The immigration of an Asian bivalve *Potamocorbula* into San Francisco Bay and the subsequent environmental change

Janet K. THOMPSON and Francis PARCHASO
(United States Geological Survey, Menlo Park, California US)

jthompso@usgs.gov

The San Francisco Bay and freshwater Delta system has undergone extensive changes in the last 150 years due to human activity. The physical habitat has been altered due to levee building, dredging, wetland reclamation, and freshwater diversion and the chemical environment has changed due to disposal of municipal and industrial waste into the system in addition to run-off of pollutants from the watershed. Coincident with these alterations, we have purposefully and inadvertently introduced over 300 non-indigenous species into the system (Cohen and Carlton 1998). These physical, chemical, and biological changes have, in sum, resulted in an ecosystem that minimally resembles the historic system and one that presents us with immense challenges in our efforts to restore the system. We will be discussing one cause of ecosystem change, the introduction of a non-indigenous bivalve, but the response of the ecosystem to this event must be understood within the context of an ecosystem that is stressed. Thus we will begin with a short history of the anthropogenic influences on the ecosystem and then discuss how one new bivalve species resulted in changes to the structure of the food web and to the transfer of contaminants within the food web of the system.

1. San Francisco Bay - An Urban Estuary

The San Francisco Bay and freshwater Delta (SFBD) is the largest U.S. estuary on the Pacific coast. San Francisco Bay (SFB) is a temperate, middle-latitude estuary located in the center of a large urban center (>8 million people), and is the natural terminus for 70% of the state of California’s annual freshwater runoff. Because 80% of the freshwater needs for the state occur in the southern portion of the state, about 50% of the freshwater that historically flowed into SFB is now being retained in reservoirs for urban and agricultural consumption and hydroelectric power (Peterson et al 1995). The alteration of freshwater flow is now considered to be one of the major stresses on the SFBD ecosystem. In addition to the decrease in volume of freshwater, there has also been a change in the hydrograph. For example, (1) peaks in flow that historically occurred in late winter are now reduced in magnitude and extend into spring, and (2) salinity intrusion up channels that have been deepened by dredging, in combination with increased freshwater use in the Delta necessitate increased freshwater flow during the historic low-flow periods (late spring through fall).

Man began to manipulate the SFBD soon after gold was discovered in the foothills and watershed of the system in 1849. The effects of the gold rush continue into the present time, as the
hydraulic mining for the placer gold washed over 400 million cubic meters of sediment into the bay along with a large portion of the ≈ 9 million kilograms of liquid mercury lost to the system during the mining process. Over the next 125 years the mercury-laden sediment was buried by newer sediment eroded from the watershed. However, this surface sediment is now eroding and the mercury is becoming biologically available as the system becomes sediment “starved”, a result of the retention of sediment behind dams in the watershed. Mercury is not the only contaminant of concern in the system as effluent from 46 wastewater-treatment plants and 65 large industrial dischargers release 36 million kilograms of over 65 contaminants into SFB each year. Most locations in SFB have sediments or water that exceed contaminant guidelines for either PCBs, PAHs, or mercury (SFEI 2003).

The influx of miners into the SFBD watershed (over 300,000 between 1849 and 1954) resulted in the earliest man-made modifications to the system as the freshwater marsh was diked to create farmland. Today the freshwater marsh is a series of diked, man-made canals surrounding drained marshland that has now subsided to 8 m below sea level in some locations. The salt marsh has also been diked, filled, and developed for highways and commercial use such that the total marshland in the system has been reduced by 91%.

Possibly because of its relatively young geologic age, active shipping port, and temperate climate, SFBD has been the recipient of so many non-indigenous species that it has been called “the most invaded aquatic ecosystem in North America” (Cohen and Carlton 1995). While some of these species were intentionally introduced, most have been accidentally introduced either with the spat of cultured oysters in the 1800’s or in ballast water, which is believed to be responsible for the dramatic increase in the rate of introductions in the last 30 years (Cohen and Carlton 1998).

