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Invasion by a Japanese marine microorganism in western North America

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Abstract

The earliest record in western North America of *Trochammina hadai* Uchio, a benthic foraminifer common in Japanese estuaries, is from sediment collected in Puget Sound in 1971. It was first found in San Francisco Bay in sediment samples taken in 1983, and since 1986 has been collected at 91% of the sampled sites in the Bay, constituting up to 93% of the foraminiferal assemblage at individual sites. The species is also present in recent sediment samples from 12 other sites along the west coast of North America. The evidence indicates that *T. hadai* is a recent introduction to San Francisco Bay, and is probably also not native to the other North American sites. *Trochammina hadai* was probably transported from Japan in ships' ballast tanks, in mud associated with anchors, or in sediments associated with oysters imported for mariculture. Its remarkable invasion of San Francisco Bay suggests the potential for massive, rapid invasions by other marine microorganisms.

Introduction

Numerous recent reports have documented sudden outbreaks of harmful marine microorganisms, including toxic dinoflagellates, primnesiophyceans and diatoms, oftentimes in regions where the species was previously unknown (Anderson, 1989; Smayda, 1990; Hallegraeff, 1993). Two explanations have been offered for these events: (1) that the organism had always been present at low and undetected densities but multiplied dramatically in response to some environmental change, with nutrient enrichment from human activities such as the discharge of sewage effluent or the deforestation and erosion of coastal watersheds often cited as the cause; or (2) that the organism was introduced from some other region of the world. Often, little evidence exists on which to choose between these two scenarios.

We here report clear evidence of the introduction and rapid proliferation of an exotic marine microorganism in western North America. This invasion event is reminiscent of the explosive growth of some recent macrofaunal introductions, such as the European zebra mussel *Dreissena polymorpha* in the Great Lakes (Nalepa & Schloesser, 1993), the Asian clam *Potamocorbula amurensis* in San Francisco Bay (Carlton et al., 1990; Nichols et al., 1990), the Atlantic comb jelly *Mnemiopsis leidyi* in the Black Sea (Vinogradov et al., 1989), and the Japanese sea star *Asterias amurensis* in the Derwent Estuary, Tasmania (Buttermore et al., 1994).

Materials and methods

In 1995 we identified the foraminifer *Trochammina hadai* Uchio, a common protozoan species in Japanese estuaries, in core-top sediments that were collected in 1993 from south and north San Francisco Bay (McGann, 1995; Sloan, unpubl. data). Following this discovery, we undertook a systematic re-examination of foraminiferal studies, cores, and recent sediment samples from the bay to determine the date of this foraminifer's first appearance in the bay; a bay-wide

