What have natural and human changes wrought on the foraminifera of San Francisco Bay late Quaternary estuaries?

Amy E. Lesen[a,*], Jere H. Lipps[b]

[a] Dillard University, Department of Biology, 2601 Gentilly Boulevard, New Orleans, LA 70122, USA
[b] Museum of Paleontology and Department of Integrative Biology University of California, Berkeley, CA 94720, USA

ARTICLE INFO

ABSTRACT

In this study we compare the foraminifera of modern South San Francisco Bay with fossils from sediments of a previous estuary at 125 ka to provide a basis for interpreting the impact of natural and human change on the benthic ecosystem. All the species found in the Pleistocene sediments of this study are estuarine and/or shallow-water species occurring commonly in San Francisco Bay today, except for the introduced foraminifer *Trochammina hadai*, a native of Japan that was not found in samples taken in San Francisco Bay before 1983. The biodiversity and species composition of the fossil and modern assemblages before the introduction of *T. hadai* are nearly identical, suggesting that the environmental and physical changes in the 125,000-year-old and modern estuaries have not had a significant effect on the meiofauna of the Bay. In contrast, modern anthropogenic change in the form of species introductions has impacted the modern foraminiferal assemblage: *T. hadai* began to dominate the modern assemblage a decade after its introduction. Similar to the recorded impacts of introductions of marine metazoan invertebrate species, the dominance of *T. hadai* changed species proportions in the post-1980s foraminiferal assemblage, however no known extinctions in the native foraminiferal fauna occurred.

© 2011 University of Washington. Published by Elsevier Inc. All rights reserved.

Introduction

San Francisco Bay (Fig. 1), the largest estuary on the eastern Pacific coast, has a dynamic and complex geologic and environmental history extending over the past million years (Atwater, 1979; Sloan, 1980; Ingram and Sloan, 1992; Sloan, 1995; Ingram, 1998; Ingram and Ingle, 1998; Byrne et al., 2001; Malamud-Roam and Ingram, 2001). At least four river valleys and four estuaries have alternately occupied the present site of the Bay as sea level rose and fell with glaciations and warming periods (Atwater, 1979). Near the close of the last glaciation, about 13,000 yr ago, humans migrated into the area (see Fagan, 2004, for a general discussion and references). At that time, sea level was 120 m lower than today and the Bay was a valley with a river that flowed across nearly 48 km of coastal plain beyond the Golden Gate to empty into the Pacific Ocean (Lindberg and Lipps, 1996). The current Bay began approximately 10 ka, as the last glaciation ended and the Pacific Ocean entered the Golden Gate. The hydrology and biota of San Francisco Bay as it is today largely developed during the last 6000 yr when the extent of the bay was similar to today's and the average depth was less than 5 m (Atwater, 1979). Humans were present along the edges of this Bay during its entire change from river valley to estuary. Today San Francisco Bay is home to approximately 7 million people (Conomos, 1979; Sloan, 1995; Bay Area Census at http://www.bayareacensus.ca.gov/bayarea.htm).

Current global warming trends and the subsequent rise in sea level are expected to result in inundation of coastal environments and in habitat change for the San Francisco Bay biota (Patrick and Delaune, 1990; Keldsen and Wilson, 1997; Kennish, 2001; Galbraith et al. 2002). Global and environmental changes must be viewed in both an evolutionary and geologic context; studying fossils and paleobiology provides this crucial historical perspective (Travis and Futuyma, 1993; Lieberman, 2000; Pataki, 2002). Foraminifera, with their long fossil record and current abundance in marine ecosystems, are very useful in understanding the evolution of ecosystems and the possible future changes on the environment and biota in San Francisco Bay and worldwide (Thierstein, 1987; Hallock, 2000).

The distribution, ecology, and paleoecology of both recent and fossil foraminifera along the California coast and in San Francisco Bay are reasonably well known (McDonald and Diediker, 1930; Bandy, 1953; Arnal and Conomos, 1962; Means, 1965; Slater, 1965; Quinterno, 1968; Locke, 1971; Arnal et al., 1980; Sloan, 1980, 1981; Erskian and Lipps, 1987; Finger et al., 1990; Sloan, 1992; Langer and Long, 1994; McCormick et al., 1994; McGann and Sloan, 1996; Sliter, 1999; Lesen, 2005). In addition, foraminifera have been valuable tools in researching and mitigating environmental degradation, pollution, and contamination of water and sediment in San Francisco Bay (van Geen et al., 1992; Sloan, 1995; van Geen and Luoma, 1999a,b; Lesen, 2005) as well as many other systems (Setty and Nigam, 1984; Nagy

and Alve, 1987; Alve, 1991; Yanko et al., 1994; Alve, 1995; Collins et al., 1995; Danovaro et al., 1995; Resig et al., 1995; Yanko et al., 1998).

The Pleistocene stratigraphy of San Francisco Bay and its ancient foraminiferal fauna are also known (Stewart and Stewart, 1933; Ingle, 1976; Sloan, 1980, 1981, 1992, 1995), thus presenting an opportunity for comparisons of fossil and recent foraminiferal assemblages in the Bay that may provide information about how the Bay's ecosystems have changed or remained resilient during the glacial/interglacial cycles of the Pleistocene. This information, in turn, can aid in predicting the response of the Bay and its biota to future environmental changes. Here we compare the species proportions, overall similarity, seasonal changes, and species diversity of the recent foraminiferal assemblage at a site in South San Francisco Bay with the fossil foraminiferal assemblage from Pleistocene samples taken at three nearby sites in South San Francisco Bay, in order to test the hypothesis that the foraminiferal assemblage in San Francisco Bay has not changed significantly since the last interglacial interval.

The late Pleistocene San Francisco Bay

San Francisco Bay is a complex environment with three major divisions: North Bay, with the chief flow of freshwater to the bay; Central Bay, with deep depths and significant ocean influence; and South Bay, a shallow, broad expanse of soft-sediment without much influence from runoff. North and Central Bay may have been significantly influenced by variations in runoff, sedimentation or other factors which we wished to avoid in an effort to make our comparisons as meaningful as possible. Instead, we chose to examine South Bay because of the relative similarity of the modern and ancient bays.

South Bay generally has retained the same form throughout its recent history and the sedimentation patterns have remained similar as well (Atwater, 1979). The Yerba Buena mud was deposited about 125,000 yr ago at a lower but rising sea level, and its depth at the time of deposition was similar to that in South Bay today because the intrusion of sea water into South Bay induced sedimentary infilling that maintained a shallow depth. The Yerba Buena mud and modern South Bay are reasonably comparable in terms of sedimentation, depth and climate, so comparisons of the foraminiferal faunas during these two time periods is justifiable.

Materials and methods

Samples of recent foraminifera

Sampling of recent foraminifera was carried out on monthly cruises on the R/V *Polaris* for 2 yr from November 1999 through November 2001, in cooperation with the United States Geological Survey (USGS) (Table 1). Foraminiferal samples were collected at USGS Station 25 (37°40.2′N, 122°19.5′W) in South San Francisco Bay (Fig. 1). Station 25 is located at a depth of 8.8 m at mean lower low water, and the surface salinity ranges from 15 to 32 psu from the rainy to the dry season (USGS, 2003). Station 25 is close to the San Bruno Shoal, an important bathymetric feature of South Bay that affects exchange between Central San Francisco Bay and the southern part of South Bay (Fig. 1).

