

CHAPTER 6. DISCUSSION

(A) THE ECOLOGICAL IMPACTS OF BIOLOGICAL INVASIONS IN THE SAN FRANCISCO ESTUARY

Nonindigenous aquatic animals and plants have had a profound impact on the Estuary's ecosystem. No habitat—with the possible exception of the deep floor of the Central Bay—remains uninvaded by exotic species, and in some habitats it is difficult to find any natives. The depth and extent of biological invasions now recognized for the Estuary is greater than for any other aquatic ecosystem in North America, a phenomenon which apparently results from a combination of factors, including: 150 years of intense human commercial activity involving both the frequent disturbance and alteration of the ecosystem and the importation of nonindigenous organisms (Nichols et al. 1986), the prior geological and ecological history of the Bay, and the amount of research into biological invasions in this system. Despite the intensity of research effort our understanding of the ecological and biological consequences of the estuary's nonindigenous biota, in terms of both the individual and the collective impacts of many species, remains strikingly limited.

A brief survey of the estuary reveals the scale of dominance by the nonindigenous biota. At the Bay's mouth, under the shadow of the Golden Gate Bridge, orange-red clumps of the Indo-Pacific bryozoan *Watersipora*, 30 centimeters across and 20 centimeters deep, covers the dock sides. To the north, in San Pablo and Suisun bays, the Chinese clam *Potamocorbula* forms thick beds in the mud while Japanese gobies and Korean shrimp swim overhead. In a brackish river a few kilometers distant large, coral-like masses formed from the calcareous tubes of an Australian serpulid worm harbor an abundant population of the Atlantic shore crab *Rhithropanopeus*. Upstream in the Delta a Eurasian freshwater hydroid forms thick colonies on ropes and marina floats. Swimming nearby may be any of several warmwater gamefish native to eastern North America, including six species of catfish, four species of sunfish and four species of bass.

Along the eastern and southern Bay shores, great masses of Atlantic and Asian seaquirts comprise the dominant fouling biota along with dense populations of bay mussels, represented in San Francisco Bay by both the native *Mytilus trossulus* and the Mediterranean *Mytilus galloprovincialis*. On the fringes of the Bay, dense beds of the New England ribbed mussel bind the upper intertidal sediments and lower marsh fringes, clonal colonies of the Atlantic cordgrass *Spartina alterniflora* encroach upon the mudflats, and a New Zealand burrowing isopod inexorably bores into the clay and mud banks of the Bay's shore. Moving in seasonal migrations over the mudflats, vast herds of the Atlantic mudsnail *Ilyanassa* rework the uppermost layers of sediment above the subsurface beds of the Atlantic softshell clam and the Japanese littleneck clam.

With seasonal changes, with dramatic interannual variation in the amount of freshwater runoff or saltwater intrusion, with the discharge of point-source or

diffuse pollutants, and with many other variables, these associations of introduced species may shift significantly, but the overall aspect remains the same: the dominant members of many of the Bay and Delta aquatic communities are organisms that were not present 150 years ago.

Considered here are the ecological and biological impacts that have been caused by the introduction of nonindigenous animals and plants into the marine, brackish, and freshwater environments of the Bay and Delta region. We review examples of communities in which introduced species are the dominant members, both in terms of diversity and biomass, consider trophic changes in the Bay as a result of invasions, and then consider additional community-level and habitat changes that have occurred. We conclude with prospects for future invasions.

1. ASSOCIATIONS OF NONINDIGENOUS SPECIES

In some regions of the Estuary, 100% of the common species are introduced.

As Carlton (1975, 1979a, 1979b), Nichols & Thompson (1985a,b) and Nichols & Pamatmat (1988) have noted, the shallow-water benthos of San Francisco Bay is dominated by nonindigenous species—indeed, Nichols & Thompson (1985b) have used the phrase, "introduced mudflat community" in reference to South San Francisco Bay. Nichols and Pamatmat (1988), in describing the Bay's soft-bottom benthic communities, state that:

"The principal contributors to biomass throughout much of the bay are the mollusks *Tapes* [now *Venerupis*] *philippinarum*, *Musculista senhousia*, *Macoma balthica* [now *petalum*], *Mya arenaria*, *Gemma gemma*, and *Ilyanassa obsoleta*. In addition, the large tube-dwelling polychaete *Asychis* [now *Sabaco*] *elongata* is a major contributor to total biomass in the muddy subtidal areas of South Bay...[Since 1987] the Asian bivalve, *Potamocorbula amurensis*...has become the dominant macroinvertebrate throughout the northern portions of the bay and is found in South Bay sloughs as well."

