- 7. Azpeitia nodulifer
- 8. Larcopyle butschlii
- 9. Litheliid group B
- 10. Spongodiscid
- 11. Larcopyle butschlii
- 12. Litheliid group A
- 13. Lithelius minor

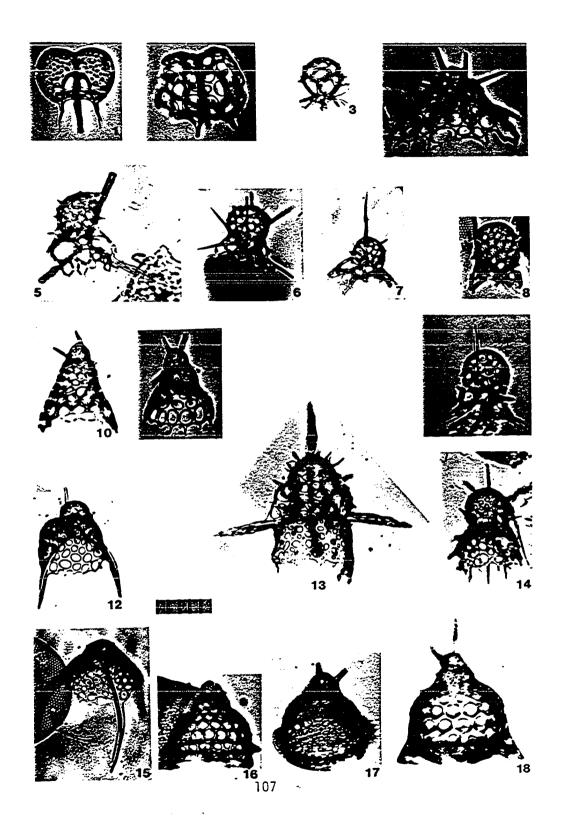


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Plate I.2

Figures 1-18 x 250 (each division on scale bar = 10 um)

- 1-2. Lophospyris/Phormospyris group
- 3. Peridium spinipes
- 4. Helotholus histricosa
- 5-7. Lophophaena group A
- 8-9. Arachnocorallium calvata group
- 10. Theocalyptra davisiana cornutoides
- 11. Theocalyptra davisiana davisiana
- 12. Dictyophimus gracilipes
- 13-14. Lophophaena group B
- 15. Dictyophimus gracilipes
- 16-17. Clathrocyclas bicornis
- 18. Theocalyptra bicornis



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DIATOM TAXONOMIC AND ENVIRONMENTAL REMARKS

The partial taxonomies given below include references to recent descriptions and illustrations of the flora, as well as references used for environmental interpretation. The taxonomy of Round et al. (1990) is followed.

Division Bacillariophyta Class Coscinodiscophyceae Subclass Coiscinodiscophyceae Order Coscinodiscales Family Coscinodiscaceae Coscinodiscus marginatus Ehrenberg Cupp, 1943, p.55, fig. 19, pl. 1, fig. 3; Schrader and Gersonde, 1978, pl. 2, fig. 9, pl. 3, fig. 1. Cold flora, Kanaya and Koizumi, 1966; Schrader and Gersonde, 1978.

Family Hemidiscaceae

Azpeitia africana (Janisch ex Schmidt) Fryxell & Watkins Fryxell et al., 1986, p. 22-23, pl. XXII, XXIII. Warm flora, Fryxell et al., 1986.

Azpeitia nodulifer (Schmidt) Fryxell and Sims

Fryxell et al., 1986, p. 19-20, figs. XVII, XVIII-1, 2, 4, 5, XXX-3, 4. Warm flora, Kanaya and Koizumi, 1966; Fryxell, et al., 1986; Lange et al., 1990.

Hemidiscus cuneiformis Wallich

Round et al., 1990, p. 192-193, figs. a-i. Warm flora, Kanaya and Koizumi, 1966; Fryxell et al., 1986; Lange et al., 1990.