2. Relevant Facts About San Francisco Bay

SFB is very shallow (median depth is 2.8 m at MSL), mesotidal, and has unequal, semi-diurnal tides. The bay can be divided into three sections, the North Bay (NB), through which the majority of freshwater enters, Central Bay where the Pacific Ocean enters the bay, and the South Bay (SB), a mostly saline system where most of the freshwater has been diverted. Freshwater flow peaks in NB in early winter or spring when snowmelt water is released from upstream reservoirs. Salinity ranges from 0-25 psu and the salinity gradient is substantial throughout NB, which is classified as a river-dominated partially mixed estuary. In contrast to the NB, the majority of the freshwater flowing into SB is from sewage effluent and periodic advection of NB water during wet years. The SB is classified as a lagoonal estuary (salinity range of 15-30 psu). Phytoplankton is the major source of organic carbon in SFB (Jassby et al 1993), but neither NB or SB are very productive despite high nutrient concentrations (20 g C m⁻² yr⁻¹ in NB and 150-200 g C m⁻² yr⁻¹ in SB, Alpine and Cloern 1992, Cloern 1987) due to the high turbidity (Cloern 2001).
Primary production (Jassby et al 2002) and zooplankton abundance (Mecum and Orsi 2001) have declined since the 1970’s in the NB and Delta, possibly as a result of the cumulative stresses on the SFBD. Some of the NB primary production reduction is due to grazing by *Potamocorbula amurensis* (see below), but this is not true for the Delta. There were earlier signs of ecosystem stress when commercial fisheries declined in the early 1900’s and disappeared in the 1950’s (Skinner 1962). It is likely that over-fishing and introduced species contributed to some of the fishery declines as 20 of the 40 species of fish in SFBD are introduced (Moyle 2002).

### 3. *Potamocorbula amurensis* Invades and Perturbs San Francisco Bay

A few individuals of *Potamocorbula amurensis* were first discovered in NB in fall 1986. Within a year, *P. amurensis* had spread throughout the NB and was the dominant (by biomass) organism in the benthic community at most locations. *P. amurensis* is native to the western Pacific and was likely transported with ballast water from The Peoples Republic of China (PRC) to SFB (Carlton et al 1990). It spread throughout the bay’s soft-sediment habitats and was common in SB by 1989. *P. amurensis* was particularly successful in the NB benthic community, which was mostly composed of seasonally ephemeral species that could live either in the fresh or estuarine salinities, but not in both. *P. amurensis*’ ability to rapidly osmoregulate as adults and larvae (Nicolini and Penry 2000) has allowed this species to live in NB throughout the seasonal salinity variations. *P. amurensis* is frequently the dominant species in the benthic community with maximum densities of \( \approx 20,000 \) individuals/m\(^2\) and maximum biomass values of 100g C/m\(^2\).

The most startling change to the ecosystem after *P. amurensis*’ arrival was the disappearance of the annual phytoplankton bloom in the NB (Figure 1a). The phytoplankton bloom historically began in late spring and continued into fall, with phytoplankton biomass values (measured as chlorophyll \( a \) concentration) peaking at 20-30 g/L of chlorophyll \( a \). *P. amurensis* is a filter feeder that is capable of filtering about four liters of water per day per adult (Cole et al 1992). This filtration rate, when combined with the large number of individuals in NB (Nichols et al 1990), resulted in sufficiently high community grazing rates (volume of water that the individuals found in a square meter of sediment can filter per day: \( m^3/m^2/d = m/d \)) to account for the reduction in phytoplankton biomass (Alpine and Cloern 1992, Thompson et al in review). A comparison of time series for grazing rates and phytoplankton biomass (Figure 1a and 1b) reveals opposing patterns for grazing rates and phytoplankton biomass. If we look at this pattern in more detail (Figure 2) we see that even small seasonal variations in phytoplankton biomass appear to be controlled by *P. amurensis* grazing.