Bottom samples were collected with a 0.10-m² Van Veen grab every month for 2 yr. Single samples were taken for the first five months of the study and replicate samples were collected every month thereafter. Foraminiferal sub-samples were taken from the Van Veen sampler using a short plastic core tube 12.5 cm in diameter. The top 1.0 cm of sediment was sliced from the core (12.5 cm³) and placed into a jar containing a solution of 10% formalin (buffered with sodium borate) to which Rose Bengal stain had already been added to a concentration of $1.0 \, g \, l^{-1}$. Rose Bengal is a standard method of
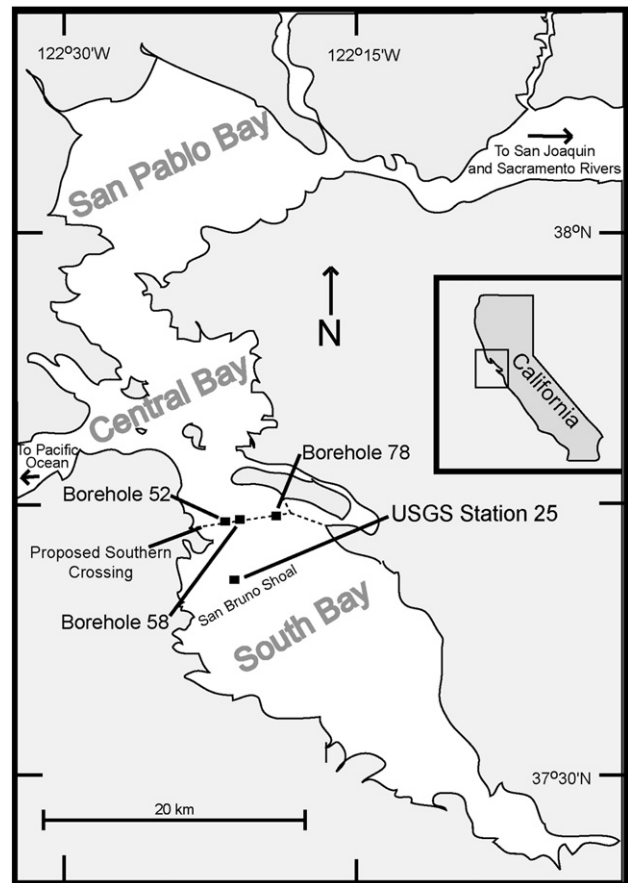
Figure 1. Map of San Francisco Bay showing the location of the site of the recent foraminiferal samples at USGS Station 25, taken in the central channel of San Francisco Bay. Also shown is the source of the fossil foraminiferal samples along the proposed Southern Crossing where boreholes 52, 58, and 78 were drilled.

determining which foraminifera contained protoplasm when stained, but it is not entirely reliable (Bernhard, 2000).

Each sample was stored at 4°C in the laboratory and allowed to stain for 1 week. Each sample was then washed over a 63-μm sieve and air dried. At the beginning of the study, approximately 15 dried samples were floated in sodium polytungstate to separate some of the sediment from the foraminifera. Floatation was then abandoned, however, because of the possible loss of foraminifera due to repeated drying before and after floatation. The remaining 33 samples were counted without flotation. The number of stained and unstained foraminifera in the >63-μm fraction from each 12.5-cm³ sample was counted.

Table 1
Sampling dates for collection of the recent foraminifera. Samples taken on the USGS R/V *Polaris* at USGS Station 25 in South San Francisco Bay.

Month/Year	1999	2000	2001
January		11–12	
February		8–9	6–7, 26–27
March		7–8	27–28
April		4–5	24–25
May		16–17	24–25
June		13–14	19–20
July		11–12	17–18
August		8–9	
September		5–6	11–12
October		10–11	15–16
November	10–11	7–8	27–28
December	14–15	12–13	

Samples of fossil foraminifera

Fossil foraminiferal samples were obtained by Sloan (1980, 1981, 1992) from cores taken from boreholes drilled along a transect by CALTRANS (formerly the California Department of Transportation) in San Francisco Bay in 1969 for the proposed Southern Crossing, a bridge between San Francisco and the island of Alameda that was never constructed (Fig. 1). Cores 75 cm long and 8 cm in diameter were subsampled at 1.5-cm intervals and stored in tubes and jars. In all, Sloan (1980, 1981, 1992, 1995) processed and analyzed foraminifera in 440 samples from 347 sample intervals. Fifty-gram splits of each core sample were washed through 20-, 120- and 230-μm sieves. Samples for foraminiferal analysis were taken from the youngest Pleistocene sediments, the Yerba Buena mud member of the San Antonio formation, which now lies between 25 and 70 m below mean sea level (Fig. 2; Sloan, 1981, 1992).

The Yerba Buena mud lies on top of Pleistocene alluvium and is overlain by alluvium and aeolian sand (Fig. 2), which were deposited during the last glaciation when San Francisco Bay was a river valley (Ingram and Sloan, 1992; Sloan, 1992). The Yerba Buena mud ranges in thickness from 5 to 32 m (Sloan, 1992) in the vicinity of the present study. Data on the thickness, extent, stratigraphic position, radiometric dates, and amino acid racemization ages in mollusk shells suggest deposition of the Yerba Buena mud during Marine Isotope Substage 5e; the Yerba Buena mud is probably the earliest estuarine deposit of the last interglacial interval, about 122.5 to 125.2 ka (Sloan, 1981; Martinson et al., 1987; Ingram and Sloan, 1992; Sloan, 1992).

Selecting samples for comparison and statistical methods

In this study, data from the fossil samples collected by Sloan (1980, 1981, 1992) were used that contained the most foraminifera and that were collected from boreholes located as close as possible to USGS Station 25, the site where recent samples were collected (Fig. 1). The fossil data reported here are from the >120-μm fraction; in order to compare samples, recent foraminifera smaller than 120 μm were excluded from the analysis.

Cluster analysis was performed with SYSTAT v. 10.2.01 on Jaccard binary similarity coefficients from presence–absence data, using the single-linkage, nearest-neighbor cluster method. Cluster analysis on recent and fossil samples was performed using Bray–Curtis dissimilarity measures (single-linkage, nearest-neighbor cluster method). To carry out statistical analyses comparing the fossil and recent assemblages, all samples that had fewer than 200 individuals (Tables 3 and 4) were eliminated.

Results

Recent foraminiferal assemblages

Nine species of benthic foraminifera were found in the >120-μm fraction at USGS Station 25 in South San Francisco Bay between November 1999 and November 2001 (Table 2, Figs. 3a and b). Sample sizes ranged from 62 to 492 individuals (Table 3).

The dominant species (as illustrated by the mean values) in the recent assemblage were *Trochammina hadai* Uchio (20%), *Ammonia beccarii* (Linné) (14%), *Bolivina striatula* Cushman (13%), *Bolivina vaughani* Natland (10%), and *Elphidium excavatum* (Terquem) (17%). All of these dominant species are calcareous foraminifera, except for *T. hadai*, which has an agglutinated test. The relative abundances of these taxa were fairly constant over the two-year collection period (Table 3).