Roperia tessellata (Roper) Grunow Round et al., 1990, p. 198-199, figs. a-k. Warm flora, Hasle, 1976; Fryxell et al., 1986; Lange et al., 1990.

Order Asterolaprales

Family Asterolampraceae

Asteromphalus archne (Breb.) Ralfs in Pritchard Hustedt, 1930, p. 493, fig. 276; Scrader and Gersonde, 1978, pl. 2, fig. 2.

Warm flora, Schimmelmann et al., 1990.

Subclass Rhizosoleniophycidae Order Rhizosoleniales Family Rhizosoleniaceae Fragilariopsis (Pseudoeunotia) doliolus (Wallich) Medlin and Sims, 1993 Barron, 1985, p. 788, fig. 13.2. Warm flora, Hasle, 1976; Lange et al., 1990.

RADIOLARIAN TAXONOMIC AND ENVIRONMENTAL REMARKS

The radiolarian taxonomy below primarily follows that of Nigrini and Moore, 1979. Included are references to the original description, recent illustrations, and environmental interpretation. The genera and species under each family are listed in alphabetical order.

Order SPUMELLARIA

Family COLLOSPHAERIDAE Collosphaerid group

This includes Siphonosphaera polysiphonia Haeckel, 1887, and Polysolenia spinosa (Haeckel, 1860).

Family ACTINOMMIDAE

Actinommid group This includes Actinomma antarcticum (Haeckel, 1887), A. medianum Nigrini, 1967. Astrosphaera spp. Hexacontium group Stylosphaera spp.

Family LITHELIIDAE

Larcopyle buetschlii Dreyer, 1889
Nigrini and Moore, 1979, p. S131, pl. 17, fig. 1A, B. Transition fauna, Kling, 1977; Sachs, 1973.
Larcospyra quadrangula Haeckel, 1887
Nigrini and Moore, 1979, S133, pl. 17, fig. 2.
Warm fauna, Kling, 1979.
Litheliid group A

Includes loosely coiled litheliids.

Litheliid group B

Includes tightly coiled litheliids.

Lithelius minor Jorgensen, 1899 Nigrini and Moore, 1979, p. S135, pl. 17, figs. 3, 4A,B. Transition fauna, Molina-Cruz, 1977.
Spongosphaera streptacantha Haeckel, 1862 Renz, 1976, p. 105, pl. 2, fig. 13; Boltovskoy and Riedel, 1987, p. II, fig. 10.

Family PYLONIIDAE

Hexapyle spp. Nigrini and Moore, 1979, p. S121, pl. 16, figs. 1A-C Warm fauna, Molina-Cruz, 1975.
Pylospyra octopyle Haeckel, 1887 Nigrini and Moore, 1979, p. S139, pl. 17, figs. 6A-C Warm fauna, Molina-Cruz, 1977.
Octopyle stenozona Haeckel, 1887 Nigrini and Moore, 1979, p. S123, pl. 16, figs. 2A, B. Warm fauna, Molina-Cruz, 1977.
Tetrapyle octacantha Mueller, 1858 Nigrini and Moore, 1979, S125, pl. 16, figs. 3A, B.

Warm fauna, Robertson, 1975.

Family SPONGODISCIDAE

Amphirhopalum ypsilon Haeckel, 1887 Nigrini and Moore, 1979, p. S75, pl. 10, figs. 1A-E. Warm fauna, Boltovskoy and Riedel, 1980. Dictyocoryne spp. Dictyocoryne profunda Ehrenberg, 1860 Nigrini and Moore, 1979, p. S87, pl. 12, fig. 1. Warm fauna, Boltovskoy and Riedel, 1980. Dictyocoryne truncatum (Ehrenberg, 1861) Nigrini and Moore, 1979, p. S89, pl. 12, figs. 2A, B. Warm fauna, Johnson and Nigrini, 1982. Euchitonia elegans (Ehrenberg, 1872a) Nigrini and Moore, 1979, p. S83, pl. 11, figs. 1A, B. Euchitonia furcata Ehrenberg, 1872a Nigrini and Moore, 1979, p. S85, pl. 11, figs. 2A, B. Euchitonia spp. Porodiscus group This includes Porodiscus sp. A and B in Nigrini and Moore, 1979, Stylochlamydium asteriscus Haeckel, 1887, and Stylodictya multispina Haeckel, 1860.