Each of these species is introduced to San Francisco Bay, arriving in the following approximate sequence:

	Time of First Observation (O) or Hypothesized Arrival (H)
Introduced with Atlantic Oysters	
Atlantic soft-shell clam <i>Mya</i>	early 1870s (O)
Atlantic tellinid clam <i>Macoma</i>	1870s-1890s (H)
Atlantic gem clam <i>Gemma</i>	before 1893 (O)
Atlantic mudsnail <i>Ilyanassa</i>	before 1907 (O)
Atlantic bamboo worm <i>Sabaco</i>	after 1912 (H)
Introduced with Japanese Oysters	
Japanese mussel <i>Musculista</i>	before 1946 (O)
Japanese clam <i>Venerupis</i>	before 1946 (O)
Introduced with Ballast Water	
Chinese clam <i>Potamocorbula</i>	before 1986 (O)

Although these nonindigenous species dominated the intertidal and subtidal mudflat communities, many other species of mollusks, crustaceans, polychaetes, and other invertebrates were added to the Bay's soft-bottom communities during these periods as well (Table 1). Each new addition or set of additions presumably altered the previously-existing community, in ways that may have prevented or facilitated the invasion of the next introduced species. While these "successional" concepts of the roles of inhibition or facilitation by preceding invaders are not well developed in invasion ecology, the assembly of these communities over a relatively long period of time, from different source regions (and thus of species that did not coevolve), may prove to be key factors in understanding the structure of invaded communities, and of which species do and do not invade.

A review of several faunal studies around the Bay conducted between the 1940s and 1970s (Carlton, 1979a; Table 4, herein) demonstrates the importance of introduced species in intertidal epifaunal (on the surface), intertidal infaunal (under the surface) and fouling communities. In locations ranging from freshwater sites in the Delta through estuarine sites in the northern bays, the Central Bay and the South Bay, introduced species account for the majority of the species diversity at most sites. On South Bay mudflats, Vassallo (1969) found that the infaunal communities could be characterized in terms of introduced species: the upper intertidal was essentially a "*Macoma balthica* community," whereas the lower intertidal was an "*Ampelisca abdita* community." At some sites, 100% of the common to abundant species were found to be introduced. We discuss later in this section the question of the replacement or displacement of a native biota by these introduced species.

Thus, extensive communities in the Bay are structured around introduced species: the abundant filter feeders, the abundant herbivores, the abundant detritivores, and the abundant carnivores are not native. With few exceptions, the introduced versus native status of the abundant primary producers (phytoplankton and algae) is not known, and thus the extent to which the entire food chain is constructed of invasions is not yet known. However, few, if any, of the estuarine phytoplankton or algae are clearly native. These communities are further composed of species originating from different regions of the world—species that evolved in the presence of other species (that did not arrive with them in San Francisco Bay) and that evolved under different environmental regimes. The extent to which these introduced species, artificially placed together in a novel environment, are undergoing coadaptation, in terms of predator-prey relationships or competitive interactions, remains unknown.

The predominance of nonnative species in the Bay's communities suggest that a vast amount of energy, in terms of dissolved organic and inorganic compounds, and in terms of primary and secondary production, now pass through and are utilized by the nonindigenous biota of the Bay. We explore some of these trophic changes below, as well as the role of competition, habitat alterations, and the regional or global extirpation of native species.

Table 4. Associations of Introduced Species in the San Francisco Estuary.

The number and percentage of introduced species (excluding cryptogenic species) in selected communities.

