SILICEOUS PHYTOPLANKTON IN THE SANTA BARBARA CHANNEL: A SEVEN-YEAR COMPARISON OF SPECIES IN A NEAR-BOTTOM SEDIMENT TRAP AND IN WATER SAMPLES FROM THE EUPHOTIC LAYER

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ABSTRACT

Biweekly sediment trap samples were collected from the Santa Barbara Basin between August 1993 and April 2000. We compare the siliceous phytoplankton species from these traps with mixed-layer phytoplankton samples from quarterly cruises. We evaluate signals from the two data sets, without regard to their specific compositions. Both data sets indicate strong, regular spring blooms. The trap data allow definition of a fall-winter flora not identified from the water samples. The water samples allow definition of an oceanic warm-water flora, not readily seen in the trap data.

Many of these differences are procedural artifacts. However, significant differences arise from the different scales of the samples. Species' relationships, which are often expressed over relatively short scales of time and space, are better captured by the small-scale water samples. Regional oceanographic and climatic signals are more efficiently captured in trap samples, which integrate over small-scale variability.

INTRODUCTION

Between 1993 and 2000, two sets of phytoplankton samples were collected from the Santa Barbara Basin at the northern end of the Southern California Bight (fig. 1). One set is a series of contiguous sediment trap samples collected from approximately 540 m depth; the second is a series of quarterly water samples from the mixed layer above the trap. Portions of both sets have been the subject of previous studies (Thunell 1998; Lange et al. 1997, 2000; Venrick 1998), and additional analyses of the trap material are underway. Although these two data sets are not well matched in number of samples or in frequency, they are both typical of the data sets commonly collected by discrete samples from the euphotic zone and by sediment traps at greater depth.

Several studies in the past have examined transformation of organic material as it sinks through the water column and settles on the seafloor (e.g., Bishop et al. 1977; Knauer et al. 1979; Deuser and Ross 1980; Honjo et al. 1982; Shipe and Brzezinski 2001). Some of these have considered species composition (Passow 1991; Passow and Peinert 1993; Sancetta 1992; Treppke et al. 1996; Scharek et al. 1999; Romero et al. 2000). We know of no other instance where the data sets include species composition over a range of several years and hence allow comparison of the long-term taxonomic information contained by samples from the euphotic zone and from a sediment trap just above the seafloor.

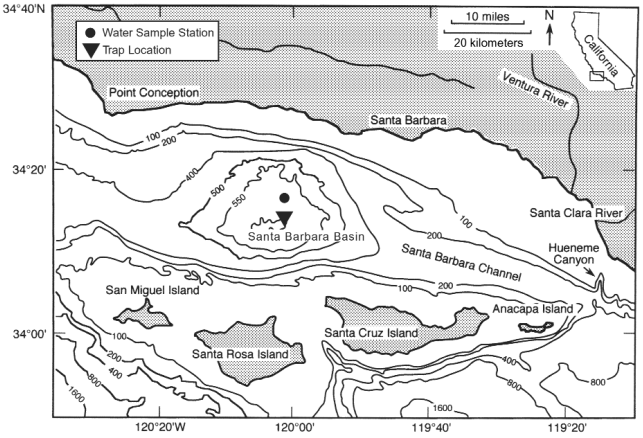

Figure 1. Geographic and topographic map of the Santa Barbara Channel and the Santa Barbara Basin showing the locations of the sediment trap and the water sample station.

We first compare estimates of abundance and flux of total siliceous phytoplankton as well as the overall species compositions of the two data sets. We then apply two different grouping procedures in an analogous manner to both sets: the first procedure identifies individual species that tend to be abundant in the same trap samples or the same water samples; the second procedure groups individual trap samples or water samples according to the similarity of their species composition.

The purpose of this article is not a detailed interpretation of either data set but rather a comparison of their primary signals. The ecological mechanisms underlying the patterns will be explored only as needed to make the comparison. The information content of each data set may be modified by several factors: the different total number and frequency of samples in the two data sets, the different temporal/spatial scales represented by a single sample from each data set, and their different species

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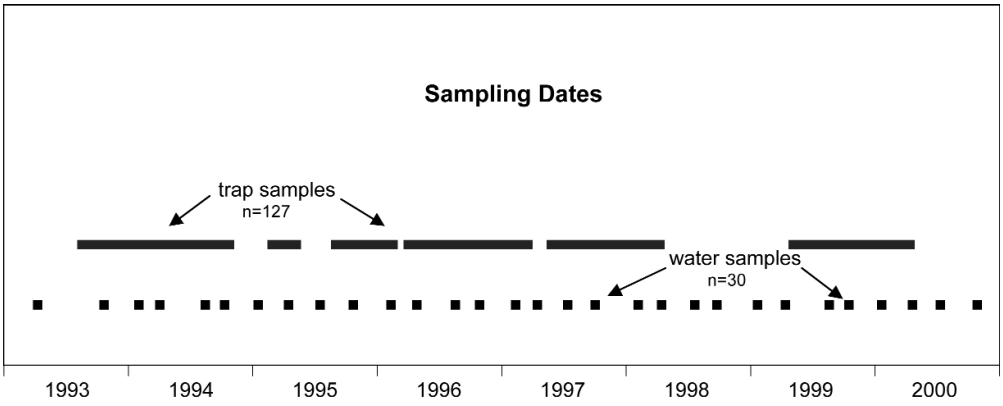

Figure 2. Sampling dates for water samples and range of consecutive dates for trap samples; *n* = number of samples.

compositions. We will attempt to differentiate between these factors.

METHODS

The sediment trap was a 13-cup trap with a 0.5 m^2 collection area, located near the center of the Santa Barbara Basin (34°14'N, 120°02'W; fig. 1) about 50 m above the bottom (Thunell 1998). One hundred and twenty-seven samples of 2-week (rarely 1-week) duration were collected sequentially between 19 August 1993 and 12 April 2000. In this article, the trap date is the midpoint of the trap collection period. Because of trap malfunctions, there are no samples between 10 April 1998 and 5 May 5 1999, as well as some shorter data gaps (fig. 2).

Trap samples were poisoned in the field with $HgCl_2$. Splits of the original sample (usually, 1/16–1/64) were washed through a 45 μm sieve, acid-cleaned (Wigley 1984), and mounted on permanent slides with Naphrax. Subareas of a slide were counted for siliceous phytoplankton skeletons (diatoms and silicoflagellates) using a phase contrast microscope and a magnification of 250×, or 650× for spores and small valves (for details on methodology, see Lange et al. 1997).

The 30 water samples were collected quarterly from 4 m to 11 m depth at CalCOFI station 82.47 (34°16.5'N, 120°1.5'W; fig. 1). Samples were preserved with neutralized formalin; volumes between 0.225 ml and 24.6 ml were settled and counted under an inverted microscope. Effort was made to identify and count all phytoplankters > 5 μm; larger and rarer taxa were counted at 100×, and smaller taxa at 250×. Some related heterotrophs were included.

We have coordinated taxonomic identification for more than 20 years. We are confident that our identifications are as comparable as possible for different workers. We have based our taxonomic nomenclature on Round et al. (1990) for diatoms and Tomas (1997) for the other groups. Because the genus *Pseudo-nitzschia* is important in both sets of data, we have lumped the species in the trap samples into the two size categories used for the water samples.

There are 19 pairs of simultaneous samples in which a trap was open when a water sample was collected. There are 17 pairs of samples where the trap opened 1 to 14 days after the collection of the water sample (lag one 2-week interval). Likewise, there are 19 pairs with lag = 2 (trap opened 2–4 weeks after collection of the water sample), 19 pairs with lag = 3, 19 pairs with lag = 4, 19 pairs with lag = 5, and 17 pairs with lag = 6. This restricted set of simultaneous samples allows direct comparison of trap and water sample data.

We measure species diversity by means of the entropy index (Legendre and Legendre 1983):

$$H = -\sum_{i=1}^{n} p_i, \log p_i,$$

where p_i is the proportion of species i in a sample of n species.

Species are clustered using the recurrent group procedure (Fager and McGowan 1963), scoring species above and below their median (Venrick 2002). For species present in less than half of the samples, presence and absence are used. Recurrent groups present in less than 10% of the samples are eliminated from further consideration.

The recurrent group procedure is based on an affinity index:

$$\alpha = [J/(N_a N_b)^{1/2}] - (1/2)(N_b)^{1/2},$$

where J is the number of joint occurrences of species a and species b out of a total of N_a occurrence of species a and N_b occurrences of species b, and $N_a > N_b$. Alpha varies from 0 (no co-occurrence) to 1 (perfect co-occurrence).

As α is relaxed, groups typically increase in size and number. At the same time, more cross-group affinities

appear. In many situations, the most informative groups are those at the lowest α that produces distinct groups or clusters of groups. In this study, groups are defined at α levels of 0.80, 0.75, 0.70, 0.65, 0.60, 0.55, and 0.50. Results are discussed for groups defined at 0.70 and 0.55.

Alpha is a proportional index, independent of sample size. If the number of occurrences of species *a* and *b* are the same in two sets of samples, and if the number of joint occurrences is the same, then α will be the same, regardless of the total number of samples. If N_a, N_b, and J are scaled up proportionately (as would happen, for instance, if additional samples were collected without error from the same population), then α is affected only by the correction for sample size, which becomes smaller as N_b increases. All else remaining the same, the effect of an increase in sample number is an increase in the value of α. Therefore, in this study we expect α values among species in the trap samples to be somewhat larger than α values among species in the water samples.