Spongaster cf. Spongaster pentas Riedel and Sanfilippo, 1970
Boltovskoy and Riedel, 1987, pl. II, fig. 21.
Spongaster tetras Ehrenberg irregularis Nigrini, 1967
Nigrini and Moore, 1979, p. S95, pl. 13, fig.2.
Transition fauna, Nigrini, 1970.
Spongocore puella Haeckel, 1887
Nigrini and Moore, 1979, p. S69, pl. 8, figs. 5A-C.
Transition fauna, Boltovskoy and Riedel, 1987, as S. cylindrica.
Spongodiscid group
Transition fauna
Spongopyle osculosa Dreyer, 1889
Nigrini and Moore, 1979, p. S115, pl. 15, fig. 1.
Intermediate fauna, Morley, 1977.
Spongotrochus glacialis Popofsky, 1908
Intermediate fauna, Boltovskoy and Riedel, 1980, p. 117, pl. 3, fig. 15.
Spongotrochus (?) venustum (Bailey, 1856)
Nigrini and Moore, 1979, p. S119, pl. 15, figs. 3A, B.
Transition fauna, Kling, 1979 (as Stylochlamydium venustum).
Spongurus cf. elliptica (Ehrenberg, 1872a)
Nigrini and Moore, 1979, p. S63, pl. 8, fig. 2.
Warm fauna, Johnson and Nigrini, 1982.

Family COCCODISCIDAE

Cypassis irregularis Nigrini, 1968
Nigrini, 1968, p. 53, pl. 1, figs. 2a-c.
Warm fauna, Kling, 1979.
Didymocyrtis tetrathalamus (Haeckel, 1887)
Nigrini and Moore, 1979, p. S49 and S53, pl. 6, figs. 1A-D, 2A, B.
Warm fauna, Kling, 1979.

Family Phacodiscidae

Heliodiscus asteriscus Haeckel, 1887 Warm fauna, Boltovskoy and Riedel, 1980, p. 115, pl. 3, fig. 8.

Order NASSELLARIA

Suborder SPYRIDA

Lophospyris pentagona pentagona (Ehrenberg) emend. Goll, 1977 Nigrini and Moore, 1979, p. N15, pl. 19, fig. 5. Warm fauna, Johnson and Nigrini, 1982. Lophospyris/Phormosypris spp.

Boltovskoy and Riedel, 1987, pl. III, fig. 14. Neosemantis distephanus Popofsky, 1913 Boltovskoy and Riedel, 1980, p. 120, pl. 4, fig. 14.] Warm fauna, Kling 1979. Phormospyris stabilis stabilis (Goll, 1968) Goll, 1976, p. 390, pl. 1, figs, 1-13. Warm fauna, Kling, 1979. Plectacantha sp. Jorgensen, 1905 Boltovskoy and Riedel, 1980, p. 122, pl. 5, fig. 5. Zygocircus productus (Hertwig, 1879) Petrushevskaya, 1971, p. 281, pl. 145, figs. 4-12. Suborder CYRTIDA Family PLAGONIIDAE Amphiplecta spp. Arachnocorallium calvata (Haeckel, 1887), group Petrushevskaya, 1971, p. 136, pl. 70. Transition fauna, Boltovskoy and Riedel, 1987, pl. III, fig. 24. Arachnocorys circumtexta Haeckel, 1862 Petrushevskaya, 1971, p. 125, figs. 65III-V, 67IJI. Warm fauna, Boltovskoy and Riedel, 1980. Callimitra carolotae Haeckel, 1887 As Callimitra emmae Haeckel; Benson, 1966, p. 390, pl. 25, fig. 12; Boltovskoy and Riedel, 1987, pl. IV, fig. 1. Cladoscenium tricolpium (Haeckel, 1887) Jorgensen, 1905, p. 134, pl. 15, figs. 71-73; Nishimura and Yamauchi, 1984, p. 44, pl. 24, fig. 6. Clathrocanium coarctatum Ehrenberg, 1860 Petrushevskaya, 1971, p. 81, pl. 39, fig. 1-4; Boltovskoy and Riedel, 1987, pl. IV, fig. 2. Helotholus histricosa Jorgensen, 1905 Benson, 1966, p. 459, pl. 31, figs. 4-8. Transition fauna, Kling, 1977. Lampromitra spp. Lampromitra quadricuspis Haeckel, 1887 Benson, 1966, p. 455, pl. 30, fig. 11, pl. 31, fig. 1. Lithomelissa setosa Jorgensen, 1900 Intermediate fauna, Kling, 1977, pl. 1, fig. 2. Lophophaena group A This includes L. sp. aff. L. capito Ehrenberg, 1874, and similar forms. Lophophaena group B