Food web responses to the decline in phytoplankton in NB have included population declines in one copepod (*Eurytemora affinis*, Figure 1c) due to a combination of food limitation and predation on its larval stages by *P. amurensis* (Kimmerer et al 1994). Another copepod, *Psuedodiaptomus forbesi*, was introduced to SFBD coincident with the decline in *E. affinis* but it has never achieved the
seasonally consistent high biomass previously seen with *E. affinas*, possibly due to food limitation with this species also. Further up the food web, an herbivorous mysid shrimp (*Neomysis mercedis*) has dramatically declined (Figure 1d) due to food limitation (Kimmerer and Orsi 1996, Orsi and Mecum 1996). A recently introduced mysid shrimp (*Acanthomysis bowermani*) may also be food limited. These population declines are troubling because mysid shrimp are the major prey item for many juvenile and adult fish in the system. Despite these changes in the food web, we have not seen a large decline in the fish in the system that can be attributed to the demise of the phytoplankton and thus to the introduction of *P. amurensis*. Some of the difficulty in making these connections is due to the long history of fishery decline in the system (Figure 1e) that began prior to the appearance of *P. amurensis*. It is possible that, given the large number of stresses in this system, food may eventually prove to be limiting to some species but that has not yet been shown (Kimmerer 2002). The most recent food web response to *P. amurensis* reflects the ease with which these bivalves are consumed by bottom feeding birds and fish. *P. amurensis* live near the surface of the sediment with one third to one half of their shell exposed at the sediment surface. Overwintering birds in SFB are exploiting this new prey item and forage less on their previous prey, *Macoma balthica*, a bivalve that lives very deep in the sediment. The combination of ease of capture and the thick shell of *P. amurensis*, which reduces the food value per clam relative to *M. balthica*, may be responsible for ducks dispersing earlier in the season as their prey disappears (Poulton et al 2002, Takekawa et al 2003). The long-term effect of this change on the over-wintering habits of the diving ducks is, as yet, not known.

The invasion of *P. amurensis* resulted in a change in the transfer of selenium through the food web. Selenium is a reproductive and developmental toxin that occurs naturally in the watershed and is concentrated in agricultural drain water that flows into the SFBD. The combination of the huge increase in benthic biomass (Nichols et al 1990) of a desirable and easily preyed upon organism and *P. amurensis*’ extraordinary ability to accumulate selenium (Schlekat et al 2000, 2002) has resulted in a selenium rich food source that is being concentrated in bottom feeding fish and birds. Some of *P. amurensis*’ major predators, such as the Sturgeon (Figure 3) have shown increased selenium concentrations coincident with their consumption of *P. amurensis* (Linville et al 2002). Diving ducks that overwinter in NB have selenium concentrations in their liver above the 10 mg/g dry tissue concentration that is associated with reproductive impairment. Furthermore, ducks foraging in SFB during winter show increasing concentrations of selenium with time spent in the system, a result of their concentrated diet on *P. amurensis* (Miles et al 2003).

There is no definitive way to document if previous invasions of non-indigenous species into SFBD resulted in ecosystem changes similar to those seen with *P. amurensis*. However it is likely that at least three introduced, filter-feeding bivalves had some effect: (1) The Atlantic Oyster (*Crassostrea virginica*) was cultured in SFB from 1870 through 1920 (Skinner 1962), and is likely to have locally reduced phytoplankton biomass, (2) The Atlantic Soft-Shell Clam (*Mya Arenaria*),
introduced in 1874, was commercially harvested through the 1930’s and may have had an effect on the phytoplankton biomass on the same spatial scale as we have seen with *P. amurensis*, and (3) *Corbicula fluminea* shown to have localized effects on phytoplankton biomass (Lucas et al 2002), is likely to have affected phytoplankton in the freshwater system following its introduction in 1945.  

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Figure 1. Chlorophyll a concentrations (data from California Department of Water Resources, CDWR) and *Potamocorbula amurensis* grazing rate (CDWR, station D7), copepod and mysid shrimp abundance in spring, and a measure of striped bass abundance in NB.

図1 クロロフィル a濃度と*Potamocorbula amurensis*の摂食速度、カイアシとアミの春における発生量、湾北部におけるシマスズキ発生量の指標。
図2 1986年にP. amurensisが侵入した後の湾北部の入り江・グリズリー湾におけるクロロフィルa濃度とP. amurensisの摂食速度。

図3 P. amurensisがサンフランシスコ湾に侵入する前（1986）と後（1990と1999）における、漂浮食性魚類（シマズキ）と底食性魚類（シロチョウザメ）の組織内セレニウム濃度。セレニウムが底生の食物網を通過するのと一致して、漂浮食性魚類ではP. amurensisが侵入後もセレニウム濃度は増加していないが、底食性魚類では組織中のセレニウム濃度が5倍に増加している。