Fossil foraminiferal assemblage

Twenty-one species of benthic foraminifera occur in the Yerba Buena mud samples used in this study, all of which are common estuarine and shallow water taxa (Table 2) (Sloan 1992). Between 125 and 3211 specimens/sample were recovered (Table 4). Seven species composed over 98% of the individuals in all samples: *Elphidium excavatum* (63%), *Elphidiella hannai* (Cushman and Grant) (20%), *Elphidium gunteri* Cole (7%), *Buccella frigida* (Cushman) (3%), *A. beccarii* (2%), *Buliminella elegantissima* (d'Orbigny) (2%), and *Elphidium magellanicum* Heron-Allen and Earland (1%) (Sloan, 1992). *Elphidium* species and *E. hannai* combined compose 83% of the individuals in all samples (Table 4) (Sloan, 1992).
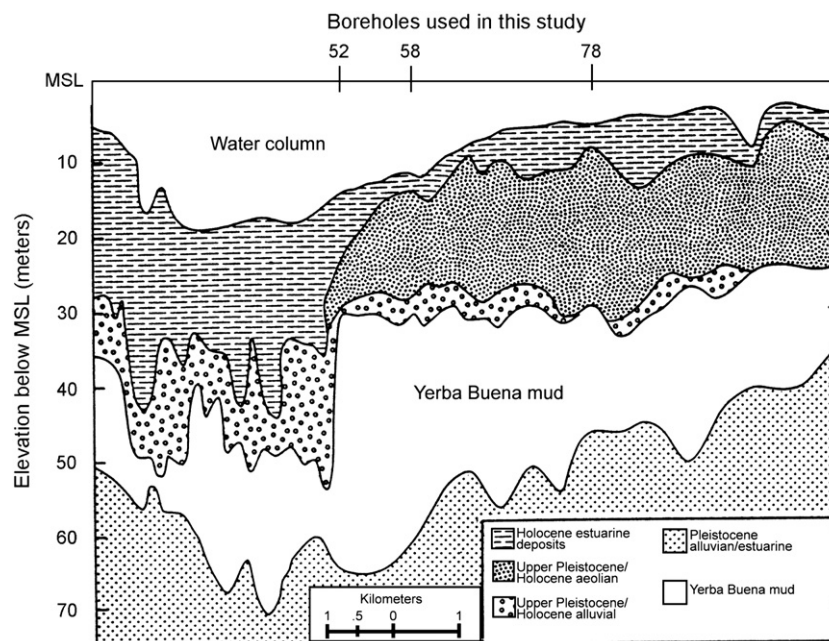
Figure 2. Sediments beneath San Francisco Bay along the proposed Southern Crossing, and location of boreholes used in this study from which fossil foraminifera samples were taken. Figure modified from Sloan (1992).

Table 2

Taxa found in recent and fossil assemblages in South San Francisco Bay. See Appendix for the complete references to these taxa.

Species names	
Recent assemblage	Fossil assemblage
Ammonia beccarii (Linné)	*Ammonia beccarii* (Linné)
Buliminella elegantissima (d'Orbigny)	*Ammotium planissimum* (Cushman)
Bolivina striatula Cushman	*Bolivina striatula* Cushman
Bolivina vaughani Natland	*Buccella frigida* (Cushman)
Elphidium excavatum (Terquem)	*Buccella tenerrima* (Bandy)
Elphidium gunteri Cole	*Buliminella elegantissima* (d'Orbigny)
Elphidiella hannai (Cushman and Grant)	*Cibicides fletcheri* Galloway and Wissler
Trochammina hadai Uchio	*Cibicides lobatulus* (Walker and Jacob)
Trochammina inflata (Montagu)	*Elphidiella hannai* (Cushman and Grant)
	Elphidium excavatum (Terquem)
	Elphidium gunteri Cole
	Elphidium magellanicum Heron-Allen and Earland
	Elphidium microgranulosum (Galloway and Wissler)
	Fissurina cucurbitasema Loeblich and Tappan
	Fissurina lucida (Williamson)
	Fursenkoina fusiformis (Williamson)
	Fursenkoina loeblichi (Feyling-Hanssen)
	Lagena amphora Reuss
	Lagena sp.
	Nonionella stella Cushman and Moyer
	Textularia sp.

Comparisons between fossil and recent assemblages

Species diversity

Species richness was higher in the Pleistocene Yerba Buena mud samples than in the recent samples (Table 2). However, species evenness was greater in the recent samples. Of all 9 species found in the recent samples, none had a relative abundance lower than 4%, whereas 18 out of the total 25 species found in the Yerba Buena samples had abundances of less than 1% (Tables 3 and 4). The fossil sample sizes were generally larger than the recent samples (Tables 3 and 4). Rarefaction analysis was performed which revealed that, at a sample size of 200, there would be an average of 9 species present in the fossil samples, which is the same number found in the recent samples (hypergeometric distribution for rarefaction [Hurlbert, 1971; Hayek and Buzas, 1997]).

Fisher's alpha (α) was used as the total diversity index because it is not sensitive to sample size (Hayek and Buzas, 1997). The mean Fisher's α for the fossil samples was 2.203 ± 0.924 and the mean for the recent samples was 1.776 ± 0.132 (Table 5). No significant difference in mean Fisher's α was found between the fossil and recent assemblages (SYSTAT 10.2.01, 2002; ANOVA, where $\alpha = 0.05$, $p = 0.144$).

Relative proportion of dominant species

The relative proportion of all the dominant species that were common between the fossil and recent assemblages were calculated using *A. beccarii*, *B. elegantissima*, *E. excavatum*, *E. gunteri*, and *E. hannai* (Table 6). The proportion of *A. beccarii* ($p \leq 0.001$) and *B. elegantissima* ($p \leq 0.001$) were significantly higher in the recent than the fossil samples. The proportion of *E. excavatum* was significantly higher in the fossil samples ($p \leq 0.001$) (Table 6) (SYSTATv.10.2.01, 2002; ANOVA). No significant difference in mean relative abundance of *E. gunteri* ($p = 0.361$) or *E. hannai* ($p = 0.070$) was found between the recent and fossil assemblages (Table 6) (SYSTAT v.10.2.01, 2002; ANOVA, where $\alpha = 0.05$).

Comparisons of overall species composition

To compare overall species composition between the fossil and recent samples, only species that were common to both assemblages

(*B. striatula*, *A. beccarii*, *B. vaughani*, *E. excavatum*, and *E. gunteri*) were included in the analysis. Cluster analysis revealed that all of the recent samples clustered with fossil samples 52–18, 52–15, and 52–17 (distance = 0.000), and this cluster was joined with sample 58–21 (distance = 0.167).

Discussion

Recent foraminiferal assemblage

With one exception, all taxa found in this study are common estuarine and shallow water species that have been found in other studies of benthic foraminifera in San Francisco Bay (Slater, 1965; Locke, 1971; Arnal et al., 1980). The exception is the introduced foraminifer *T. hadai*, which is native to Japan and was not found in samples taken in San Francisco Bay before 1983 (McGann and Sloan, 1996; McGann et al., 2000). *T. hadai* has proliferated in many regions of San Francisco Bay and was found to constitute as much as 56% of all foraminifera in sediment samples collected from South San Francisco Bay in the 1990s (McGann and Sloan, 1996; McGann et al., 2000).

South San Francisco Bay can reach near open ocean salinities (up to 32 psu) in the summer when there is little or no freshwater input (Conomos et al., 1985; USGS, 2003). The recent foraminiferal assemblage in South Bay is dominated by taxa that are representative of shallow water marine habitats and habitats with little freshwater influence or taxa that are able to survive in a wide range of estuarine conditions (Quinterno, 1968; Arnal et al., 1980).

Quinterno (1968) and Arnal et al. (1980) separated recent foraminifera of South San Francisco Bay into four ecologic zones based on depth distributions. This study's USGS Station 25 could be assigned to their Zone III, the deep bay zone between 8 and 15 m depth, based on the species composition, although they found higher relative abundances of *E. gunteri* (~5–10%), *E. excavatum* (over 40% in some samples), and *A. beccarii* (as much as 40% between 8 and 9 m) (Quinterno, 1968; Arnal et al., 1980). Their samples were collected between 1961 and 1963 before the introduction of *T. hadai* whereas the recent assemblage collected for this study was obtained between 1999 and 2001, over a decade after the species' introduction, and included 20% *T. hadai*. This introduction significantly altered the relative abundance of species all over San Francisco Bay (McGann and Sloan, 1996; McGann et al., 2000).

Fossil foraminiferal assemblage and implications for San Francisco Bay paleoenvironments

All of the dominant fossil taxa found in the Yerba Buena mud are present in San Francisco Bay assemblages today except for *B. frigida* (Arnal and Conomos, 1962; Quinterno, 1968; Locke, 1971; Arnal et al., 1980). Sloan (1992) identified three foraminiferal associations in different layers of the Yerba Buena mud (Fig. 4). The fossil samples used in our study were taken from regions of the Yerba Buena mud where the *E. excavatum* and the *E. hannai* associations are found.