This includes L. hispida (Ehrenberg, 1872a), L. sp. aff. L. apiculata Ehrenberg, 1875, and similar forms. Peridium longispinum Jorgensen, 1900 Jorgensen, 1900, p. 75, pl. XV, fig. 76. Peridium spinipes Haeckel, 1887 Haeckel, 1887, p. 1154, pl. 53, fig. 9. Nishimura and Yamauchi, 1984, as P. longispinum, pl. 23, figs. 1-3, pl.55, fig. 1. Peromelissa spp. This includes P. phalacra Haeckel. Pseudocubus obeliscus Haeckel, 1887 Petrushevskaya, 1971, p. 150, pl. 76, figs. 1-6; Boltovskoy and Riedel, 1987, pl. IV, fig. 16. Trisulcus triacanthus Popofsky, 1913 Petrushevskaya, 1971, p. 141, pl. 72, figs. 8-13; Boltovskoy and Riedel, 1987, pl. IV, fig. 18. Family THEOPERIDAE Clathrocyclas bicornis Hays, 1965 Nishimura and Yamauchi, 1984, p. 49, pl. 36, figs. 8a, b,12. Transition fauna, Kling, 1979, as Theocalyptra bicornis. Cornutella profunda Ehrenberg, 1854 Boltovskoy and Riedel, 1980, p. 123, pl. 5, fig. 6. Intermediate fauna, Kling 1979. Corocalyptra columba (Haeckel, 1887) Boltovskoy and Jankilevich, 1985. Corocalyptra kruegeri Popofsky, 1913 Renz, 1976, p. 119, pl. 4, fig. 6; Boltovskoy and Riedel, 1987, pl. IV, fig. 22. Dictyocephalus (?) papilosus (Ehrenberg, 1872) Petrushevskaya, 1967, p. 114, figs. 66, I-III. Dictyophimus crisiae Ehrenberg, 1854 Nigrini and Moore, 1979, p. N33, pl. 22, figs. 1A, B. Dictyophimus gracilipes Bailey, 1856 Boltovskoy and Riedel, 1980, p. 124, pl. 5, fig. 8. Transition fauna, Kling, 1977; Boltovskoy and Riedel, 1987. Dictyophimus hirundo (Haeckel, 1887) Boltovskoy and Riedel, 1980, p. 124, pl. 5, fig. 20. Intermediate fauna, Riedel, 1958. Dictyophimus infabricatus Nigrini, 1968