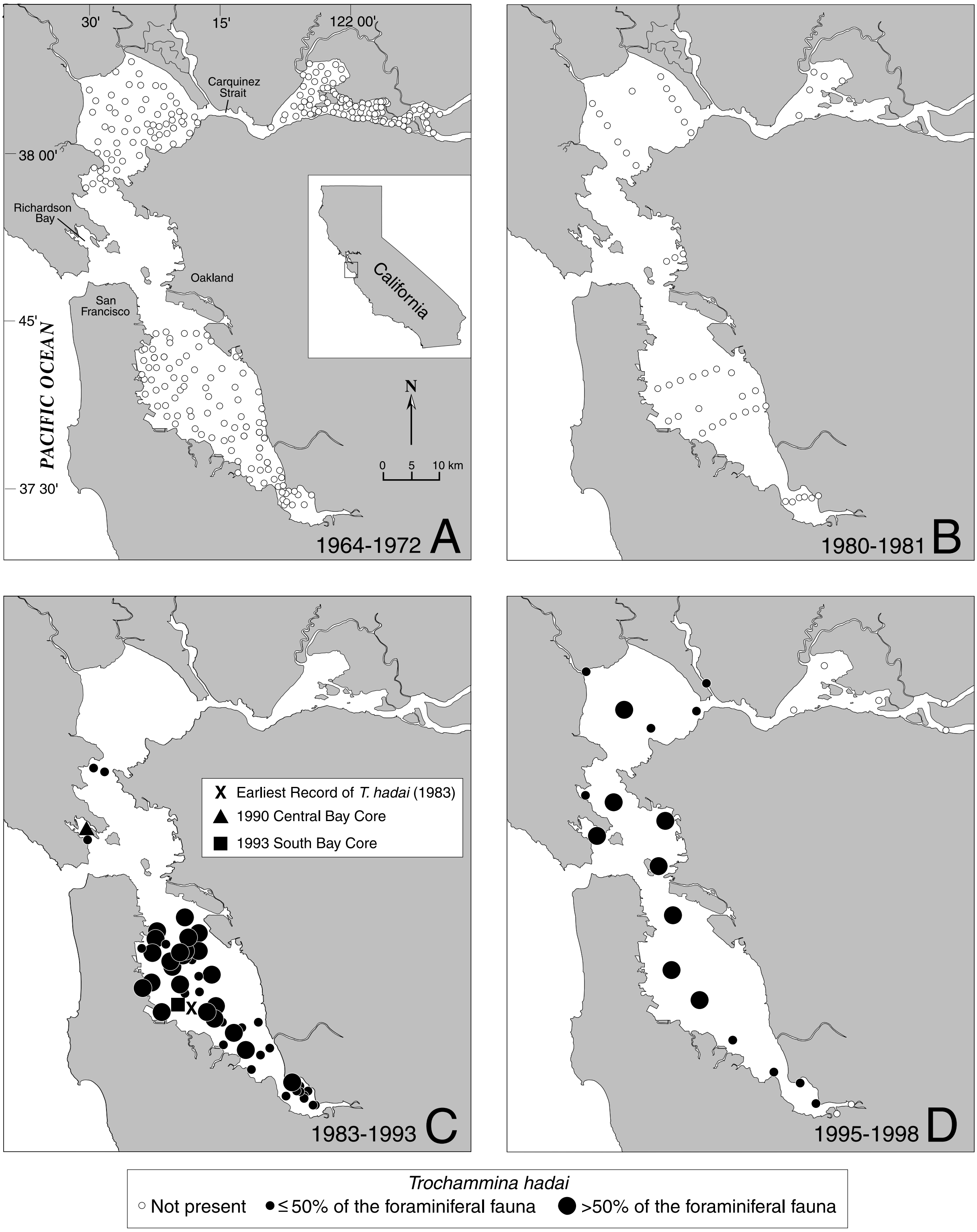

Figure 1. Trochammina hadai in sediment samples from San Francisco Bay. Where a station was sampled more than once during a period, the highest recorded abundance is mapped. (**A**) Stations sampled between 1964 and 1972 for foraminiferal studies in San Francisco Bay (Means, 1965; Slater, 1965; Locke, 1971; Quinterno, 1968; Arnal et al., 1980; Ingle, unpubl. data); 75 stations from Richardson Bay in which no *T. hadai* were reported, are too closely spaced to be shown here. (**B**) Stations sampled in 1980–81, examined by Sloan. (**C**) Stations sampled in 1983–93, examined by McGann & Sloan. (**D**) Stations sampled in 1995–1998, examined by McGann & Sloan.

sampling program in 1995–98 to determine its present status in the bay; and an exploratory sampling of protected coastal waters and examination of other available sediment samples in western North America to determine its current range. Samples of about 200–300 cc were collected and processed according to standard techniques. Splits of ~300 specimens were analyzed from each sample.

Results

The first detailed studies of San Francisco Bay foraminifers were conducted between 1964 and 1972, and characterized foraminiferal faunas from 288 sites (Means, 1965; Slater, 1965; Quinterno, 1968; Locke, 1971; Arnal et al., 1980; Ingle, unpubl. data). These faunas were dominated by *Elphidium excavatum* (Terquem), *Ammonia beccarii* (Linné), *Elphidiella hannai* (Cushman and Grant), and *Trochammina inflata* (Montagu), with other minor constituents, including *Elphidium gunteri* Cole, *Haynesina germanica* (Ehrenberg), *Trochammina kellettae* Thalmann, *Trochammina macrescens* Brady and *Miliammina fusca* (Brady). With the exception of *H. germanica*, which is only present in restricted areas, all of these species are also present in San Francisco Bay in sediments dated ~125 000 years B.P. (Sloan, 1980, 1992; Ingram & Sloan, 1992). No *T. hadai* were reported in any of these studies (Figure 1A).