The *E. excavatum* association consists of *E. excavatum* and *A. beccarii* which comprise more than 50% of all individuals, as well as *B. frigida*, *B. elegantissima*, *E. hannai*, *E. gunteri* and *E. magellanicum* in smaller abundances. This association is found in the middle part of the Yerba Buena unit. Of the samples used in the present study, samples 52–11, 52–17, 52–18, 58–18, 58–20, 58–21, 58–22, and 58–23 were taken from sections that are dominated by the *E. excavatum* association (Fig. 4). *Elphidium excavatum* is common in the more saline South Bay today, and *A. beccarii* is found in all parts of San Francisco Bay, suggesting that the middle part of the Yerba Buena mud represents a similar environment to today's South San Francisco Bay (Quinterno, 1968; Locke, 1971; Wagner, 1978; Arnal et al., 1980; Sloan, 1980).
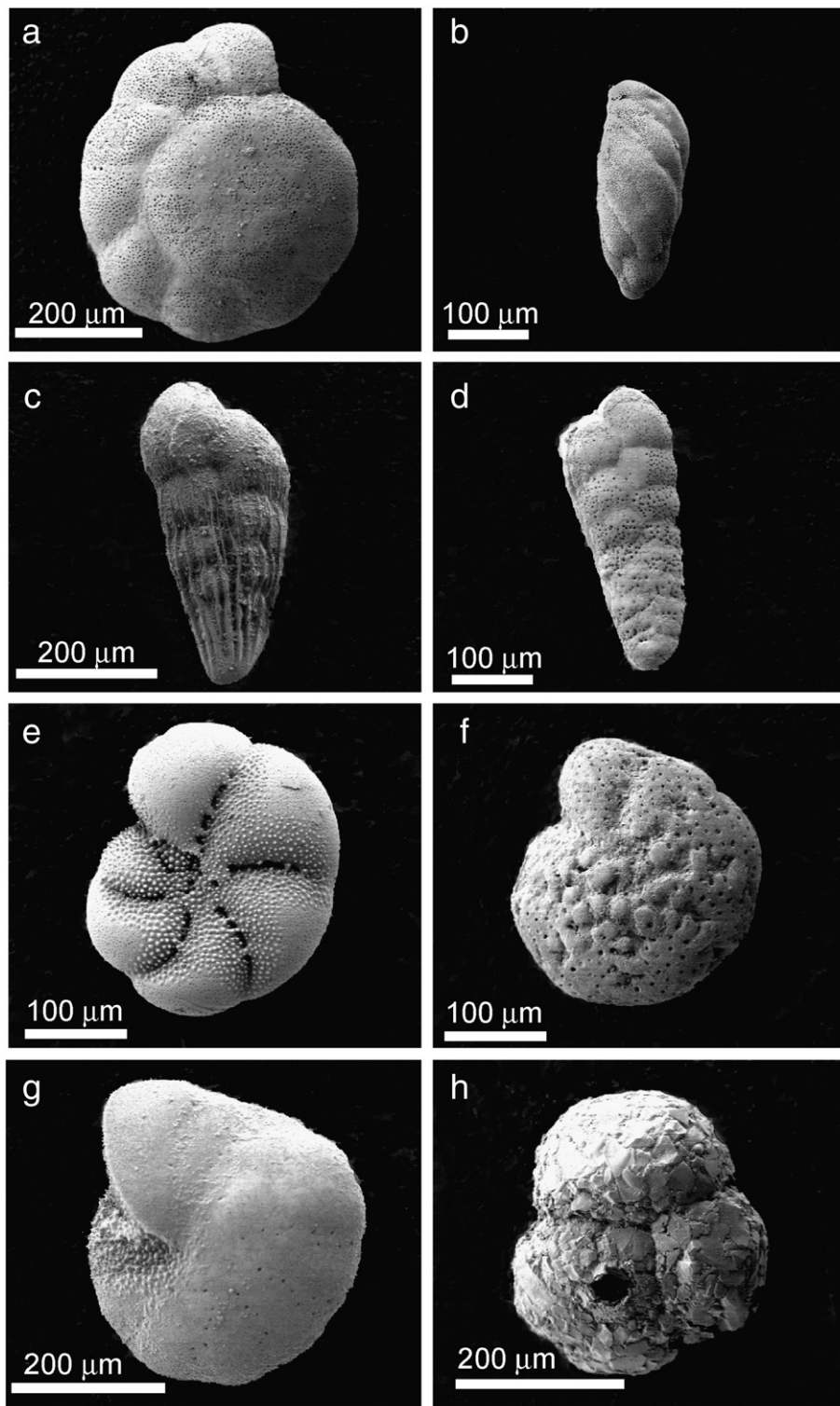
Figure 3. Fig. 3a: SEM images of recent foraminifera found in this study, a) *Ammonia beccarii*, b) *Buliminella elegantissima*, c) *Bolivina striatula*, d) *Bolivina vaughani*, e) *Elphidium excavatum*, f) *Elphidium gunteri*. Fig. 3b: SEM images of recent foraminifera found in this study, g) *Elphidiella hannai*, h) *Trochammina hadai*. Not pictured: *Trochammina inflata*. SEM micrographs of fossil foraminifera are included in Sloan (1980).

The second association is dominated by *E. hannai* along with less abundant *B. frigida* and *E. excavatum* and is found in the upper part of the Yerba Buena unit (samples 52–14, 52–15, 58–19, and 78–21; Fig. 4) (Sloan, 1992). In the early 1960s, tests of *E. hannai* constituted as much as 30% of all individuals in the deep channel zones (>12 m) in South San Francisco Bay (Quinterno, 1968; Arnal et al., 1980), yet constituted only 7% of the recent assemblage from USGS Station 25.

However, few of these tests stained with Rose Bengal. Neither were any living specimens found in a vertical distribution study of foraminifera at two other sites in South San Francisco Bay (McGann, 1999). This indicates that *E. hannai* is not actually living today in this region, but rather the tests are transported there by currents (Quinterno, 1968; McGann, 1999). Indeed, other workers have found living or Rose Bengal-stained specimens of *E. hannai* only in

Table 3
Relative abundances of species in recent foraminiferal samples taken in South San Francisco Bay. Numbers reported are percentages of the total number of individuals in each sample. Samples taken in Nov-99 through Mar-00 were single samples; all other data are averages of two replicate samples. Foraminifera counted were from the >120 μm fraction.