Correlations are Spearman's nonparametric correlations (Conover 1999). Cluster analyses of samples use the method of unweighted average linkages (Legendre and Legendre 1983).

Because many of the following analyses involve multiple tests with nonindependent data sets, the assumptions underlying the usual statistical "probability" values are violated. In these cases, we base our conclusions on the patterns of the statistics rather than on the usual tests of significance.

PHYSICAL SETTING

The Santa Barbara Channel is an elongated channel bounded by Southern California on the north and east and by the Channel Islands on the west and south. The Santa Barbara Basin is a bottom depression in the western center of the channel, reaching depths in excess of 500 m (fig. 1). Because of a unique combination of bottom topography, hydrography, and biology, the seasonal patterns of production are well preserved in the sediments, making it an important location for high-resolution studies of paleoecology and paleoceanography (e.g., Soutar and Isaacs 1974; Baumgartner et al. 1992; Kennett and Ingram 1995; Schimmelman and Lange 1996). The present data come from one of two sediment trap studies currently underway in the Santa Barbara Basin (e.g., Thunell et al. 1995; Thunell 1998; Lange et al. 1997, 2000; Shipe and Brzezinski 2001; Shipe et al. 2002).

Since 1993, a number of moorings have been in place in and north of the Santa Barbara Channel. These, together with drifter releases, hydrographic surveys, and anemometer measurements have provided detailed information about the near-surface current patterns (e.g., Hendershott and Winant 1996; Dever et al. 1998; Harms and Winant 1998; Bray et al. 1999; Winant et al. 1999, 2003). At the eastern entrance, annual mean flow into the channel at the surface is poleward. However, this reverses seasonally, being generally equatorward between February and June. At the western mouth, annual mean flow is poleward along the northern shore and equatorward along the southern. Overall, equatorward transport is greatest during the spring and weakest during the winter. There is a tendency for downwind transport during upwelling-favorable winds, with consequent transport of newly upwelled water into the channel from the northwest. The Santa Barbara Channel has a mean tendency for cyclonic rotation of the near-surface currents. This tendency is strongest in summer, weakest in winter. Superimposed on the mean patterns is a complex pattern of near-surface currents and reversals, filaments, and eddies. These have been described as synoptic states (Harms and Winant 1998; Dever et al. 1998; Winant et al. 2003) that have seasonal cycles as well as fluctuations on smaller time scales.

Of 235 drifters released at various locations within the Santa Barbara Channel, the average residence time was 7 days (Winant et al. 1999). This estimate may be biased downward by the proportion of drifters that ran aground before exiting the channel—about one-third. One drifter was caught in a local eddy for 21 days; nevertheless, it is clear that the Santa Barbara Channel cannot be considered a closed system.

There are two primary sources of water in the Santa Barbara Channel. From the north, water is coastal and includes cold, upwelled water from the region between Point Conception and Point Arguello. This source is most pronounced in the spring when upwelling is most consistent and surface flows through the channel are primarily equatorward. However, upwelling along the coast at Point Conception and north can occur throughout the year, and there remains the possibility of sporadic incursions of upwelled water in other seasons. From the south, water is warm saline water from the California Bight. This water has a complex origin that includes the Central Pacific, the East Tropical Pacific, and modified water from the California Current. The core of the California Current rarely penetrates into the Santa Barbara Channel directly.

RESULTS

Total Siliceous Phytoplankton

The time series of total siliceous phytoplankton cells from both data sets show distinct peaks of flux or abundance in the spring, but the relative magnitudes differ (fig. 3). The trap data show occasional peaks in the fall. Both data sets indicate very low values from mid-1997 through early 1998; these have been interpreted as an

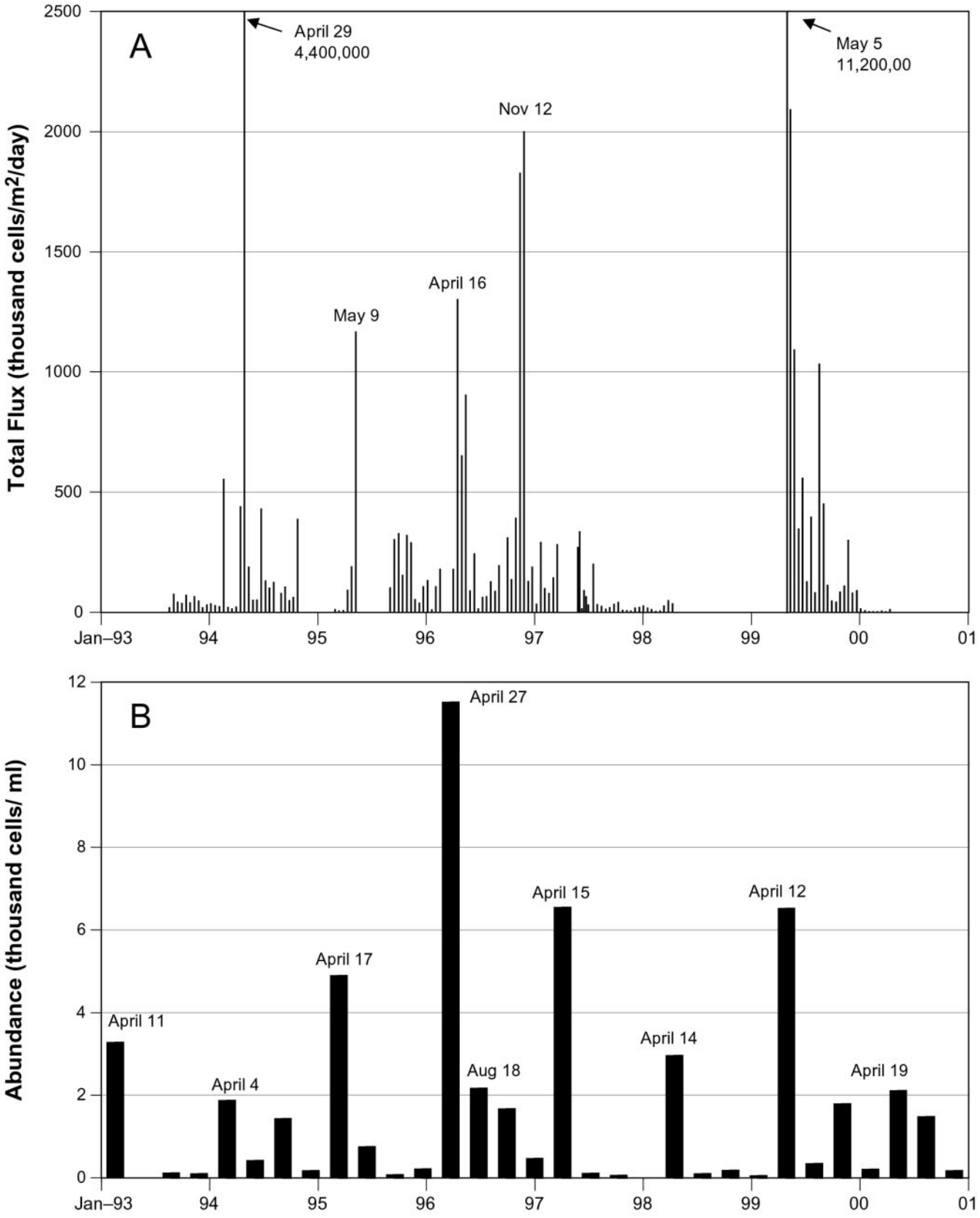

Figure 3. Fluctuations of flux and abundance of total siliceous phytoplankton, 1993–2000: *A*, trap samples; *B*, water samples. Dates of major peaks of flux or abundance are given.

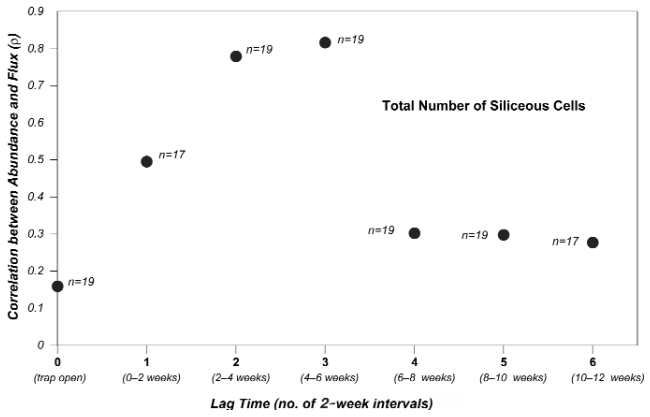

Figure 4. Correlation between abundance and flux of total siliceous phytoplankton at lag times from zero to six 2-week intervals, with abundance leading flux.

effect of the 1997–98 El Niño (Lange et al. 2000). Low flux values at the start of the series have been explained as a consequence of the El Niño conditions just preceding the data collection (Thunell 1998).

Correlation between abundance of total siliceous phytoplankton in the water column and flux into the trap is examined quantitatively by comparing the 19 data pairs where the trap was open when the water sample was collected (fig. 4). Correlation between simultaneous samples is poor. Lagging the trap samples by successive intervals causes the correlation to increase to maximum values at two and three trap intervals ($\rho = 0.78$ and 0.82), that is, intervals of 2–4 and 4–6 weeks between the collection of the water sample and the opening of the trap. The relatively smooth parabolic pattern of ρ versus lag time, as well as the high maximum correlations, gives strength to this interpretation.