We examined 118 sediment samples collected bimonthly between March 1980 and February 1981 from 47 stations throughout San Francisco Bay. Of these, 26 samples taken at the five stations nearest where *T. hadai* would eventually be found for the first time yielded the same four common estuarine species present in earlier studies, and no *T. hadai* (Sloan, unpubl. data) (Figure 1B). However, *T. hadai* was found in one of four samples collected in 1983 from the south bay, where it constituted 3% of the foraminiferal fauna (Figure 1C). By 1986–87, *T. hadai* was present at all of the 46 stations sampled in the south bay, dominating the assemblage with up to 89% of the foraminifers at these sites (Figure 1C). *Trochammina hadai* was found in all of nine sediment samples collected from central and south bay stations in 1990–93, constituting up to 56% of the foraminifers (Figure 1C). In six surveys from 1995–98, *T. hadai* was found at 17 sites, where it constituted up to 93% of the foraminiferal fauna, but was not found at seven sites in the extreme northern and southern ends of the bay (McGann & Sloan, 1999) (Figure 1D). In all, *T. hadai* has been found at 91% of 79 stations sampled between 1986 and 1998. Outside of San Francisco Bay, we found *T. hadai* in core-top samples from Prince William Sound collected in 1989–92 after the *Exxon Valdez* oil spill, and in surface sediments from 12 bays and harbors from San Diego to Puget Sound collected in 1996–99 (Figure 2). The earliest sample containing *T. hadai* that we found was a 1971 surface sample from Puget Sound.

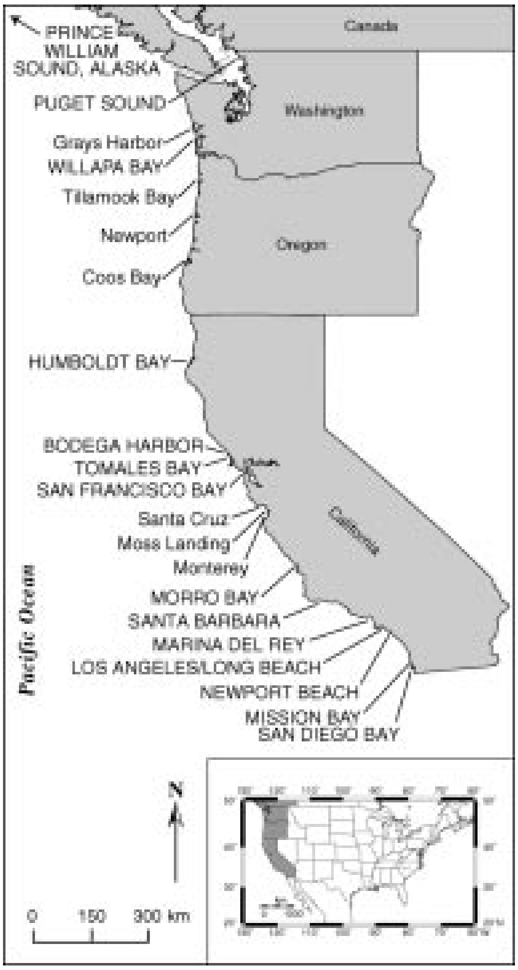

Figure 2. Bays and harbors sampled for *T. hadai*. Uppercase – *T. hadai* present in samples; lowercase – not present in samples.

We examined two sediment cores from San Francisco Bay that provided further evidence of the prior absence and recent proliferation of *T. hadai* (Figure 1C). In a 1990 central bay core, *T. hadai* accounted for 21% of the foraminifers at the top of the core, 8% at 20 cm depth, and 6% at 40 cm depth (Sloan, unpubl. data). Similarly, in a 1993 south bay core, *T. hadai* constituted 52% of the foraminifers at the top, 9% at 10 cm , <1% at 20 cm, and was absent from the remaining 33 samples down to the bottom of the 352 cm core (McGann, 1995).

Discussion

Since its first record in San Francisco Bay, *T. hadai* has been found in 96% of the surface sediment samples collected west of Carquinez Strait. It has been collected from the intertidal zone to 17 m water depth, in areas with typical summer bottom salinities of 20–33 psu and typical summer bottom temperatures of 15–20 °C (Conomos, 1979). However, it was most abundant in areas with typical summer bottom salinities of 28–32 psu and in mud rather than sand. These environmental parameters are consistent with its distribution in Japan's estuaries and harbors (Uchio, 1962; Matoba, 1970; Matsushita & Kitazato, 1990). The proliferation of *T. hadai* in San Francisco Bay is associated with a decline in relative abundance of one of the most common native foraminifers, *Elphidium excavatum*. For example, in the south bay core described above which represents an estimated 3800 years of deposition based on six AMS ^{14}C dates (McGann, 1995; unpubl. data), *E. excavatum* declined from at least 55% of the foraminifers in all samples prior to the first appearance of *T. hadai* in the core, to 19% of foraminifers at 1–2.5 cm depth, to a present average of 5% in the south bay area (McGann & Sloan, unpubl. data).