	A. beccarii	B. elegantissima	B. striatula	B. vaughani	E. excavatum	E. gunteri	E. hannai	T. hadai	T. inflata	Sample size
Nov 1999	19.3	8.2	10.5	12.3	15.8	4.1	6.4	19.9	3.5	214
Dec 1999	17.7	7.9	15.6	11.9	13.5	5.2	7.3	12.5	8.3	120
Jan 2000	16.3	5.3	20.0	7.9	15.0	5.6	5.6	18.1	6.3	200
Feb 2000	14.0	10.7	15.4	12.5	11.4	1.3	9.2	16.2	9.2	285
Mar 2000	12.9	6.3	18.9	9.4	15.7	4.5	5.9	21.7	4.5	358
Apr 2000	17.9	4.8	17.7	7.2	18.4	3.8	5.7	18.1	6.3	237
May 2000	10.1	4.4	15.3	6.6	24.2	5.8	5.8	23.0	4.6	163
Jun 2000	12.1	2.6	12.9	3.9	23.4	3.2	7.3	31.5	3.2	62
Jul 2000	18.3	5.0	15.0	7.5	20.7	4.2	10.5	15.0	3.9	167
Aug 2000	15.9	7.3	17.9	11.0	17.6	5.2	11.7	10.3	3.1	145
Sep 2000	10.8	6.8	13.7	10.2	21.6	4.6	7.5	19.0	5.9	153
Oct 2000	15.6	4.2	17.7	6.3	17.2	7.7	6.6	18.7	6.1	190
Nov 2000	10.7	6.6	21.4	9.9	15.5	7.2	6.9	15.9	5.9	145
Dec 2000	10.3	7.9	19.8	11.9	17.4	9.0	5.4	13.0	5.2	184
Jan 2001	10.0	15.3	10.3	9.8	12.1	2.7	6.8	24.4	8.4	219
Feb 2001	17.1	2.7	3.4	4.1	14.9	4.6	6.3	37.1	9.7	175
Mar 2001	9.9	6.1	11.2	9.1	21.7	8.6	8.6	19.7	5.3	152
Apr 2001	12.5	12.1	8.9	3.9	16.7	6.4	8.9	27.0	3.6	281
May 2001	19.5	4.1	3.9	13.6	21.5	2.0	9.1	24.4	1.8	492
Jun 2001	12.1	13.6	7.6	6.7	18.8	9.4	7.0	17.9	7.0	330
Jul 2001	11.2	17.5	4.0	11.7	11.7	1.3	9.4	22.9	10.3	223
Sep 2001	15.0	7.9	20.9	17.7	11.0	2.0	5.9	19.7	0.0	254
Oct 2001	17.3	2.0	16.2	10.2	29.4	0.5	6.1	16.2	2.0	197
Nov 2001	16.9	0.0	16.1	26.3	19.5	0.8	8.5	11.9	0.0	118

colder, deeper parts of North and Central San Francisco Bay, or along the outer California coast (Bandy, 1953; Locke, 1971; Lankford and Phleger, 1973; Sloan, 1992). This "E. hannai paradox" in South Bay suggests two possible explanations for the paleoenvironment of the upper part of the Yerba Buena unit: 1) the upper part of the Yerba Buena unit indicates a different environment than that found in South Bay today, with greater depths, higher salinities, or lower temperatures (Sloan, 1992); or 2) the upper Yerba Buena mud was a similar environment to that found today, and E. hannai tests were also somehow transported in great abundances to the South Bay during the Pleistocene.

Comparing the fossil and recent assemblages

The greater species richness in the Pleistocene Yerba Buena mud samples compared to the recent samples is probably reflective of sample size, since all but seven species were rare, and since rarefaction analysis found that only nine species would be present at sample sizes of 200 individuals. Studies of fossil foraminifera indicate that, over time, the fossil record of abundant species may remain relatively static until there is a large-scale disturbance (McKinney et al., 1996). Fossil samples are time averaged, so the difference in species diversity could also be due to the fact that a greater period of time is represented by the fossil samples during which conditions favored larger populations of a few species.

Species diversity shows no difference between fossil and recent assemblages in this study, as is consistent with other studies which have found similar species diversity patterns in Plio-Pleistocene and recent foraminiferal assemblages (Aoshima, 1979). These findings indicate that the environments in the 125 ka and modern estuaries were similar and that human activities have not resulted in an increase or decrease in species diversity in San Francisco Bay. The dynamic nature of estuaries on a spatial and temporal scale may not be conducive to increases in species diversity over both geologic and shorter time scales (Whitfield, 1994).

The relative abundances of taxa in the fossil versus recent assemblages, in contrast, were significantly different for three out of five dominant taxa. The foraminiferal assemblage shifted from dominance by E. excavatum in the Pleistocene to greater dominance

by A. beccarii and B. elegantissima today. Buliminella elegantissima is found in lagoons where near-marine conditions prevail (Phleger and Ewing, 1962). Ammonia beccarii is a common estuarine and shallow-water marine species with a cosmopolitan distribution and a tolerance for a range of marine conditions (Phleger, 1960; Lankford and Phleger, 1973). Bolivina striatula and B. vaughani, possible morphological environmental variants of the same species (Quinterno, 1968), were also abundant in recent samples; B. striatula is very rare in the fossil samples used in this study, and B. vaughani is completely absent. Both taxa are restricted to depths of less than 100 m, and to areas with little freshwater influence (Natland, 1957; Uchio, 1960; Means, 1965). The greater abundances of these taxa in the recent assemblages may reflect environmental shifts in depth, salinity, or temperature between the recent and the Pleistocene.

Elphidium excavatum was the most abundant species in the fossil samples, making up 63% of all individuals. Today it still reaches its greatest abundances in South San Francisco Bay, as opposed to North or Central Bay (Arnal et al., 1980), but it only accounts for 17% of the assemblage at USGS Station 25. Similarly, E. excavatum makes up 19% of the assemblage at the top of a core (DJ6-93SF-6) with a 3900-year record obtained in South San Francisco Bay near San Francisco International Airport (McGann, 2008).

E. excavatum no longer dominates the assemblage as it did in the Pleistocene. One possible explanation for this is the increase in abundance of T. hadai. This native of Japan is the most abundant species in the recent assemblage, in agreement with other studies that found a significant shift in the San Francisco Bay assemblage since its anthropogenic introduction in the early 1980s (McGann and Sloan, 1996; McGann et al., 2000). In fact, the microfaunal record for the last ca. 200 yr in core DJ6-93SF-6 demonstrates that this introduction is the single most important factor contributing to the loss in dominance by E. excavatum (McGann, 2008). Just prior to the introduction of T. hadai, E. excavatum accounted for more than 75% of the assemblage. The species' abundance dropped 56% between 18 and 20 cm downcore and the core-top sediments, whereas T. hadai increased by 52%. No other species recovered in this South San Francisco Bay core recorded such a dramatic shift in abundance over the entire 3900-year record. Trochammina hadai commonly lives in highly polluted areas and is an indicator of eutrophication in its native estuaries (Tsujimoto

Table 4
Relative abundances of species in fossil foraminiferal samples taken in South San Francisco Bay. All relative abundances are percentages of total individuals in each sample. Foraminifera counted were from the >120 μm fraction.

CORE	A. beccarii	A. planissimum	B. striatula	B. frigida	B. tenerrima	B. elegantissima	C. fletcheri	C. lobatulus	E. excavatum	E. hannai	E. gunteri	E. magellanicum	E. microgranulosum	L. amphora	Lagena sp.	N. pachyderma	N. stella	Textularia sp.	Sample size
52–11	1.9	–	–	1.9	–	0.9	0.5	–	52.6	12.3	23.7	5.2	0.9	–	–	–	–	–	211
52–14	0.4	0.2	–	4.8	–	0.1	–	–	31.5	62.4	0.2	0.3	0.1	–	–	–	0.1	–	902
52–15	0.4	0.1	0.2	13.9	0.5	11.1	–	0.4	47.3	21.6	0.2	2.6	0.1	–	–	–	–	–	1623
52–17	3.1	–	0.03	0.06	–	0.2	–	0.06	84.2	3.3	9.8	0.2	–	–	–	0.03	–	–	3211
52–18	29.5	–	0.5	1.9	1	1.4	–	0.3	31	2.3	34	2.8	0.5	0.5	–	0.9	–	–	213
58–18	–	0.8	–	8.8	–	1.3	0.3	–	53	33.6	0.3	2.8	0.3	–	0.3	–	–	–	384
58–19	0.7	0.7	–	–	–	–	–	–	30.1	68.5	–	–	–	–	–	–	–	–	146
58–20	1.8	0.6	–	–	0.2	–	–	–	59.3	37.3	1	–	–	–	–	–	–	–	614
58–21	3	–	0.1	0.6	–	–	–	–	57.9	36.1	2.9	0.1	–	–	–	–	–	0.1	854
58–22	4.5	–	–	0.8	–	–	–	–	69.8	–	24.8	–	–	–	–	–	–	–	467
58–23	16.8	–	–	–	–	–	–	–	68	0.8	13.6	–	–	–	–	–	–	–	125
78–21	0.2	–	–	0.2	0.3	0.1	0.3	0.2	75.2	14.4	8.2	0.5	–	–	–	–	0.1	–	942

Table 5
Fisher's alpha diversity index and means for the recent and fossil sample with a sample size of at least 200 individuals. The means of recent and fossil diversity indices were not significantly different from one another (SYSTAT v.10.2.01, ANOVA, $\alpha = 0.05$, $p = 0.144$).