Species Composition

Analysis of total particles neglects the rich taxonomic data contained in both data sets. A total of 204 species was identified from the trap samples, 178 from the water samples. The data sets have 112 taxa in common. One obvious source of difference between the two data sets is the removal of smaller and nonsiliceous cells from the trap samples during sample preparation. In the water samples 42% of the taxa are nonsiliceous, and these account for 10% of the cell totals. Another difference is the absence of benthic species from the water samples. In the trap samples, 30% of the species are benthic, but these represent less than 1% of the total number of cells. In addition, the process of acid cleaning and mounting cells before enumeration of the trap material facilitates the identification of several groups of diatoms that are problematic in water samples, such as species in the genera *Coscinodiscus* and *Thalassiosira*. The high frequency of *Chaetoceros* resting spores in the trap material also allows identification of Hyalochaete species that are difficult to identify in vegetative phase and may not have been consistently recognized in the water samples. In addition to the methodologically caused differences, discrepancies are expected to arise from dissolution of cells below the euphotic zone, influx of cells into traps from other areas, and undersampling of the euphotic zone.

The ten dominant species in the two data sets are given in Table 1. In the case of the Hyalochaete species, the dominant forms in the sediment trap are resting spores; these were almost never observed in water samples. *Chaetoceros radicans* is the most abundant species in both data sets. *Ch. debilis* is the third most abundant in both data sets and *Ch. compresses* is ranked eighth. Other taxa agree less well. Many discrepancies can be attributed to the analytical differences (pennate 1 and *F. pseudonana* are too small to be retained by the 45 μm sieve used in preparing the trap samples; "slim" *Pseudo-nitzschia* spp. may be too delicate to reach the trap intact or may pass through the sieve end-first; *Ch. diadema* and *Ch. vanheurckii* are difficult to identify in vegetative form). One unexpected discrepancy is *Coscinodiscus radiatus*, which occurs in every trap sample (ranking sixteenth in abundance) but occurs only twice in the water samples. This is unlikely to be an identification problem. In the water column, this species may be most abundant below the mixed layer and thus be missed by the water samples.

A comparison of sample diversity for the two sets of data (fig. 5) shows that 23% of the trap samples have a diversity of less than $H = 1.38$, the lowest diversity in a water sample. The lowest trap values ($H = 0.35$ and 0.36) are from two trap samples collected during late April–early May 1994 in which *Ch. radicans* resting spores comprised more than 90% of the flux. The previous water sample (5 April 5 1994) was also dominated by *Ch. radicans* (vegetative cells), but these only accounted for 39% of the total cells. Only 2.5% of the remaining cells in that water sample were nonsiliceous, so the broader range of floral types counted in the water samples does not explain the relatively low proportion of *Ch. radicans*.

Of the 29 low-diversity trap samples ($H < 1.38$), 90% are dominated by Hyalochaete resting spores, which are rarely observed in water samples. Resting spores dominate in only 67% of the higher diversity trap samples (χ^2; $p < 0.005$). Thus, the low diversity of some trap samples appears to be due to a very high proportion of Hyalochaete resting spores. The absence of resting spores from the water samples suggests that spores may develop at depths below the mixed layer, and/or over very short time scales, and are not captured by the water samples. Their extreme dominance in some trap samples, compared with the dominance of vegetative cells in the mixed layer, suggests some concentrating mechanism, such as

TABLE 1
Comparison of the Ten Most Abundant Species in Trap and Water Samples

a. Trap Samples

Species	Proportion of all species (%)	Abundance in water samples		Notes
		%	Rank	
Chaetoceros radicans	51.4	18.90	1	Includes *Ch. cinctus*
Chaetoceros vanheurckii	23.6	0.25	32	
Chaetoceros debilis	5.3	14.50	3	
Chaetoceros diadema	3.5	0.25	31	
Chaetoceros concavicornis	2.3	0.25	32	
Chaetoceros affinis	1.6	0.10	43	
Bacteriastrum delicatulum	1.6	0.52	19	Includes *B. furcatum*
Chaetoceros compressus	1.4	4.10	8	
Chaetoceros "peanuts"	1.3	0.00		Unidentified resting spores
Chaetoceros 1	1.0	0.00		Possibly *Ch. lorenzianus* or *diadema*

b. Water Samples

Species	Proportion of all species (%)	Proportion of siliceous species (%)	Abundance in trap samples		Notes
			%	Rank	
Chaetoceros radicans	18.9	19.7	51.40	1	Includes *Ch. cinctus*
slim *Pseudo-nitzschia* spp.	18.2	18.9	0.08	70	Sum of 5 slim species
Chaetoceros debilis	14.5	15.1	5.30	3	
Chaetoceros socialis	8.4	8.7	0.00		Not found in trap samples
Dactyliosolen fragilissimus	5.9	6.2	0.00		Not found in trap samples
Skeletonema costatum	5.0	5.2	0.18	23	
robust *Pseudo-nitzschia* spp.	4.2	4.4	0.57	12	"Sum of 5 species, *P. australis* most abundant"
Chaetoceros compressus	4.1	4.3	1.40	8	
Pennate 1	1.8	1.9	0.00		Unidentified small pennate
Fragilariopsis pseudonana	1.6	1.6	0.00		Too small to be retained during trap sample preparation

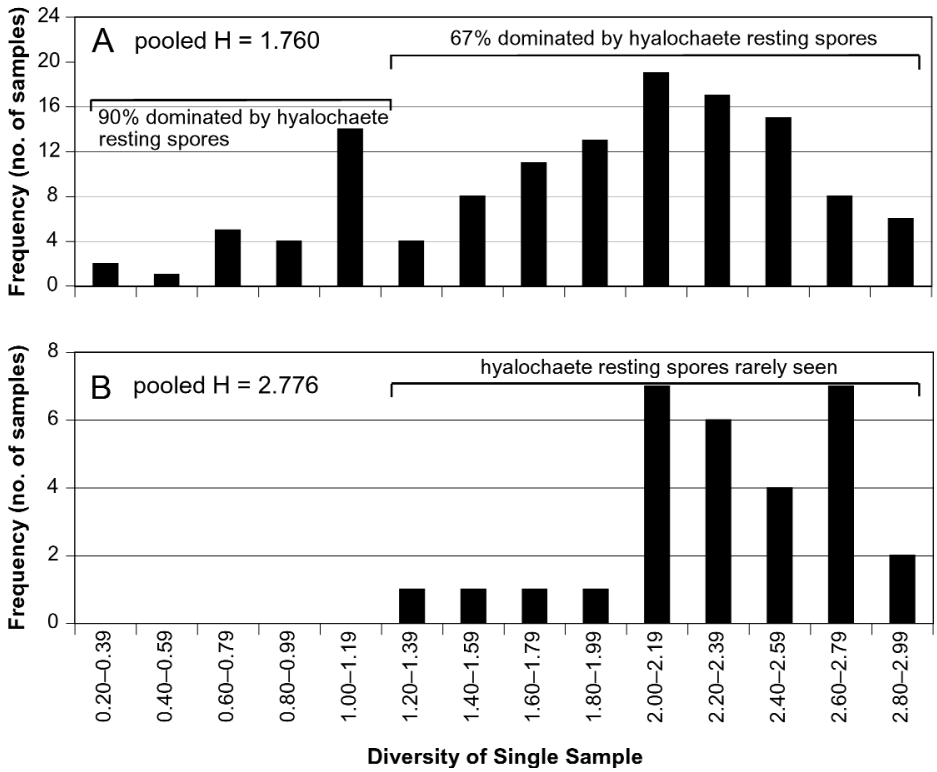

Figure 5. Frequency of diversity (*H*) of individual trap and water samples: *A*, trap samples; *B*, water samples. Traps with *H* values < 1.38 are strongly dominated by hyalochaete resting spores.

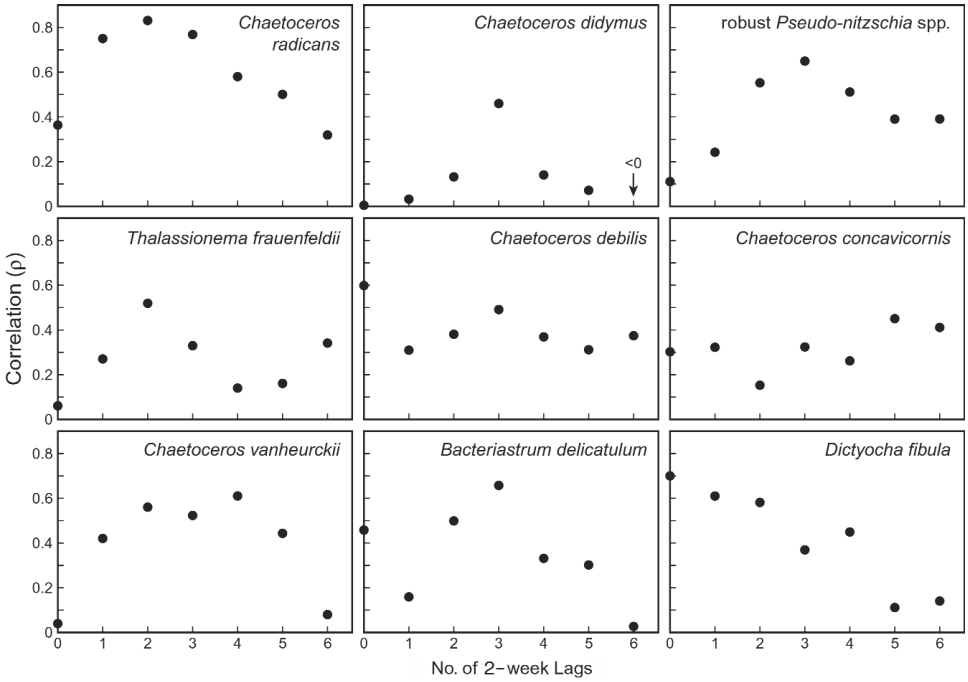

Figure 6. Correlations between abundance and flux of nine species at lag times from zero to six 2-week intervals with abundance leading flux.

an accumulation of cells at some horizon below the mixed layer prior to spore formation or accumulation of spores on the sediment at shallower depth and subsequent advection into the basin (Sancetta 1992).