Evidence from surface sediment samples and from sediment cores indicates that *T. hadai* is recently established in San Francisco Bay. It was absent from all sediment samples taken from hundreds of stations throughout San Francisco Bay through 1981, present at one of four stations sampled in 1983, and present in all of 46 stations sampled in 1986–87, dominating the assemblage at some of them. In two cores, taken from the central bay and the south bay, *T. hadai* is absent from the lower sections of the cores but present in the uppermost sections, where its relative abundance declines steadily downward from the surface. We interpret the lowest presence of *T. hadai* in these cores not as representing its first appearance in the sediments, but rather its displacement downward by bioturbation or by physical disturbance of individuals initially deposited in layers at or near the surface.

Furthermore, except for the proliferation of *T. hadai* in the uppermost samples in these cores, their faunal composition is remarkably stable. For example, in the south bay core, other than *T. hadai* none of the minor species (those absent from one-fifth or more of the samples) ever constitutes more than 1% of the fauna in any one sample. *Trochammina hadai*, in contrast, is absent from 92% of the samples, but in the few samples where it is present constitutes up to 52% of the fauna. The depth distribution of *T. hadai* in these cores is thus entirely unlike that of the other, presumably native, foraminifer species present.

The native or introduced status of *T. hadai* at other sites in western North America is less clear. Three possibilities are: (1) *T. hadai* may be native to sites both north and south of San Francisco Bay, but not to San Francisco Bay itself; (2) *T. hadai* may initially have had a boreal Pacific distribution, ranging as a native species from Japan northward through Siberia to North American shores and southward to some point north of San Francisco Bay, and been recently introduced by human activities or carried by currents to sites south of that point; or (3) *T. hadai* may be native to Asian shores and introduced to all North American sites where it is now found. The first two possibilities would require some change in environmental conditions to enable *T. hadai* to become widespread and abundant in San Francisco Bay since the early 1980s, despite its apparent absence for roughly 3800 years previously (McGann, 1995; unpubl. data). As no environmental change that would account for this is known, the third possibility – requiring only an available transport mechanism such as those discussed in the next paragraph – is the most parsimonious interpretation of the currently available data. Ongoing investigations by the authors of *T. hadai* in surface sediments and sediment cores in North America may shed further light on this question.

If *T. hadai* is an introduction to western North America, then it could have been transported via oysters or ships. Oysters have been imported from Japan to sites on the west coast of North America for commercial mariculture since 1902 (Carlton, 1979). Initially these were carried in boxes or barrels that frequently contained substantial sediment capable of hosting benthic foraminifers, but for several decades such shipments have been generally free of significant quantities of sediment, making oyster shipments less likely as a transport mechanism. On ships, foraminifers have been collected as dried specimens on an anchor chain (Carlton et al., 1995), in ballast water (Carlton & Geller, 1993; Smith et al., 1996; Chu et al., 1997) and from sediments in ballast tanks (Galil & Hülsmann, 1997; Gollasch et al., 1998; Macdonald, 1998). For example, we found *T. hadai* and other foraminiferal species in sediments collected in January 1996 from the ballast tank of a gasoline tanker in Long Beach Harbor that routinely traveled between western U.S. ports. Further research on the time of arrival of *T. hadai* in different western North America sites may clarify whether ships or shellfish are the more likely transport vector.

Conclusion

Surface sediment and core data clearly indicate that *T. hadai* is a recent introduction to San Francisco Bay and probably was also introduced to other bays and harbors in western North America. Three lessons may be drawn from this analysis. First, data from sediment cores may prove useful in identifying invasions by benthic microorganisms within historic time, and in deciphering possible impacts on species composition. Second, marine microorganisms introduced to a region may very quickly exhibit high abundances and distribution over a broad area. And third, although microfossil faunal changes similar in scale to that described here have generally been interpreted as evidence of an alteration in environmental conditions, in some cases such changes could result from a natural invasion following a seaway opening, a change in ocean currents, or a stochastic transport event carrying a wayward organism across or between oceans.

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