Sampling date	Fisher's α	CORE	Fisher's α
Nov 1999	1.912	52–11	2.469
Jan 2000	1.937	52–14	1.956
Feb 2000	1.761	52–15	3.655
Mar 2000	1.674	52–17	1.901
Apr 2000	1.846	52–18	3.377
Jan 2001	1.888	58–18	2.859
Apr 2001	1.777	58–20	0.927
May 2001	1.565	58–21	1.592
Jun 2001	1.708	58–22	0.97
Jul 2001	1.888	78–21	2.328
Sep 2001	1.577		
Mean recent	1.776	Mean fossil	2.203

et al., 2006). Its dominance at Station 25 and throughout San Francisco Bay may reflect changes in the environmental quality of the region in recent years.

The mean relative abundances of *E. gunteri* and *E. hannai* were not significantly different between fossil and recent assemblages. *Elphidium gunteri* had a total abundance of approximately 7% in both the fossil and recent assemblages; however, the fossil samples used in this study were not from the deepest layers of the Yerba Buena mud where Sloan (1992) found an *E. gunteri* association (Figs. 3a, b and 4). Stained specimens of *E. gunteri* were completely absent or extremely rare in the recent samples and in the vertical distribution study of McGann (1999), suggesting that, similar to *E. hannai*, *E. gunteri* may not be living in South San Francisco Bay, but rather tests are transported there by currents. *Elphidium gunteri* is found alive today in North San Francisco Bay, marshy habitats, and shallow areas with salinities below 10 psu (Slater, 1965; Locke, 1971). As discussed earlier, *E. hannai* and *E. gunteri* are not present in living populations in South Bay today, whereas dead tests are still found in appreciable numbers in recent samples. Therefore, whether or not the statistical similarity between the fossil and recent abundances of these two taxa indicates that populations lived in the Pleistocene South Bay or that a similar current regime, which, like today, may have transported dead tests to South Bay is unclear.

For overall similarity, four out of the five fossil samples that clustered with the recent samples came from the *E. excavatum* association layer of the Yerba Buena mud. Only one sample (52–15) that clustered with the recent samples was from the *E. hannai* association layer. Sloan (1992) suggested that the *E. hannai* middle layer of the Yerba Buena mud indicates colder, possibly deeper and more saline conditions during this phase of the Pleistocene bay, since this is the environment favored by *E. hannai* today. She also suggested that the *E. excavatum* upper layer of the Yerba Buena mud may indicate a shift back to more estuarine environments, since that is the present preference of living *E. excavatum* populations. The cluster

Table 6
Mean relative abundances of the dominant taxa common to both the recent and fossil assemblages. The mean relative abundance was calculated by taking an average of the relative abundance of each dominant taxon from all samples with at least 200 individuals.

Species name	Mean% recent	Mean% fossil	P value
A. beccarii	0.390	0.174	≤0.001[*]
B. elegantissima	0.308	0.065	≤0.001[*]
E. excavatum	0.400	0.839	≤0.001[*]
E. gunteri	0.191	0.255	0.361
E. hannai	0.272	0.455	0.070

[*] Taxa with significant difference in relative abundance between recent and fossil assemblages (SYSTAT v.10.2.01, ANOVA, $\alpha = 0.05$).

Boreholes used in this study
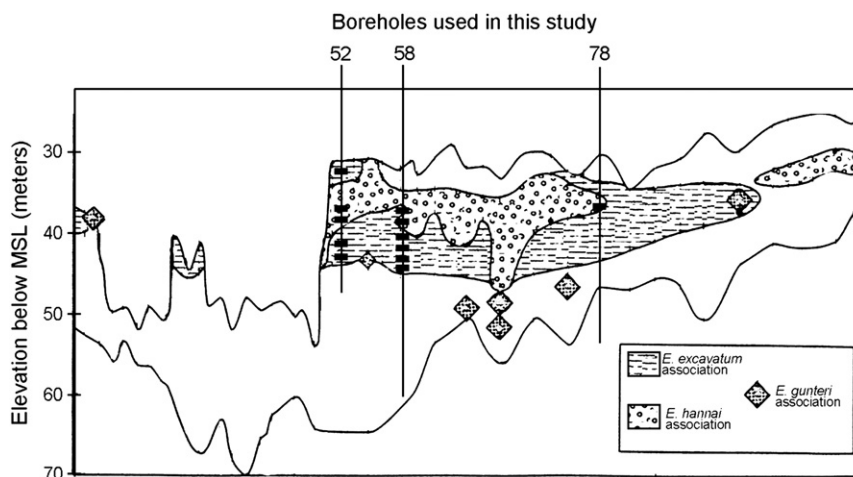
Figure 4. Cross section of the sediment beneath San Francisco Bay showing the Yerba Buena mud foraminiferal associations (see box), and location of borehole samples used in this study: Borehole 52 (sample locations, top to bottom: 52–11, 52–14, 52–15, 52–17, 52–18); Borehole 58 (sample locations, top to bottom: 58–18, 58–19, 58–20, 58–21, 58–22, 58–23); Borehole 78 (sample 78–21). Figure modified from Sloan (1992).

analysis supports her hypothesis, since the recent samples clustered primarily with the samples from the *E. excavatum* layer.

Conclusion

Although San Francisco Bay has been subjected to significant natural and human impacts, a comparison of meiofaunal diversity and species abundances indicates that the modern benthic foraminiferal biota was similar to that of the late Pleistocene until the early 1980s introduction and subsequent domination by the anthropogenically introduced species *T. hadai*. The overall similarity between the modern assemblage and the Yerba Buena assemblage, in terms of foraminiferal species composition, indicates that the benthic environmental conditions 125 ka were similar to those in today's South San Francisco Bay. Further, species diversity has neither decreased nor increased between the Pleistocene and the present day in South San Francisco Bay, suggesting that environmental change has not affected species diversity of the benthic foraminiferal fauna. In terms of anthropogenic effects on the assemblage, the introduction of the Japanese foraminifer *T. hadai* has shifted the modern assemblage away from the dominance of *E. excavatum* found in the Pleistocene and the latest Holocene, although overall species richness has not changed significantly. These data show that comparisons between fossil and recent assemblages are powerful tools in interpreting paleoenvironments, and they may help us to understand the impact of human activity on estuarine and other marine systems.

Acknowledgments

Appendix A

Alphabetic list of recent genera and species found in this study. Generic assignments follow Loeblich and Tappan (1988).

Ammonia beccarii (Linné) = *Nautilus beccarii* Linné, 1758, p. 710.

Ammotium planissimum (Cushman) = *Haplophragmoides planissima* Cushman, 1927, p. 135, Pl. 1, Fig. 6.

Bolivina striatula Cushman, 1922, p. 27, Pl. 3, Fig. 10.

Bolivina vaughani Natland, 1938, p. 146, Pl. 5, Fig. 11.

Buliminella elegantissima (d'Orbigny) = *Bulimina elegantissima* d'Orbigny, 1839, p. 51, Pl. 7, Figs. 13 and 14.

Cibicides fletcheri Galloway and Wissler, 1927, p. 64, Pl. 10, Figs. 8 and 9.

Cibicides lobatulus (Walker and Jacob) = *Nautilus lobatulus* Walker and Jacob, 1798, p. 642, Pl. 14, Fig. 36.

Elphidiella hannai (Cushman and Grant) = *Elphidium hannai* Cushman and Grant, 1927, p. 78, Pl. 8, Fig. 1.