Although 112 taxa occur in both data sets, only 16 species occur in 20% or more of the samples in each set. The correlations between flux and abundance of these 16 species are compared at various time lags using the reduced set of simultaneous samples, as explained in the Methods section. To maintain the power of the correlation, we require that the species be present in at least 20% of the samples in each reduced data set. Only 9 species are frequent enough to meet this criterion. There is a spectrum of relationships between mixed-layer abundance and flux into the traps (fig. 6). For *Ch. concavicornis*, there is no discernable relationship. For *Dictyocha fibula*, the relationship appears tight; the period of maximum flux includes the time of maximum abundance in the water above. Other species, however, show indications of the parabolic relationship that occurs when there is a lag time between abundance and flux. The overall median and modal lag is three 2-week intervals (4–6 weeks). However, correlations at two 2-week intervals are often high.

With only nine species abundant in both data sets, the challenge of this study is to compare the information content using the species composition drawn from two different pools of species. After some consideration, we have retained *all* species in both data sets, even those with serious methodological biases. This avoids drawing an arbitrary line between "biased" and "unbiased." More importantly, it is the only way to objectively evaluate the loss of information arising from procedural practices.

Groupings of Species

The recurrent group procedure was applied to each set of data to define groups of species that tend to be abundant together. The question in the present study is not whether groups of the same species are formed from each data set but whether analogous groups are formed.

Trap Samples. At the higher affinity level ($\alpha = 0.70$), ten species are grouped into four recurrent groups (fig. 7a). The groups can be distinguished on the basis of their seasonal cycles (fig. 8) and are concordant with respect to their mean annual fluxes (Kendall concordance test, $p < 0.05$). Thus, they are separated primarily on the basis of their seasonal cycles. At the lowest affinity index ($\alpha = 0.55$), 32 species or categories are associated into ten recurrent groups with 10 associated species (fig. 9a, tab. 2). At this affinity there is a large amount of connectivity between all recurrent groups; there are no distinct recurrent groups or clusters of recurrent groups. Two of the original four recurrent groups (groups I and III) have been split into different groups (groups I, III, and IV; fig. 7).

The largest group at $\alpha = 0.55$, group I (fig. 7 and tab. 2), consists of Hyalochaete *Chaetoceros* and *Coscinodiscus*

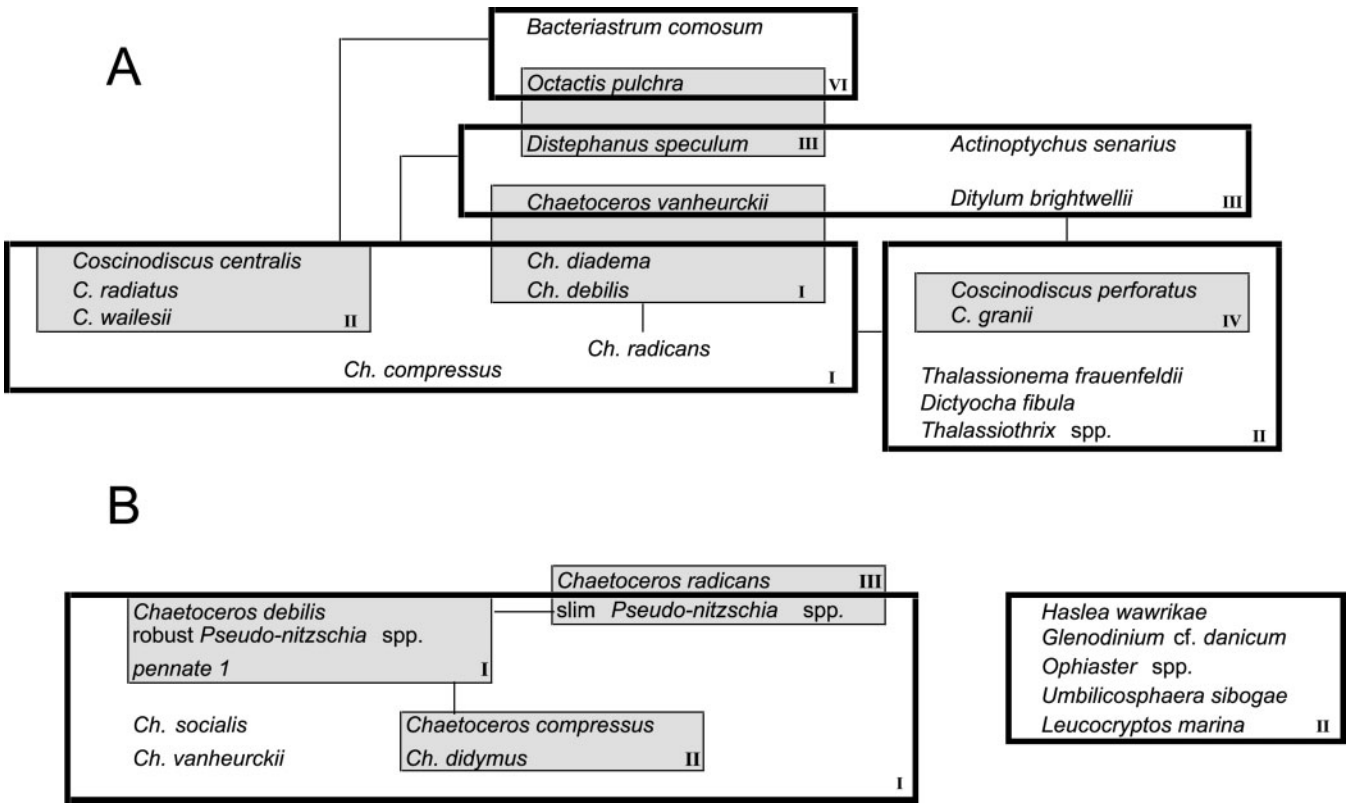

Figure 7. Recurrent groups of species defined at $\alpha = 0.70$ (*shaded boxes*) and at $\alpha = 0.55$ (*unshaded boxes*): *A*, trap samples; *B*, water samples. Composition of a recurrent group is indicated within a box. Lines between boxes (or between a species and a box) indicate association between groups or between a species and a group. Thus, in the trap samples, the species of group II and IV at $\alpha = 0.70$ continue to be associated at $\alpha = 0.55$. Groups I and III at $\alpha = 0.70$ are each split into two groups at $\alpha = 0.55$. Not all groups at $\alpha = 0.55$ are shown.

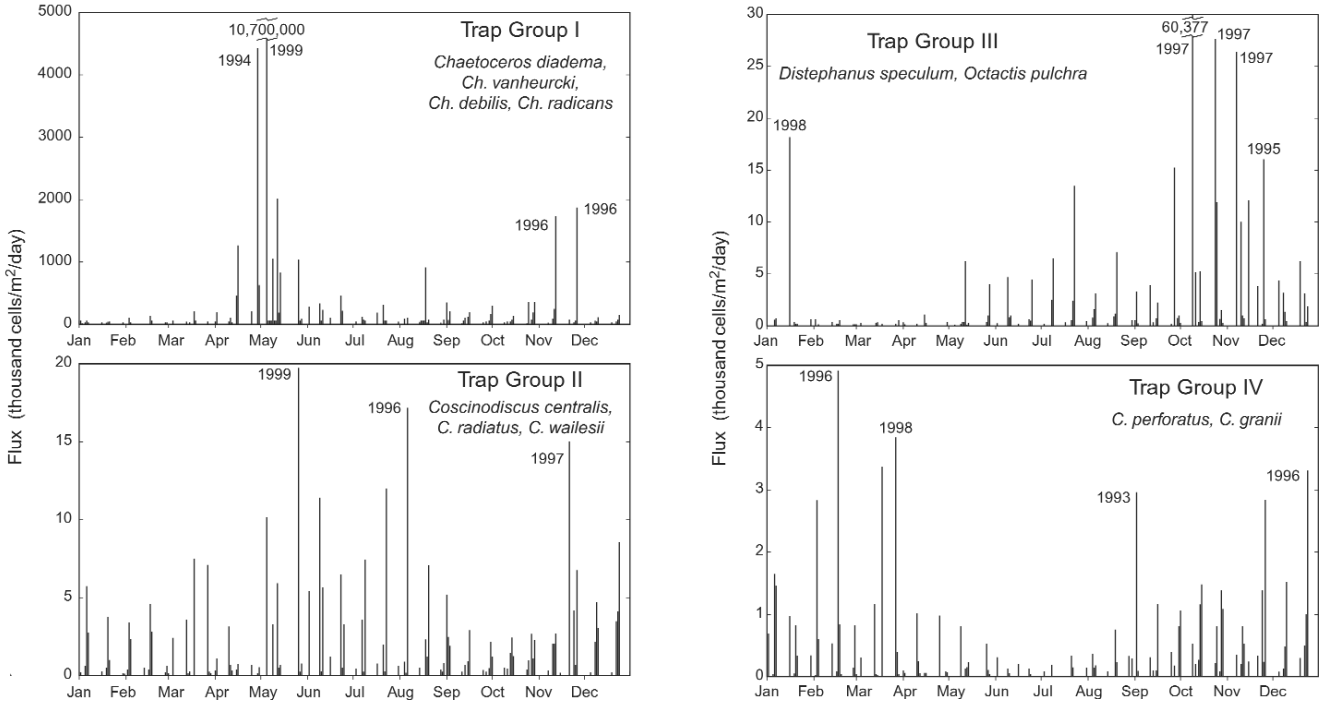

Figure 8. Seasonal cycles of the total flux of recurrent groups and associated species formed from trap samples at $\alpha = 0.70$. Years of major peaks are given.