Location	Number of Introduced Species	Reference [date of collections]
DELTA & SUISUN BAY		
Antioch and Bradford	6 out of 7 (= 86%) epibenthic/fouling species are introduced.	Aldrich, 1961
Sacramento River, Decker Is. to Chipps Is.	3 out of 5 (=60%) dominant benthic species are introduced.	Siegfried et al., 1980 [1976]
Delta to Grizzly Bay	2 out of 4 (=50%) dominant benthic species are introduced.	Markmann, 1986 [1975-81]
Suisun Bay	4 out of 7 (=57%) common benthic species are introduced.	Nichols & Thompson, 1985a
Grizzly Bay to Old River	2 out of 5 (=40%) dominant benthic species are introduced.	Herbold & Moyle 1989 [1983-84]
Delta	26 out of 52 (=50%) fish present, and 25 of 36 (=69%) fish resident, in the Delta are introduced.	Herbold & Moyle, 1989
Delta: Old River, Frank's Tract and Sherman Lake	6 out of 22 (=27%) benthic invertebrate species are introduced.	Hymanson et al., 1984 [1980-90]
Sacramento River at Sherman Island	10 out of 17 (=59%) benthic invertebrate species are introduced.	Hymanson et al., 1984 [1980-90]
Grizzly Bay	16 out of 19 (=84%) benthic invertebrate species are introduced.	Hymanson et al., 1984 [1980-90]
SAN PABLO BAY		
San Pablo Bay east to the Delta	8 out of 13 (= 62%) epifaunal species, and 16 out of 17 (= 94%) infaunal species are introduced.*	Filice, 1959
Carquinez Strait	7 out of 7 (=100%) of common benthic species are introduced.	Markmann, 1986 [1975-81]
San Pablo Bay shallows	9 out of 9 (=100%) common benthic species are introduced.	Nichols & Thompson, 1985a
CENTRAL BAY		
Oakland Estuary	All 4 species (= 100%) dominant in the fouling fauna are introduced.*	Graham & Gay, 1945 [1940-42]
Lake Merritt	31 out of 35 (= 88%) epifaunal species, and 6 out of 8 (= 75%) infaunal species are introduced.*	Carlton, 1979a [1962-72]

Table 4. Associations of Introduced Species - continued

Location	Number of Introduced Species	Reference [date of collections]
SOUTH BAY		
Hayward	4 out of 5 (= 80%) upper intertidal infaunal species are introduced. The infauna is numerically dominated by the introduced clam <i>Macoma petalum</i> ; the epifauna is numerically dominated by the introduced mudsnail <i>Ilyanassa obsoleta</i> .	Vassallo, 1969
	7 out of 9 (= 77%) lower intertidal infaunal species are introduced. The community is numerically dominated by the introduced amphipod <i>Ampelisca abdita</i> .	
Palo Alto	14 out of 14 (=100%) species of mudflat infauna and epifauna are introduced.	Nichols, 1977
South Bay channels	10 out of 10 (=100%) common benthic species in the channels, and 6 out of 6 (=100%) dominant benthic species in the shallows are introduced.	Nichols & Thompson (1985a)

* For these calculations, all mussels reported as *Mytilus edulis* were assumed to be native.

2. TROPHIC CHANGES IN THE BAY

In the 1990s, introduced and cryptogenic species dominate the Estuary's food webs.

We consider here trophic alterations to the Bay's ecosystem by introduced species utilizing different feeding levels and strategies: the phytoplankton, the zooplankton, water column consumers (filter feeders), epibenthic and shallow-infaunal grazers and deposit feeders, and carnivores.

(a) Phytoplankton

Although various mechanisms have transported and continue to transport large numbers of nonindigenous phytoplankton to the San Francisco Bay and Delta (today mainly via ballast water, but in the past including settled diatoms transported with oysters and freshwater phytoplankton in the water used to transport game fish), and researchers have identified introduced diatoms and dinoflagellates in other areas of the world (in Australia: Hallegraeff, 1993; Hallegraeff and Bolch, 1992; in Europe: Bolch, 1994; in the Great Lakes: Mills et al., 1993), none of the phytoplankton in the estuary have yet been reported as introduced species. We consider at least 31 species of phytoplankton to be cryptogenic (Table 2), which is

probably only a small fraction of the total number of planktonic, benthic, and epibiotic species that have been introduced to the Bay and Delta system.