Elphidium excavatum (Terquem) = *Polystomella excavata* Terquem, 1876, p. 429, Pl. 2, Figs. 2a–d.

Elphidium gunteri Cole, 1931, p. 34, Pl. 4, Figs. 9 and 10.

Elphidium incertum (Williamson) = *Polystomella umbiculata* var. *incerta* Williamson, 1858, p. 44, Pl. 3, Figs. 82 and 82a.

Elphidium magellanicum Heron-Allen and Earland, 1932, p. 440, Pl. 16, Figs. 26–28.

Fissurina cucurbitasema Loeblich and Tappan, 1953, p. 76, Pl. 14, Figs. 10 and 11.

Fissurina lucida (Williamson) = *Entosolenia lucida* Williamson, 1848, p. 30, Pl. 5, Figs. 16–18.

Fursenkoina fusiformis (Williamson) = *Bulimina pupoides* var. *fusiformis* Williamson, 1858, p. 63, Pl. 5, Figs. 129, 130.

Fursenkoina loeblichi (Feyling-Hansen) = *Virgulina loeblichi* Feyling-Hansen, 1954, p. 191, Pl. 1, Figs. 14–18.

Fursenkoina pontoni (Cushman) = *Virgulina pontoni* Cushman, 1932, p. 17, Pl. 3, Fig. 7.

Globigerina bulloides d'Orbigny, 1826, p. 3, Pl. 1, Figs. 1–4.

Globigerina quinqueloba Natland, 1938, p. 149, Pl. 6, Fig. 7.

Lagena amphora Reuss, 1850.

Neogloboquadrina pachyderma (Ehrenberg) = *Aristerospira pachyderma* Ehrenberg, 1861, pp. 276, 277, and 303.

Nonionella stella Cushman and Moyer = *Nonionella miocenica* Cushman, var. *stella* Cushmans and Moyer, 1930, p. 56, Pl. 7, Figs. 17a–c.

Trochammina hadai Uchio, 1962, pp. 387–388, Pl. 18, Figs. 9a–c.

Trochammina inflata (Montagu) = *Nautilus inflatus* Montagu, 1808, p. 81, Pl. 18, Fig. 3.

References

Alve, E., 1991. Benthic foraminifera in sediment cores reflecting heavy metal pollution of Sorfjord, western Norway. Journal of Foraminiferal Research 21 (1), 1–19.

Alve, E., 1995. Benthic foraminiferal responses to estuarine pollution: a review. Journal of Foraminiferal Research 25 (3), 190–203.

Aoshima, M., 1979. Depositional environment of the Plio-Pleistocene Kakegawa Group Japan a comparative study of the fossil and the recent foraminifera. Journal of the Faculty of Science University of Tokyo Section II Geology Mineralogy Geography Geophysics 19 (5), 401–441.

Arnal, R.E., Conomos, T.J., 1962. Sedimentary and foraminiferal aspects of southern San Francisco Bay. Geological Society of America Special Paper 73, 21–22.

Arnal, R.E., Quinterno, P.J., Conomos, T.J., Gram, R., 1980. Trends in the distribution of recent foraminifera in San Francisco Bay. Cushman Foundation for Foraminiferal Research Special Publication 19, 17–39.

Atwater, B.F., 1979. Ancient processes at the site of southern San Francisco Bay: movement of the crust and changes in sea level. San Francisco Bay: The Urbanized Estuary. AAAS, San Francisco.

Bandy, O.L., 1953. Ecology and paleoecology of some California foraminifera, Part I. Journal of Paleontology. 27, 161–182.

Bernhard, J.M., 2000. Distinguishing live from dead foraminifera: methods review and proper applications. Micropaleontology 46 (Supplement 1), 38–46.

Byrne, R., Ingram, B.L., Starratt, S., Malamud-Roam, F., Collins Joshua, J., Conrad, M., 2001. Carbon-isotope, diatom, and pollen evidence for late Holocene salinity change in a brackish marsh in the San Francisco Estuary. Quaternary Research 55 (1), 66–76.

Collins, E.S., Scott, D.B., Gayes, P.T., Medioli, F.S., 1995. Foraminifera in Winyah Bay and North Inlet marshes, South Carolina: relationship to local pollution sources. Journal of Foraminiferal Research 25 (3), 212–223.

Conomos, T.J. (Ed.), 1979. San Francisco Bay: The Urbanized Estuary. : Investigations into the Natural History of San Francisco Bay and Delta With Reference to the Influence of Man. Pacific Division of the American Association for the Advancement of Science, San Francisco.

Conomos, T.J., Smith, R.E., Gartner, J.W., 1985. Environmental setting of San Francisco Bay California, USA. Hydrobiologia 129 (1), 1–12.

Danovaro, R., Fabiano, M., Vincx, M., 1995. Meiofauna response to the Agip Abruzzo Oil Spill in subtidal sediments of the Ligurian Sea. Marine Pollution Bulletin 30 (2), 133–145.

Erskian, M.G., Lipps, J.H., 1987. Population dynamics of the foraminiferan Glabratella ornatissima (Cushman) in northern California [USA]. Journal of Foraminiferal Research 17 (3), 240–256.

Fagan, B.M., 2004. Before California: an archaeologist looks at our earliest inhabitants. Alta Mira Press, Walnut Creek, California. Revised edition, 399 pp.

Finger, K.L., Lipps, J.H., Weaver, J.C.B., Miller, P.L., 1990. Biostratigraphy and depositional environments of calcareous microfossils in the lower Monterey Formation (Lower to Middle Miocene), Graves Creek area, central California [USA]. Micropaleontology 36 (1), 1–55.

Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B., Page, G., 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. Waterbirds 25 (2), 173–183.

Hallock, P., 2000. Symbiont-bearing foraminifera: harbingers of global change? Micropaleontology (New York) 46 (Supplement 1), 95–104.

Hayek, L.A.C., Buzas, M.A., 1997. Survyeing Natural Populations. Columbia University Press, New York.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52 (4), 577–586.

Ingle Jr., J.C., 1976. Late Neogene paleobathymetry and paleoenvironments of Humboldt Basin, northern California. The Neogene symposium: In: Ter Best, H., Wornardt, W.W. (Eds.), Pacific Section, Soc. Econ. Paleont. Mineral. San Francisco, California, pp. 53–81.

Ingram, B.L., 1998. Differences in radiocarbon age between shell and charcoal from a Holocene shellmound in northern California. Quaternary Research (Orlando) 49 (1), 102–110.

Ingram, B.L., Ingle, J.C., 1998. Strontium isotope ages of the Marine Merced Formation, near San Francisco, California. Quaternary Research (Orlando) 50 (2), 194–199.

Ingram, B.L., Sloan, D., 1992. Strontium isotopic composition of estuarine sediments as paleosalinity–paleoclimate indicator. Science 255, 68–72.

Keldsen, T.J., Wilson, K.R., 1997. The potential impacts of climate change on California clapper rail habitat. Bulletin of the Ecological Society of America 78 (4 SUPPL.), 122.

Kennish, M.J., 2001. Coastal salt marsh systems in the U.S.: a review of anthropogenic impacts. Journal of Coastal Research 17 (3), 731–748.

Langer, M., Long, D.J., 1994. Association of benthic foraminifera with a gammarid amphipod on tidal flats of San Francisco Bay, California. Journal of Coastal Research 10 (4), 877–883.

Lankford, R.R., Phleger, F.B., 1973. Foraminifera from the nearshore turbulent zone, western North America. Journal of Foraminiferal Research 3 (3), 101–132.

Lesen, A.E., 2005. Relationship between benthic foraminifera and food resources in South San Francisco Bay, USA. Marine Ecology Progress Series 297, 131–145.

Lieberman, B.S., 2000. Topics in Geobiology. Paleobiogeography: Using Fossils to Study Global Change, Plate Tectonics, and Evolution. Plenum Publishing Corporation, New York.