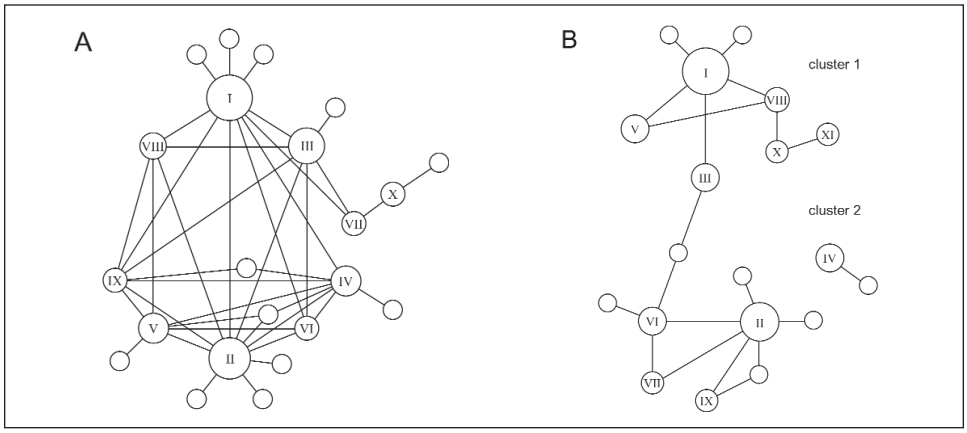

Figure 9. Recurrent groups and associated species formed from trap and water samples at $\alpha = 0.55$: *A*, trap samples; *B*, water samples. Numbers in circles are group numbers; circle size reflects group size; blank circles represent associated species. Lines connecting groups and associated species indicate cross-group affinities, and clusters represent groups of associated recurrent groups.

TABLE 2
Composition of Recurrent Groups at $\alpha = 0.55$

Trap samples	**Water samples**	**Trap samples**	**Water samples**
GROUP I *Chaetoceros compressus* *Ch. debilis* *Ch. diadema* *Ch. radicans* *Coscinodiscus centralis* *C. radiatus* *C. wailesii* Associated species: *Ch. decipiens* *Chaetoceros* sp 1 *Pleurosigma normanii*	GROUP I (CLUSTER 1) *Chaetoceros compressus* *Ch. vanheurckii* *Ch. debilis* *Ch. didymus* *Ch. socialis* robust *Pseudo-nitzschia* spp. slim *Pseudo-nitzschia* spp. pennate 1 Associated species: *Thalassiosira aestivalis* *T. rotula*	GROUP V *Bacteriastrum elongatum* *B. delicatulum* *Chaetoceros messanensis* Associated species: *Asterolampra marylandica* *Rhabdonema adriaticum*	GROUP V (CLUSTER 1) *Chaetoceros decipiens* *Ch. cf. laciniosus* *Skeletonema costatum* GROUP VI (CLUSTER 2) *Leptocylindrus mediterraneus* *Proboscia alata* *Nitzschia cf. closterium* Associated species: *Bacteriastrum delicatulum* *Rhizosolenia setigera*
GROUP II *Coscinodiscus granii* *C. perforatus* *Dictyocha fibula* *Thalassiothrix frauenfeldii* *Thalassiothrix* spp. (fragments) Associated species: *Azpetia nodulifera* *C. cf. concinnus*	GROUP II (CLUSTER 2) *Haslea wawrikae* *Glenodinium danicum* *Ophiaster* spp. *Umbilicosphaera sibogae* *Leucocryptos marina* Associated species: *Mastogloia capitata* *Gephyrocapsa* spp. *Dictyocha fibula*	GROUP VI *Bacteriastrum comosum* *Octactis pulchra* GROUP VII *Chaetoceros concavicornis* *Thalassiosira eccentrica* GROUP VIII *Chaetoceros affinis* *Rhizosolenia robusta* GROUP IX *Actinocyclus octonarius* *Biddulphia biddulphiana* Associated species: *Chaetoceros didymus* GROUP X *Asteromphalus heptactis* robust *Pseudo-nitzschia* spp. Associated species: *Thalassiosira oestrupii*	GROUP VII (CLUSTER 2) *Chaetoceros anastomosans* *Prorocentrum vaginulum* GROUP VIII (CLUSTER 1) *Chaetoceros radicans* *Dactyliosolen cf. phuketensis* GROUP IX (CLUSTER 2) *Glenodinium* spp. *Octactis pulchra* Associated species: *Dictyocha fibula* GROUP X (CLUSTER 1) *Emiliania huxleyi* *Thalassionema nitzschioides* GROUP XI (CLUSTER 1) *Asteromphalus sarcophagus* *Thalassionema frauenfeldii*
GROUP III *Actinoptychus senarius* *Chaetoceros vanheurckii* *Distephanus speculum* *Ditylum brightwellii* Associated species: *Thalassiosira eccentrica* (small)	GROUP III (CLUSTER 1) *Dactyliosolen fragilis* *Leptocylindrus danicus/minimus* *Nitzschia* sp. 1 Associated species: *Rhizosolenia setigera*		
GROUP IV *Amphitetras antediluviana* *Coscinodiscus marginatus* *Triceratium formosum f. quadrangularis* Associated species: *C. oculis-iridis* *Ch. didymus* *Asterolampra marylandica*	GROUP IV (CLUSTER 2) *Bacteriastrum hyalinum* *Lingulodinium polyedra* *Peridinium cf. steinii* Associated species: *Mesoporos perforatus*		

Note: Cluster memberships, where they exist, are indicated in parentheses. Nomenclature is based on Round (1990) and Tomas et al. (1997).

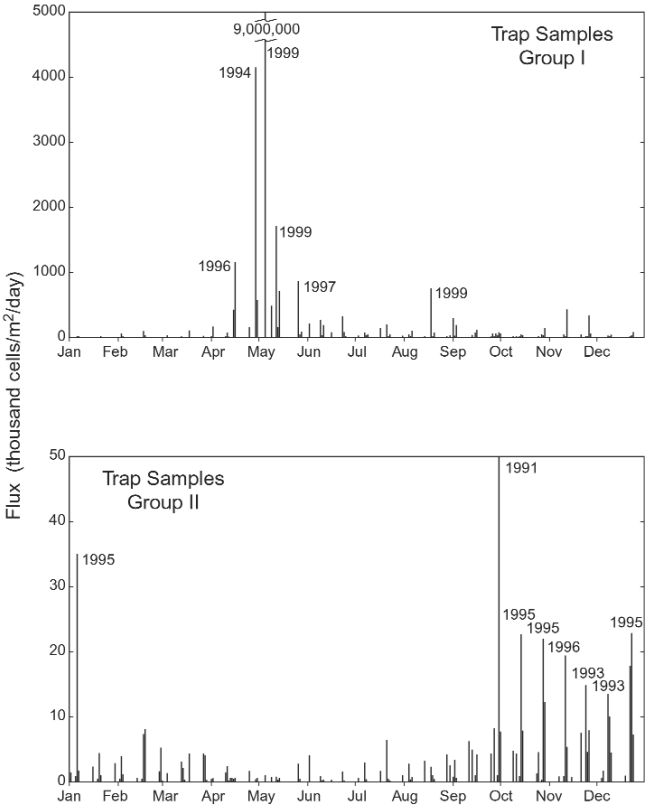

Figure 10. Seasonal cycles of the total flux of the largest two recurrent groups formed from trap samples at α = 0.55. Years of major peaks are indicated.