The diatoms *Cyclotella caspia*, *Coscinodiscus* spp., *Aulacoseira* (= *Melosira*) spp., *Aulacoseira* (= *Melosira*) *distans* variety *lirata*, *Skeletonema costatum* and *Thalassiosira decipiens* and the microflagellate *Chroomonas minuta* are dominant and important members of the phytoplankton in San Francisco Bay (Cloern et al., 1985). All are broadly distributed globally and are cryptogenic species in San Francisco Bay. The diatom *Aulacoseira granulata* (= *Melosira granulata*, Round et al., 1990) has recently come to dominate phytoplankton blooms in the San Joaquin River (Herbold & Moyle, 1989). In Suisun Bay, the diatom *Thalassiosira decipiens* alternates between dominating the water column or the benthos, apparently depending upon the degree of water column mixing (Cloern et al., 1985; Nichols and Pamatmat, 1988). Both *Aulacoseira granulata* and *Thalassiosira decipiens* are cosmopolitan species (e.g., Cholnoky, 1968) and may well be introductions in the Bay system.

While these taxa are also often reported from open-ocean systems, including upwellings, the possibility remains that these brackish water and freshwater diatoms represent estuarine genotypes transported by oysters and ships around the world, and may be distinct from the oceanic genotypes transported by ocean currents. A similar example has been provided by Greenberg (1995), who found that the estuarine populations of the jellyfish *Aurelia aurita* in San Francisco Bay are closely related to those from Japan (and thus probable ship-borne introductions as attached fouling scyphistomae or planktonic ephyrae), and less similar genetically to coastal populations from Monterey Bay.

Thus, it remains possible that many of the estuary's major phytoplankton species, accounting for the bulk of the estuary's primary production, are in fact introduced. Resolution of these cryptogenic diatoms as native or exotic would significantly improve our understanding of the origin and structure of the Bay and Delta's food webs; and is essential to developing a correct interpretation of their biology and their patterns of distribution and abundance in terms of, on the one hand, adaptation to and co-evolution with the estuary's physical conditions and other biota, or on the other, opportunistic establishment and exploitation of available resources.

(b) Zooplankton

The planktonic secondary producers are represented by a diverse zooplankton community in San Francisco Bay. Many copepod species in San Francisco Bay are considered widespread if not cosmopolitan, and thus those susceptible to human transport mechanisms should be considered cryptogenic species. Notable in this regard, for example, are the abundant estuarine copepod *Eurytemora affinis* and the estuarine rotifer *Synchaeta bicornis*, which often characterize the zooplankton communities of the Sacramento-San Joaquin Delta (Orsi & Mecum, 1986) and whose biogeographic status remains unresolved. *Eurytemora affinis* in particular has been suspected of being an introduced species (Orsi, 1995). Similarly, some microplankton in the Bay are candidate cryptogenic species: the cosmopolitan estuarine ciliate

Mesodinium rubrum, for example, caused red tides in South San Francisco Bay in spring 1993 (Cloern et al., 1994).

While the diverse meroplanktonic larvae of the large numbers of introduced benthic invertebrates and fish must play a role in water column dynamics, no studies appear to be available on this aspect of zooplankton trophic dynamics for the Bay. Mills and Sommer (1995) have noted that the introduced hydromedusae *Maeotias inexpectata* and *Blackfordia virginica* in San Francisco Bay estuarine tributaries fed almost exclusively on barnacle larvae, copepods, and the larvae of the introduced crab *Rhithropanopeus*. Whether these jellyfish decrease the abundance of their prey in an ecologically significant manner remains to be determined. *Maeotias* and *Blackfordia* are two of a large number of new invasive zooplanktonic organisms that have been recorded from the estuary since the 1970s, including another hydromedusan (*Cladonema uchidai*), the Japanese stock of the moon jelly *Aurelia aurita*, eight species of Asian copepods, three species of mysids and the demersal (vertically migrating) Japanese cumacean *Nippoleucon* (= *Hemileucon*) *hinumensis*.