Nigrini and Moore, 1979, p. N37, pl. 22, fig. 5. Transition fauna, Kling, 1979. Dictyophimus spp. Eucecryphalus sestrodiscus (Haeckel, 1887) Nishimura and Yamauchi, 1984, p. 51, pl. 26, figs. 3a, b, 4a, b. Eucyrtidium acuminatum (Ehrenberg, 1844) Nigrini and Moore, 1979, p. N61, pl. 24, figs. 3A, B. Warm fauna, Petrushevskava, 1971. Eucyrtidium anomalum Haeckel, 1862 Petrushevskaya, 1971, p. 219, pl. 98, figs. 1-4. Warm fauna, Renz, 1976. Eucyrtidium hexagonatum Haeckel, 1887. Nigrini and Moore, 1979, p. N63, pl. 24, figs. 4A, B. Warm fauna, Renz, 1976. Eucyrtidium spp. This includes E. hexastichum (Haeckel, 1887) Lipmanella dictyoceras (Haeckel, 1860) Kling, 1973, p. 636, pl. 4, figs. 24-26. Warm fauna, Kling, 1979. Lipmanella spp. Litharachnium tentorium Haeckel, 1862 Petrushevskaya, 1971, p. 227, pl. 108, 109, figs. I-IV. Warm fauna, Kling, 1979. ?Lithomitra infundibulum Haeckel, 1887 ?Benson, 1966, p. 502, pl. 34, figs. 10-12; Boltovskoy and Riedel, 1987, pl. V, fig. 9. Lithomitra lineata (Ehrenberg, 1838) group Riedel and Sanfilippo, 1971, p. 1600, pl. 1I, figs. 1-11, pl. 2I, figs. 14-16, pl. 3E, fig. 14; Kling, 1977, pl. I, fig. 1. Lithopera bacca Ehrenberg, 1873 Nigrini, 1967, p. 54, pl. 6, fig. 2. Warm fauna, Kling, 1979. Lithostrobus hexagonalis Haeckel, 1887 Benson, 1966, p. 508, pl. 35, figs. 1, 2; Boltovskoy and Riedel, 1987, pl. V, fig. 11. Warm fauna, Renz, 1976. Lophocorys polyacantha Popofsky, 1913 p. 400, text-fig. 122; Kling, 1979, pl. I, fig. 27. Warm fauna, Kling, 1979. Peripyramis circumtexta Haeckel, 1887 Nigrini and Moore, 1979, p. N29, pl. 21, figs. 4A, B.

Intermediate fauna, Kling, 1979. Pterocanium korotnevi (Dogiel, 1952) Nigrini and Moore, 1979, p. N39, pl. 23, fig. 1A, B Transition fauna, Nigrini, 1970. Pterocanium praetextum (Ehrenberg, 1872a) eucolpum Haeckel, 1887 Nigrini and Moore, 1979, p. N43, pl. 23, fig. 3. Transition fauna, Nigrini, 1970. Pterocanium praetextum praetextum (Ehrenberg, 1872a) Nigrini and Moore, 1979, p. N41, pl. 23, fig. 2. Warm fauna, Johnson and Nigrini, 1982. Pterocanium trilobum (Haeckel, 1860) Nigrini and Moore, 1979, p. N45, pl. 23, figs. 4A-C. Sethoconus tabulatus (Ehrenberg, 1872b) Boltovskoy and Riedel, 1987, pl. V, fig. 16. As Sethoconus (?) tabulatus, Petrushevskaya, 1971, pl. 92, figs. 9-11. Theocalyptra bicornis (Popofsky, 1908) Nigrini and Moore, 1979, p. N53, pl. 24, fig. 1. Intermediate fauna, Morley, 1989. Theocalyptra davisiana (Ehrenberg, 1862) cornutoides (Petrushevskaya, 1967) Transition fauna, Kling, 1977, pl. 1, fig. 20. Theocalyptra davisiana davisiana (Ehrenberg, 1862) Riedel, 1958, p. 239, pl. 4, figs. 2-3. Intermediate fauna, Kling, 1977. Theocalyptra gegenbauri (Haeckel, 1860) Intermediate fauna, Boltovskoy and Riedel, 1980, p. 126, pl. 5, fig. 18. Trictenartus elegans Haeckel, 1887 Nishimura and Yamauchi, 1984, p. 54, pl. 30, figs. 13-15, pl. 55, fig. 11.