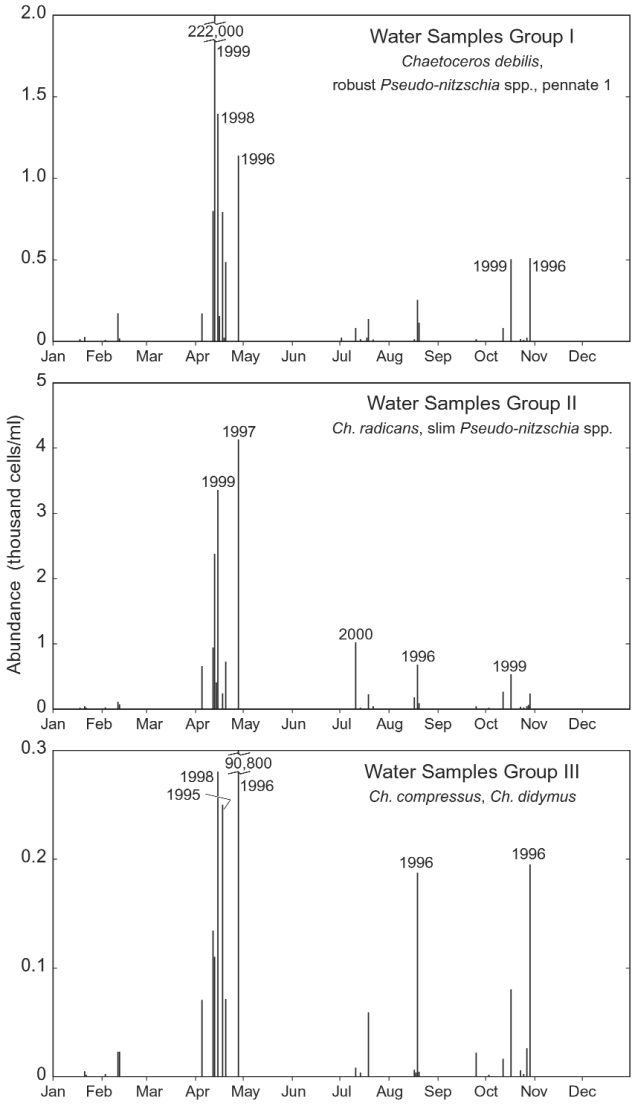

Figure 11. Seasonal cycles of the total abundance of recurrent groups formed from water samples at α = 0.70. Years of major peaks are indicated.

species. The flux of this group peaks in the spring and early summer (fig. 10), echoing the seasonal pattern of group I at α = 0.70 (fig. 8). Maximum fluxes were observed during the recent La Niña event in 1999. The second largest group, group II (fig. 7 and tab. 2) has abundance maxima in fall and winter, showing some of the features of group II at α = 0.70. The fluxes of group II were especially high in 1995. Of the five taxa in group II, *Thalassionema frauenfeldii* is a warm-temperate cosmopolite (Tomas 1997), and *Dictyocha fibula* is a widespread silicoflagellate (Sancetta 1990; Tomas 1997). However, two of the remaining species, *Coscinodiscus perforatus* and *C. granii* (group IV at α = 0.70), are thought to be restricted to coastal environments, and it is possible that the seasonal pattern of this group reflects local conditions.

There are no recurrent groups of benthic species at either level of α. The trio, group IV (α = 0.55, tab. 2), consists of two benthic species and a cold/temperate oceanic species with an associated warm-water species. Other benthic species are associated singly with groups. None can be interpreted as a "benthic" signal.

Water Samples. From the water samples, the highest affinity level (α = 0.70) defines three interrelated groups of seven diatom species (fig. 7). All of these groups have maximum abundances in April (fig. 11), like group I from the trap samples. Since the three recurrent groups are also concordant with respect to interannual abundance, their differentiation into recurrent groups must be due to an interaction between seasonal and interannual signals.

When the affinity index is lowered to α = 0.55, 35 species are grouped into 11 recurrent groups, with 8 associated species (fig. 9 and tab. 2). The initial three groups at α = 0.70 merge completely into the largest recurrent group, group I (fig. 7). Ten of the 11 recurrent groups form two clusters of interrelated recurrent groups of species each centered about one of the two largest recurrent groups. With the sole exception of one

associated species, *Rhizosolenia setigera*, that has an affinity with one recurrent group in each cluster, there are no associations between a species in one cluster and one in the other cluster. Thus, at $\alpha = 0.55$, two distinct signals are clear.

Group I at $\alpha = 0.55$ (tab. 2) is composed of eight diatoms characteristic of spring blooms. The 22 species of the larger cluster of recurrent groups, cluster I (fig. 9 and tab. 2), are diatoms, with the exception of one coccolithophore (*Emiliania huxleyi*) that is a member of a species pair (group X). The seasonal pattern of the cluster as a whole mirrors the seasonal cycle of the largest group, group I, with maximum abundances in the spring (fig. 12). The second-largest group, group II (fig. 7 and tab. 2) contains only a single diatom. As a whole, the second cluster of recurrent groups and associates is composed of seven diatoms, three coccolithophores, three dinoflagellates, two silicoflagellates, and a heterotrophic chromophyte. A seasonal cycle is not well defined for this group (fig. 12). The most prominent feature of its temporal distribution is the very low abundances during 2000, following a major La Niña event.

Comparison of Trap and Water Samples. The numbers and sizes of recurrent groups from both data sets are quite similar. Both data sets have a strong signal from spring-bloom species. To examine the relationship between the spring groups, we examine the total abundance of the largest recurrent group in each data set at $\alpha = 0.55$ (fig. 7 and tab. 2) using the reduced set of comparable samples and calculating correlations at lags between group totals between zero and six 2-week intervals. The maximum correlations between the spring recurrent group in the traps samples and in the water samples are high. As expected from previous analyses, the correlation peaks at a lag time of three 2-week intervals (trap opens 4–6 weeks after collection of the water sample). A high correlation also occurs at a lag of two 2-week intervals. The species composition suggests that these groups in both data sets are indicators of nearshore upwelling, which characteristically occurs in the spring in this region (Venrick 1998).

There are three major differences between the complete trap sample and water sample data sets. The first is the difference in compositions of the second largest groups at $\alpha = 0.55$ (groups II, tab. 2). Neither have a counterpart in the other data set. Clearly this is due to the absence of important species from each data set: the large *Coscinodiscus* species from the water samples and the nonsiliceous species, which were removed from the trap samples during preparation. As discussed previously for *C. radiatus*, the absence of many of the *Coscinodiscus* species from the water samples is surprising. Given that the populations of trap group II are best developed in the fall and winter (fig. 10), when the thermocline is

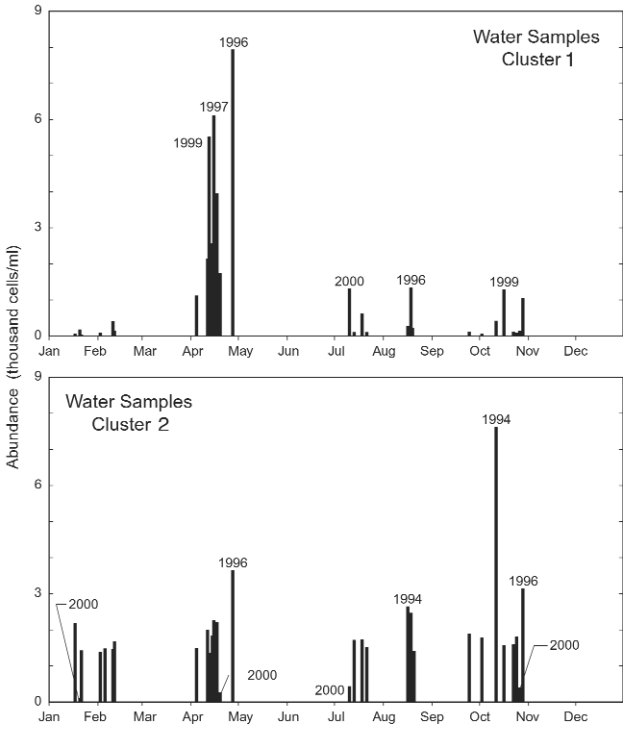

Figure 12. Seasonal cycles of the abundance of the two clusters of recurrent groups formed from water samples at $\alpha = 0.55$. Years of major peaks are indicated as are the low abundance samples from 2000.

strong and nitrate is low or absent from the mixed layer, we speculate that these species may develop below the mixed layer (i.e., below the sampling depth). We have no direct evidence that this is so. The absence of a warm-water oceanic signal from the trap data appears because much of this signal comes from nonsiliceous species that are removed from the trap material by acidification during sample preparation. In siliceous deposits, advective signals from central or equatorial species are likely to be much weaker than signals from coastal, diatom-dominated environments.

The second difference is the degree to which the spring species are delineated from the rest of the species. In the trap samples, the signal is clear at the higher level of α (0.70; fig. 7) but becomes increasingly diffuse as α is relaxed. At $\alpha = 0.55$, all groups have cross-group affinities with most of the other groups (fig. 9). In contrast, in the water samples, the initial group of spring species increases in size as α is relaxed. Several smaller spring groups appear, but these, together with group I, form a cluster of recurrent groups. The signal from spring species remains distinct from other groups even at $\alpha = 0.55$.