The role of this new guild of often abundant Asian copepods and mysids in the upper estuary is of particular interest. Complicating both speculations and interpretations, however, are the number and interrelationships of the potential factors that control copepod abundance. Changing densities and distributions of copepods may be correlated with fluctuations in environmental parameters (such as salinity, temperature and chlorophyll concentration), predator abundance (including carnivorous zooplankton, fish and benthic filter-feeders (such as the Asian clam *Potamocorbula*) capable of zooplanktivory), selective predation on different copepod species, competition between copepod species (the intensity of which may be moderated by food availability), and declines in the overall abundance of zooplankton (reducing interspecific competition and making more food available).

Orsi et al. (1983) speculated that competition between the Chinese copepod *Sinocalanus doerri* and the "native" copepod *Eurytemora affinis* (considered here to be cryptogenic) was not likely because they preferred different salinity regimes; rather, competition and/or predation between *Sinocalanus* and the presumably native freshwater copepods *Cyclops* and *Diatomus* appeared to be more likely. Herbold et al. (1992) noted that the introduction of *Sinocalanus* and *Pseudodiaptomus forbesii* was followed by a decline in *Eurytemora* and almost complete elimination of *Diatomus*, implying potential interactions between these new invaders and the previous copepod residents. Meng and Orsi (1991) further found in laboratory experiments that the larvae of striped bass (itself an introduced species) selected *Cyclops* and *Eurytemora* over *Sinocalanus* (perhaps because of differences in copepod swimming and escape behavior). Thus, the possibility arises that the striped bass larvae's preferred prey is being replaced by an introduced, and less preferred, prey.

A further complication, however, arises when the role of the newly introduced clam *Potamocorbula* is considered, which involves both the consumption of phytoplankton, thereby removing a significant portion of the potential food resource for water-column zooplankton, and the consumption of the

zooplankton themselves. Thus, as reviewed below, Kimmerer et al. (1994) show that the decline in *Eurytemora* was likely due to consumption by *Potamocorbula*, rather than by interspecific copepod competition. Indeed, *Potamocorbula* consumes *Eurytemora* and not *Pseudodiaptomus* (Kimmerer, 1991), further reducing the preferred copepod resource of striped bass larvae.

(c) The Filter Feeding Guild

Introduced clams can filter the entire volume of the South Bay and Suisun Bay at least once a day.

A large number of nonindigenous suspension-feeding organisms are now filtering the waters of the estuary. In the intertidal and sublittoral soft-bottom sediments these include the introduced bivalves *Macoma petalum* (= "balthica"), *Venerupis*, *Mya*, *Potamocorbula*, *Theora*, *Petricolaria*, *Gemma*, *Arcuatula*, *Musculista* and *Corbicula*, most of which are abundant to extremely abundant in the estuary. Introduced, suspension-feeding polychaete worms, especially spionids, and suspension-feeding tubicolous gammarid amphipods may occur by the thousands per square meter at and near the sediment surface. Intertidal and subtidal hard substrates are often thickly-coated, sometimes several organisms deep, with dense populations of introduced macrofilterers (including the seasquirts *Molgula*, *Styela clava*, *Botryllus* spp., *Ciona* spp. and *Ascidia*—see Whitlatch et al., 1995, regarding the complex roles of *Styela clava* and *Botrylloides diegensis*, both introduced into Long Island Sound, in regulating community dynamics) and introduced microfilterers (including bryozoans and sponges). Introduced carnivorous suspension feeders, such as hydroids and sea anemones, can also be abundant: dense populations of the Indian Ocean hydroid *Bimeria franciscana* occur on floats in brackish tributaries, while the exotic sea anemone *Diadumene franciscana* is sometimes found in dense clonal clusters on marina floats on the southwestern shore of the Bay. Both doubtless have an impact on adjacent plankton communities. In some parts of the estuary the Mediterranean mussel *Mytilus galloprovincialis* and two introduced barnacles, *Balanus improvisus* and *Balanus amphitrite*, are exceedingly abundant filter-feeders on all hard substrates.