Family CARPOCANIIDAE

Carpocanistrum spp.
This includes Carpocanistrum sp. A and B in Nigrini and Moore, 1979, p. N25, pl. 21 figs. 1A-C, 2.
Warm fauna, Boltovskoy and Riedel, 1987.

Family PTEROCORYTHIDAE

Anthocyrtidium ophirense (Ehrenberg, 1872a) Nigrini and Moore, 1979, p. N67, pl. 25, fig. 1. Warm fauna, Johnson and Nigrini, 1982.
Anthocyrtidium zanguebaricum (Ehrenberg, 1872a) Nigrini and Moore, 1979, p. N69, pl. 25, fig. 2.

Warm fauna, Johnson and Nigrini, 1982. Lamprocyclas maritalis Haeckel, 1887 Subspecies were not distinguished. Nigrini and Moore, p. N75-N79, pl. 25, figs. 4-6. Lamprocyrtis nigrinae (Caulet, 1971) Nigrini and Moore, 1979, p. N81, pl. 25, fig. 7. Intermediate fauna, Kling, 1979. Lamprocyrtis spp. Pterocorys hertwigii (Haeckel, 1887) Nigrini and Moore, 1979, p. 85, pl. 25, fig. 9. Warm fauna, Johnson and Nigrini, 1982. Pterocorys minythorax (Nigrini, 1968) Nigrini and Moore, 1979, p. N87, pl. 25, fig. 10. Warm fauna, Molina-Cruz, 1977. Pterocorys spp. Pterocorys zancleus (Mueller, 1858) Nigrini and Moore, 1979, p. N89, pl. 25, fig. 11A, B. Warm fauna, Petrushevskaya, 1971. Pteroscenium pinnatum Haeckel, 1887 Haeckel, 1887, p. 1152, pl. 53, figs. 14, 16; Boltovskoy and Riedel, 1987, pl. VI, fig. 4. Stichopilium bicorne Haeckel, 1887 Renz, 1976, p. 125, pl. 4, fig. 9. Warm fauna, Kling, 1979. Stichopilium variable Popofsky, 1908 Nishimura and Yamauchi, 1984, p. 62, pl. 39, figs. 8a, b. Theocorythium trachelium (Ehrenberg, 1872a) Warm fauna, Boltovskoy and Riedel, 1980, p. 127, pl. 5, fig. 22.

Family ARTOSTROBIIDAE

Botryostrobus auritus/australis (Ehrenberg, 1844) group Nigrini and Moore, 1979, N101, pl. 27, figs. 2A-D.
Botryostrobus aquilonaris (Bailey, 1856) Nigrini and Moore, 1979, p. N99, pl. 27, fig. 1. Intermediate fauna, Kling, 1979.
Phormostichoartus corbula (Harting, 1863) Nigrini and Moore, p. N103, pl. 27, fig. 3. Warm fauna, Kling, 1979.
Spirocyrtis scalaris Haeckel, 1887 Renz, 1976, p. 142, pl. 6, fig. 1. Warm fauna, Johnson and Nigrini, 1982. Tricolocampe cylindrica Haeckel, 1887

Boltovskoy and Riedel, 1987, pl. VI, fig. 9. As Siphocampium cf. cylindrica Haeckel, Benson, 1966, p. 520, pl. 35, figs. 10, 11.

Family CANNOBOTRYIDAE

Botryocyrtis scutum (Harting, 1863) Nigrini and Moore, 1979, p. N105, pl. 28, figs. 1A, B. Warm fauna, Johnson and Nigrini, 1982.
Botryopyle spp.
Cannobotryid spp.

Family SETHOPHORMIDIDAE

Enneaphormis rotula (Haeckel, 1887) Petrushevskaya, 1971, p. 68, fig. 31. Sethophormis aurelia Haeckel, 1887 Petrushevskaya, 1971, p. 66, figs. 29.II, 30.