The performances of the recurrent group procedure in both sets of samples are characteristic: as the value of α is lowered, groups increase in size and number, and the number of cross-group affinities tends to increase. It is often the case that the most informative groups are

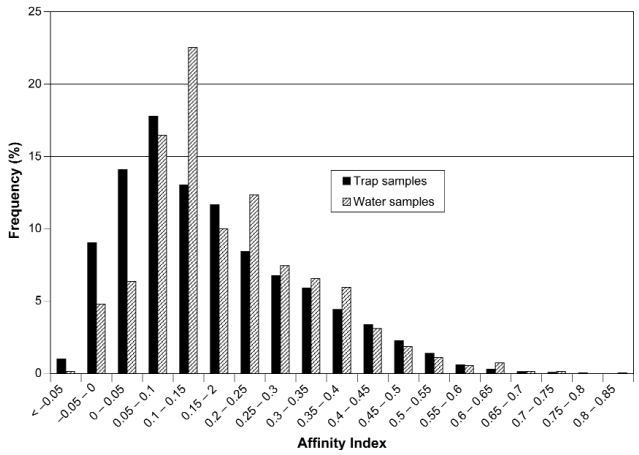

Figure 13. Frequency distribution of affinity indexes (α) between all species pairs in trap samples and in water samples.

the largest recurrent groups or group clusters that retain a level of separation. In the trap samples, the distinction between groups begins to weaken when α is as high as 0.65 (not shown). In the water samples, a distinction is clear at α = 0.55. Thus, the most meaningful recurrent groups from the trap samples are those at α = 0.70, and these are small groups of two and three species. The meaningful groups from the water samples are much larger, both because of the larger recurrent groups at α = 0.55 and because the groups themselves are clearly clustered.

There are 127 trap samples and 30 water samples. We expect the influence of sample numbers on the affinity index to tend to reduce the observed values of α between species in the water samples. Thus, the effect of the smaller numbers of samples should reduce the size and number of groups in the water sample data. This does not appear to be the case. We examine this directly by plotting the frequency distributions of α values for trap samples and water samples (fig. 13). Contrary to prediction, the frequency distribution of α values in the water samples is shifted to higher values relative to the trap samples (χ^2; $p < 0.001$). Thus, the greater number of trap samples in this comparison does not appear to be a factor in explaining the results.

Groupings of Samples

Spearman's rank order correlation coefficient, ρ, is the basis for constructing dendrograms that show the similarity of samples with respect to their species compositions (rank order of abundance).

Trap Samples. A ρ value of 0.23 was subjectively selected as that which defines the most meaningful groups of trap samples. When this value is considered, the traps are clearly grouped by date of collection (fig. 14). Ninety-four percent of the traps are included in a group, and only 6% of the clustered traps are clustered out of sequence. The longest series of traps include 9 months of data: 2 September 1993 through 13 May 1994. However, the median sequence length is less than 2 months—about five traps. Unexpectedly, this analysis does not indicate the annual cycle seen in the fluxes of some recurrent groups. In the dendrogram, spring samples are more similar to other samples in the same year than to spring samples of different years. (In a separate study it will be shown that this is, in part, a function of the use of a nonparametric correlation coefficient as the basis for clusters. Rho weights all species equally, whereas the spring bloom is an increase in a relatively few species.)

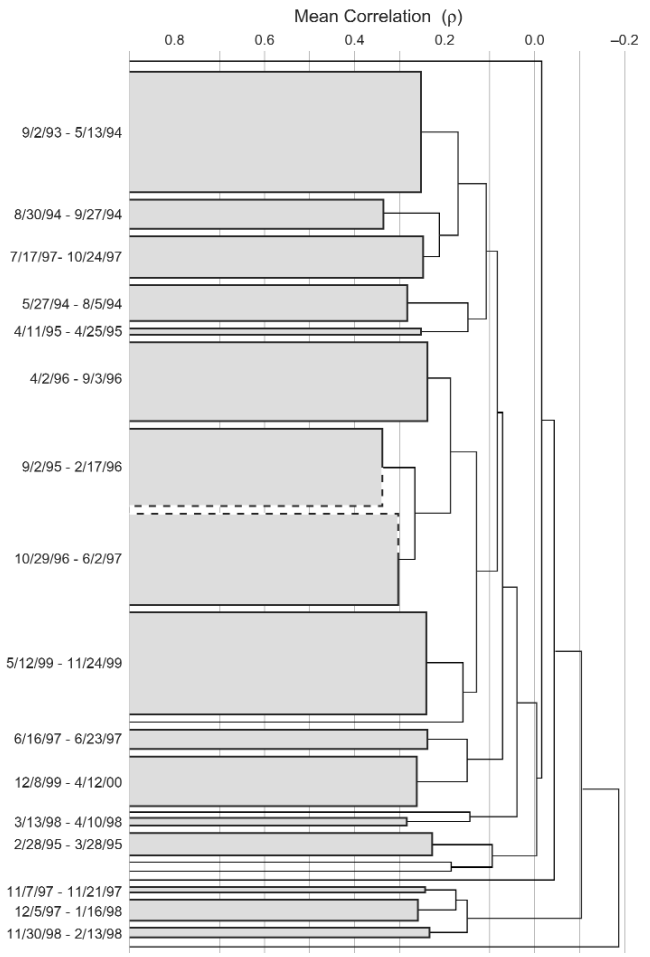

Figure 14. Abbreviated ρ-based dendrogram showing similarity of species structure of trap samples. Shaded areas indicate groups of traps similar at ρ ≥ 0.23, and dates indicate the midpoints of collection dates of the component trap samples. Dashed lines indicate possible subgroups, defined by dates.

Water Samples. In the dendrogram of water samples, no value of ρ produces informative groups of water samples (fig. 15). At ρ = 0.23, only 19 of the 30 water samples are related to other samples. The largest group consists of 7 samples that were collected in different seasons of different years. All other related samples at ρ = 0.23 are sample pairs.

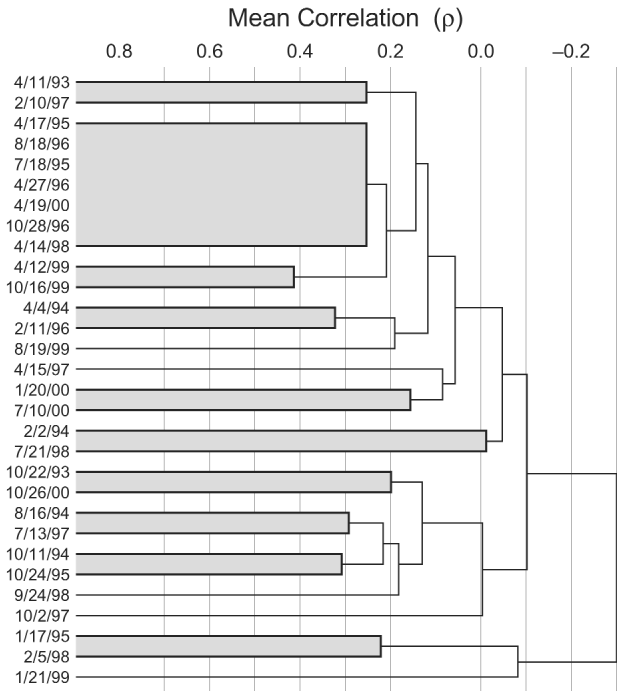

Figure 15. Rho-based dendrogram showing similarity of species structure of water samples. Dates indicate the collection dates of the samples.

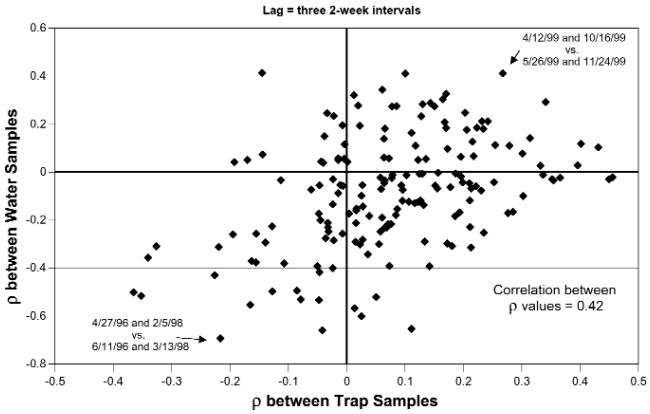

Figure 16. Relationship of the correlation (ρ) between pairs of trap samples to the correlation between the corresponding pairs of water samples, where the trap samples are lagged 4–6 weeks behind the water samples. Thus, water samples collected on 12 April 1999 and 16 October 1999 were similar in their rank order of species abundances. Trap samples collected 4–6 weeks later (mid-dates 26 May 1999 and 24 November 1999) also had similar species composition. Both trap and water samples indicate similar flora in the spring and fall of 1999; they do not necessarily indicate that the species compositions in the trap samples were similar to those in the water samples. In the same way, both trap and water samples indicate that the flora in the spring of 1996 was different from the flora in the winter of 1998.

Comparison of Trap and Water Samples. No evidence of the trap clusters can be found in the water sample dendrogram. To some extent, this may be a function of sample frequency in that many of the trap series are too short to include more than a single coincident water sample. On the other hand, there are three water samples collected during the 9-month trap series, 2 September 1993–13 May 1994. None of these water samples are related by the dendrogram criterion; nor are the three water samples collected during the 29 October 1996–2 June 1997 trap series.

A more direct approach to this problem considers the restricted sets of coincident water and trap samples to determine whether pairs of similar (or dissimilar) water samples are coincident with pairs of similar (or dissimilar) trap samples. In other words, we ask, If the correlation between a pair of trap samples indicates a similar (or dissimilar) flora, does the correlation between corresponding water samples also indicate similar (or dissimilar) flora? As a measure of similarity, we use Spearman's correlation coefficient, ρ, between the correlations of the trap sample pairs and the water sample pairs. Maximum similarity is seen when trap samples are lagged three 2-week periods behind the water samples (fig. 16), but there remains considerable scatter. The relationship accounts for only 16% of the variability. There is also a clear tendency for trap samples to be more similar than water samples (i.e., more values in the lower-right quadrant than in the upper-left).