We consider in detail below the role of the benthic filter-feeding bivalve guild in regulating phytoplankton production in San Francisco Bay. The holistic role of the entire nonindigenous filter-feeding guild—clams, mussels, bryozoans, barnacles, amphipods, seasquirts, spionids, serpulids, sponges, hydroids, and sea anemones—in altering and controlling the trophic dynamics of the Bay-Delta system remains unknown. The potential role of just one species, the Atlantic ribbed horsemussel *Arcuatula demissa*, provides insight into the potentially profound impact of introduced filter feeders on the estuary's ecosystems. Studying the energy flow in these mussels in a Georgia marsh, Kuenzler (1961) reported that,

"The mussels... have a definite effect upon the water over the marsh, daily removing one-third of the particulate phosphorus from suspension. They regenerate a small part of this into phosphate, and reject the remainder in pseudofeces and feces which drop to the mud

surface. It appears, therefore, that the mussel population may be very important in the phosphate cycle as a depositional agent, furnishing raw materials to deposit-feeders which regenerate the phosphorus." The potential tantalizing role of *Arcuatula* in the economy of Bay marshes as a biogeochemical agent remains to be investigated.

The Control of Phytoplankton in South San Francisco Bay by Introduced Clams

In two fundamental papers, Cloern (1982) and Officer et al. (1982) demonstrated that the primary mechanism controlling phytoplankton biomass during summer and fall in South San Francisco Bay is "grazing" (filter feeding) by benthic organisms, in particular the introduced Atlantic gem clam *Gemma gemma* and the introduced Japanese bivalves *Musculista* (as *Musculus*) *senhousia* and *Venerupis philippinarum* (as *Tapes japonica*).¹ [footnote on page 209]

Cloern (1982) calculated that "suspension-feeding bivalves are sufficiently abundant to filter a volume equivalent to the volume of South Bay at least once daily" (emphasis added). This remarkable process must have a significant impact on the standing phytoplankton stock in the South Bay; and with nearly the entire primary production of the South Bay potentially passing through the guts of introduced clams, this may have fundamentally altered the energy available for native biota.

The Control of Phytoplankton in Northern San Francisco Bay by Introduced Clams: The Pre-Potamocorbula Years

Nichols (1985) extended this model of benthic control of water column production to the northern Bay. He noted that during the central California drought of 1976-1977, several species typically more common west of Carquinez Strait invaded and became abundant in Suisun Bay (including four introduced Atlantic species: the clam *Mya arenaria* (which Nichols noted was introduced), the amphipods *Corophium acherusicum* and *Ampelisca abdita*, and the spionid polychaete *Streblospio benedicti*). In addition, a resident species, the tellinid clam *Macoma balthica* (now *Macoma petalum*, see Chapter 3), increased in abundance; this species too is introduced. With the arrival of these species and the increase in *Macoma*, total community abundance peaked at 153,000/m² at one site in 1976 and 20,000/m² at one site in 1977. During these two years, the usual summer diatom bloom failed to appear (Cloern et al. 1983). Nichols (1985) proposed that this guild of estuarine invaders led to increase benthic "grazing" (filter feeding), particularly by the clam *Mya*, but also by the other species (Nichols noted, for example, that the worm *Streblospio* switches from deposit feeding to suspension feeding at higher phytoplankton concentrations). Indeed, Nichols estimated that *Mya* alone "could have filtered all of the particles (including the diatoms) from the water column on the order of once per day" (emphasis added).

Cloern et al. (1983) noted that the presumably native phytoplanktivorous mysid (opossum) shrimp *Neomysis mercedis* suffered a "near-complete collapse" in the Suisun estuary in 1977, which they describe in part as a potential result of food limitation. In turn, 1977 was a year of record low abundance of juvenile striped bass

in the north Bay; larval bass rely heavily on the mysid *Neomysis* (Cloern et al. 1983). Both collapses may have been "a direct consequence of low phytoplankton biomass" (Nichols, 1985), which, if Nichols is correct in linking the decline of the phytoplankton standing stock to a rise in benthic bivalve grazing, provides a direct and remarkable example of the potential impact of an introduced species on the Bay's food web. Thus:

Populations of the Atlantic Clam *Mya arenaria*

>>Significantly Reduces Phytoplankton Standing Stock

>>Leads to a Decline in Zooplankton (e. g. Mysids)

>>Leads to a Decline in Fish (e. g. Juvenile Striped Bass)