Lindberg, D.R., Lipps, J.H., 1996. Reading the Chronicle of Quaternary Temperate Rocky-Shore Faunas, pp. 161–182. In: Jablonski, D., Erwin, D., Lipps, J.H. (Eds.), Evolutionary Paleobiology. Univ. Chicago Press.

Locke, J.L., 1971. Sedimentation and foraminiferal aspects on the recent sediments of San Pablo Bay. San Jose State University, San Jose, California, p. 100.

Malamud-Roam, F., Ingram, B.L., 2001. Carbon isotopic compositions of plants and sediments of tide marshes in the San Francisco Estuary. Journal of Coastal Research 17 (1), 17–29.

Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore, T.C.J., Shackleton, N.J., 1987. Age dating and the orbital theory of the Ice Ages: development of a high resolution 0 to 300,000-year chronostratigraphy. Quaternary Research 27, 1–29.

McCormick, J.M., Severin, K.P., Lipps, J.H., 1994. Summer and winter distribution of foraminifera in Tomales Bay, northern California. Cushman Foundation for Foraminiferal Research Special Publication 32, 69–101.

McDonald, J.A., Diediker, P.L., 1930. A preliminary report on the foraminifera of San Francisco Bay, California. Micropaleontology Bulletin 2, 33–37.

McGann, M., 1999. Vertical distribution of foraminifers, including the non-indigenous species Trochammina hadai, in south San Francisco Bay. Fourth Biennial State of the Estuary Conference, p. 77.

McGann, M., 2008. High-resolution faunal, isotopic, and trace metal records from Holocene estuarine deposits of San Francisco Bay, California. Journal of Coastal Research 24 (5), 1092–1109.

McGann, M., Sloan, D., 1996. Recent introduction of the foraminifer Trochammina hadai Uchio into San Francisco Bay, California, USA. Marine Micropaleontology 28 (1), 1–3.

McGann, M., Sloan, D., Cohen, A.N., 2000. Invasion by a Japanese marine microorganism in western North America. Hydrobiologia 421 (1–3), 25–30 (Type D 1 AB to see abstract).

McKinney, M.L., Lockwood, J.L., Frederick, D.R., 1996. Does ecosystem and evolutionary stability include rare species? Palaeogeography, Palaeoclimatology, Palaeoecology 127 (1–4), 191–207.

Means, K.D., 1965. Sediments and Foraminifera of Richardson Bay, California. University of Southern California, Los Angeles, California, p. 83.

Nagy, J., Alve, E., 1987. Temporal changes in foraminiferal faunas and impact of pollution in Sandebukta, Oslo Fjord [Norway]. Marine Micropaleontology 12 (2), 109–128.

Natland, M.L., 1957. Paleoecology of West Coast Tertiary sediments. Geological Society of America Memoir 67, 543–572.

Pataki, D.E., 2002. Atmospheric CO2, climate and evolution: lessons from the past. The New Phytologist 154 (1), 10–12.

Patrick, W.H.J., Delaune, R.D., 1990. Subsidence accretion and sea level rise in South San Francisco Bay California USA Marshes. Limnology and Oceanography 35 (6), 1389–1395.

Phleger, F.B., 1960. Ecology and Distribution of Recent Foraminifera. The Johns Hopkins Press, Baltimore.

Phleger, F.B., Ewing, G.C., 1962. Sedimentology and oceanography of coastal lagoons in Baja California. Mexico. Geological Society of America Bulletin 73, 145–182.

Quinterno, P.J., 1968. Distribution of recent foraminifera in Central and South San Francisco Bay. Department of Geology. San Jose State College, San Jose, p. 83.

Resig, J.M., Ming, K., Miyake, S., 1995. Foraminiferal ecology, Ala Wai Canal, Hawai'i. Pacific Science 49 (4), 341–366.

Setty, M.G.A.P., Nigam, R., 1984. Benthic foraminifera as pollution indices in the marine environment of west coast of India. Rivista Italiana di Paleontologia e Stratigrafia 89 (3), 421–436.

Slater, R.A., 1965. Sedimentary environments in Suisun Bay, California. University of Southern California, Los Angeles, California, p. 101.

Sliter, W.V., 1999. Cretaceous planktic foraminiferal biostratigraphy of the Calera Limestone, northern California, USA. Journal of Foraminiferal Research 29 (4), 318–339.

Sloan, D., 1980. Foraminifera of Sangamon(?) estuarine deposits beneath Central San Francisco Bay, California. Quaternary Depositional Environments of the Pacific Coast, Pacific Coast Paleogeography Symposium, 4, pp. 1–12.

Sloan, D., 1981. Ecostratigraphic Study of Sangamon Sediments beneath Central San Francisco Bay. Department of Paleontology. University of California, Berkeley, California, p. 338.

Sloan, D., 1992. The Yerba Buena mud; record of the last-interglacial predecessor of San Francisco Bay, California. Geological Society of America Bulletin 104 (6), 716–727.

Sloan, D., 1995. Use of foraminiferal biostratigraphy in mitigating pollution and seismic problems, San Francisco, California. Journal of Foraminiferal Research 25 (3), 260–266.

Stewart, R.E., Stewart, K.C., 1933. Notes on the foraminifera of the type Merced at Seven Mile Beach, San Mateo County, California. San Diego Natural History Transactions 7 (21), 259–272.

Thierstein, H.R., 1987. Paleooceanography global change in the history of the Earth. Vierteljahrsschrift der Naturforschenden Gesellschaft in Zuerich 132 (2), 88–103.

Travis, J., Futuyma, D.J., 1993. Global Change: Lessons from and for Evolutionary Biology. In: Kareiva, P.M., Kingsolver, J.G., Huey, R.B. (Eds.), Biotic interactions and global change. Sinauer Associates, Inc., Sunderland, MA, pp. 251–261.

Tsujimoto, A., Nomura, R., Yasuhara, M., Yamazaki, H., Yoshikawa, S., 2006. Impact of eutrophication on shallow marine benthic foraminifers over the last 150 years in Osaka Bay, Japan. Marine Micropaleontology 60 (4), 258–268.

Uchio, T., 1960. Ecology of living benthic foraminifera from the San Diego, California area. Cushman Foundation for Foraminiferal Research Special Publication 5, 1–72.

USGS, 2003. San Francisco Bay Water Quality data. USGS, Menlo Park, CA http://sfbay.wr.usgs.gov/access/wqdata/index.html.

van Geen, A., Luoma, S.N., 1999a. The impact of human activities on sediments of San Francisco Bay, California: an overview. Marine Chemistry 64 (1–2), 1–6.

van Geen, A., Luoma, S.N., 1999b. A record of estuarine water contamination from the Cd content of foraminiferal tests in San Francisco Bay, California. Marine Chemistry 64 (1–2), 57–69.

van Geen, A., Luoma, S.N., Fuller, C.C., Anima, R., Clifton, H.E., Trumbore, S., 1992. Evidence from cadmium calcium ratios in foraminifera for greater upwelling off California 4000 years ago. Nature (London) 358 (6381), 54–56.

Wagner, D.B., 1978. Environmental history of San Francisco Bay with emphasis on foraminifera paleontology and clay minerology. Department of Paleontology. University of California, Berkeley, p. 274.

Whitfield, A.K., 1994. Fish species diversity in Southern African estuarine systems: an evolutionary perspective. Environmental Biology of Fishes 40 (1), 37–48.

Yanko, V., Ahmad, M., Kaminski, M., 1998. Morphological deformities of benthic foraminiferal tests in response to pollution by heavy metals: implications for pollution monitoring. Journal of Foraminiferal Research 28 (3), 177–200.

Yanko, V., Kronfeld, J., Flexer, A., 1994. Response of benthic foraminifera to various pollution sources: implications for pollution monitoring. Journal of Foraminiferal Research 24 (1), 1–17.