One explanation for the greater similarity between trap samples, which integrate through time, is that they smooth out small-scale variability in the distributions of the individual species, whereas the water samples, which are point samples in time and space, capture all but the smallest scales. Unless a large proportion of species fluctuations are correlated on a small scale, the variability of individual species among water samples will reduce sample similarity and, hence, lower the mean value of ρ. At the same time, the variability of ρ (about this reduced mean) will be increased. Thus, if the temporal averaging of the trap samples is important, we expect ρ between trap samples to be higher than ρ between water samples, especially at smaller scales. That this is the case can be seen by comparing the distributions of ρ from trap and water sample pairs as the interval between samples increases (fig. 17). Using a 168-day running average, trap samples close in time are similar, and the similarity decreases somewhat asymptotically to zero at about 4.5 years. Only 19% of the values are negative. In contrast, among the water samples, even averaging over 168-day intervals fails to obscure the noise in the data (fig. 17). This may be partly due to the fewer number of water samples and hence the fewer number of samples contributing to each mean value.

Local maxima in the running average at intervals of 1, 2, 3, 4, and even 5 years reveal the annual cycle in both data set. Only the trap samples show maximum similarity (ρ) at the shortest separation intervals. In the water sample data, samples separated by intervals less than 1 year are, on the average, less similar than samples separated by 1 year. At intervals less than about 4 years, trap

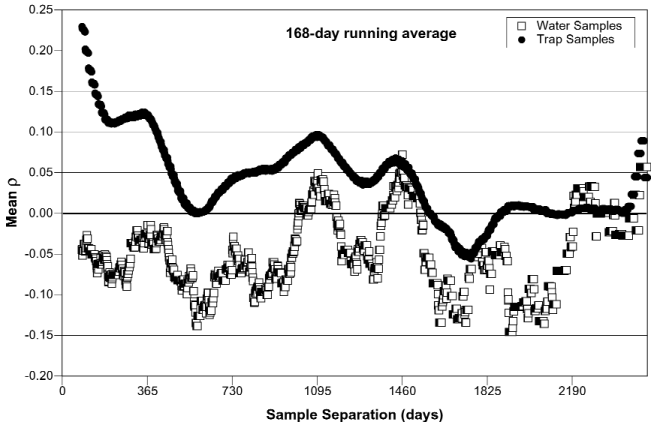

Figure 17. Frequency spectra of the similarity of sample pairs separated by increasing periods of time. Similarity is the correlation (ρ) of the rank order of species abundances in two samples. Running averages (168 days) have been taken to emphasize major trends.

samples are consistently more similar than water samples. Both data sets also show increasing correlations at the longest intervals, but the meaning of this is uncertain.

Both the higher mean ρ and the presence of a maximum at the shortest sampling intervals in the trap samples are evidence that significant small-scale spatial/temporal variability is effectively removed by the trap samples. More frequent sampling of the water column in time would not substantively change this conclusion until the sampling became so frequent that averaging could duplicate the integration of the traps.

DISCUSSION AND CONCLUSIONS

We did not expect that samples from the water column and from near-bottom traps would provide identical representations of the phytoplankton assemblage in the euphotic zone. Nevertheless, we are surprised at the magnitudes of the differences. Out of a combined species list of 260 taxa, only 9 were frequent enough in both sets of samples and were identified with sufficient reliability to provide the basis for direct comparison. If we restrict the original list to siliceous species that are partly or wholly planktonic, the proportion of comparable species improves slightly, from 0.03 to 0.06, but it is still low. Even allowing random chance its fair share, not all discrepancies have an adequate explanation. The seeming disproportionate dominance of Hyalochaete resting spores in the trap samples and the absence of many large *Coscinodiscus* species from the water samples need further study.

Several of our analyses indicate a lag time of three 2-week intervals (4–6 weeks) between water sample and trap sample. Many of these analyses also show correlations at two 2-week intervals (2–4 weeks) that are only slightly less high. The fact that these two values recur suggests an intermediate lag time (on the order of 4 weeks) as the best estimate from our data. However, our analyses are highly interdependent, so the recurrence of the same estimated lag provides little power for generalizing.

A number of studies have used diverse approaches to estimate sinking velocities or lag times between the euphotic zone and the sediment. (e.g., Eppley et al. 1967; Shanks and Trent 1980; Bienfang 1985; Deuser et al. 1990; Passow 1991; Kiørboe 1993). Estimates vary widely, in part due to different environments and different particle morphology and physiology. Species differ in their tendency to form aggregates before settling, and single cells or chains may sink more slowly than aggregates or fecal pellets (Riebesell 1989; Kiørboe 1993). Some of the range in our estimated lag times may reflect this inherent variability.

In a study from the Santa Barbara Basin that included "flocculent conglomerates of living, senescent diatoms, particularly chain-forming species, and frustules which formed following a diatom bloom," Alldredge and Gotschalk (1988) estimated a mean sinking velocity of 74 ± 39 m/day (5–15 days). Shipe and Brzezinski (2001), working at a trap site 6–8 nmi northeast of this study, estimated a 2-week lag between biogenic silica production in the upper 75 m and deposition into a trap at 470 m. Shipe et al. (2002) observed a lag interval of 2–4 weeks for several chemical measures of particulate composition. Our estimate of 4 weeks is high compared with these. It is possible that a large proportion of cells settle as single cells or single chains, but this contradicts many other observations about the importance of aggregations in vertical transport (Smetacek 1985; Fowler and Knauer 1986) and our own observations of packed aggregates in raw trap material.

Whether the estimated time lag is 2 weeks or 6 weeks, all estimates are longer than the estimated 7-day residence time of near-surface particles in the Santa Barbara Channel (Winant et al. 1999). This suggests that most of the material reaching the sediment traps is produced outside of the Santa Barbara Channel. The correlations between the spring signal in water samples and sediment traps suggest that the spring bloom is a quasi-simultaneous occurrence over a broad region. Flow into the Santa Barbara Channel during the spring is primarily from the north, which characteristically supports much stronger wind-driven coastal upwelling than the Southern California Bight to the south (Huyer 1983). In contrast, the prevailing currents from the southeast in summer, fall, and winter suggest the trap receives flora primarily from the central and southern California Bight. The influence of the prevailing currents will be modified by mesoscale diffusive processes (Siegel et al. 1990). The geographical extent of the trap's footprint remains to be determined.

A surprising result of our comparison is the fundamentally different behavior of methods that group

species with similar patterns of abundance (here, recurrent group analysis) and those that group samples according to similarity of species composition (here, dendrograms). In the first case, the water samples seem to produce clearer signals; in the second, the trap samples give clear results while the water samples do not. We interpret this as reflecting the underlying differences in the temporal/spatial scales sampled by individual water and trap samples.

Recurrent group analyses of both data sets capture the spring bloom. Although analogous groups (groups I at $\alpha = 0.55$) share only a few dominant species, their fluctuations through time are correlated. The two sets of samples, however, each produce at least one group that has no analogy to groups in the other set—for instance, the winter coastal flora in the trap samples and the warm-water oceanic flora in the water samples.

Much of the difference between traps and water samples is clearly related to different species compositions of the two data sets. Discrete water samples (especially a single near-surface sample) may miss significant populations that develop in restricted vertical strata; whether this is, in fact, the reason for the absence of a coastal fall-winter group in the water samples remains to be determined. Alternatively, studies that are focused on a restricted component of the phytoplankton, such as the siliceous component, risk diluting and distorting important environmental signals. In fact, the warm-water diatoms are often used as evidence for El Niño conditions (Lange et al. 1987, 1990, 2000). Clearly, their presence or absence must be judged by a different criterion than, for instance, the presence or absence of the spring-bloom species. It is interesting that the warm-water group identified from the water samples showed little change in abundance during the 1993 and 1997–98 El Niño conditions but showed a strong reduction in abundance following the 1999 La Niña event.

Analysis of trap data consistently produces interrelated recurrent groups. Except for species pairs, which are difficult to evaluate, it is not possible to isolate distinct recurrent groups or clusters of groups from the trap data. In contrast, in the water sample analyses, species were consistently grouped with the same species regardless of the affinity level used. At α of 0.55, two clusters of recurrent groups were clearly separated. We speculate that the more distinct relationships between species groups emerging from the water samples reflect the fact that species relationships are best preserved in smaller-scale features, which are better samples by water bottles; the temporal (and hence spatial) averaging by the trap samples smears these small-scale relationships between species.

In contrast, analyses that evaluated the species compositions of individual samples (dendrograms) produce clear signals from the trap data and no interpretable signal from the water sample data. To some extent, this is due to the larger number and higher frequency of the trap samples. However, a comparison of the behavior of ρ in the two data sets shows a higher mean value of similarity between trap samples at virtually all frequencies. This is evidence that the 2-week integration accomplished by each trap sample effectively removes small-scale variability. A single trap sample represents some substantially larger region (Deuser et al. 1990; Siegel et al. 1990), although the precise footprint of this region is uncertain. From the perspective of paleoecological interpretations, this broad representation should be an advantage, although the direction and magnitude of the source region, as well as the lag-time itself, certainly vary through time and probably have strong seasonal components. At the same time, the dendrograms from the water samples suggest limits on the amount of information about seasonal and interannual changes of assemblages that should be expected from water samples from a single location.

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