The Control of Phytoplankton in Northern San Francisco Bay by Introduced Clams: *Potamocorbula* and the Disappearance of the Summer Phytoplankton

At about the same time (1985) that Nichols first proposed that introduced clams could be controlling primary productivity in Suisun Bay, a ship inbound from China was deballasting into Suisun Bay a species of clam that would vastly overshadow the trophic impact of the existing guild of benthic phytoplanktivores. In October 1986 three specimens of *Potamocorbula amurensis*, a species previously known only from Asian waters, were collected in Suisun Bay. By the following summer, *Potamocorbula* was the most abundant benthic macro-organism in Suisun bay, achieving average densities of over 2,000/m², and peak densities at some sites of over 10,000/m². *Potamocorbula* has since spread and become the dominant subtidal clam in San Pablo Bay and South Bay as well.

What has been the impact of adding *Potamocorbula* to the Bay's ecosystem? Alpine and Cloern (1992) calculated that the mean annual primary production in Suisun Bay during the years of lower benthic clam density (<2,000 clams/m²) was 106 grams of carbon/m², compared to an estimated mean annual production of only 39 grams/m² when clams were dense (>2,000 clams/m²; these clams were mainly *Potamocorbula*, but included some *Mya*, whose densities declined sharply after the arrival of *Potamocorbula*—Nichols et al., 1990). Thus, since the proliferation and spread of *Potamocorbula* in 1987, the summer phytoplankton biomass maximum in the northern estuary (the diatom bloom) has disappeared, presumably because of feeding by this new invader. Thus since 1987, the invasion of the Bay by *Potamocorbula* has added a striking and persistent "top down" level of control to biological productivity in the estuary.

Werner and Hollibaugh (1993) may have recently provided the answer to one of the puzzles associated with the radical alteration of the estuary by *Potamocorbula*: if the phytoplankton bloom has been eliminated by *Potamocorbula*'s filter feeding, then what are those billions of clams now eating? (Cohen, 1990). Werner and Hollibaugh showed that *Potamocorbula* consumes bacteria as well as phytoplankton. Though it consumes bacteria at lower efficiency than diatoms,

Potamocorbula assimilates both with high efficiency. At present densities in northern San Francisco Bay, Potamocorbula is capable of filtering the entire water column over the deep channels more than once per day and over the shallows almost 13 times per day, a rate of filtration which exceeds the phytoplankton's specific growth rate and approaches or exceeds the bacterioplankton's specific growth rate.

Kimmerer et al. (1994) have now provided evidence that *Potamocorbula* substantially reduces zooplanktonic copepod populations in the North Bay by direct predation. Thus, *Potamocorbula* operates at multiple levels in the food chain: not only does it reduce phytoplankton (which would indirectly lead to reductions in zooplankton), but it also directly consumes zooplankton. It will be both critical to our understanding of the trophic dynamics of the estuary and inordinately challenging to sort out the complex and changing interrelationships of (a) these two levels of *Potamocorbula*'s interaction with the food chain, (b) competition between *Potamocorbula* and other introduced and native benthic filter feeders, (c) the roles of additional first and second order consumers introduced to the zooplankton (copepods and mysids) in reducing phytoplankton stocks, (d) the role of interspecific competition between and among introduced and native copepods and mysids, (e) selective predation by higher order consumers, many of them introduced fish species, on the zooplankton, and (f) competition between and among both introduced and native higher order consumers. Invasions by new species of phytoplankton, zooplankton, and benthic filter feeders in the Bay—invasions that can be predicted with some degree of confidence (Chapter X)—will add further complexities to this framework.

(d) Epibenthic and Shallow-Infaunal Grazers and Deposit Feeders

Benthic non-filter feeding invaders in San Francisco Bay include a number of carnivores and omnivores (considered below) as well as epibenthic and shallow infaunal grazers on surface sediments. The latter include a number of species of introduced polychaetes (such as the extremely abundant maldanid worm *Sabaco*) which act as selective or non-selective deposit feeders, interfacial bivalves such as *Macoma petalum*, which uses its siphons to graze on the mud surface but can also suspension feed, grazing peracarid crustaceans (including many introduced species of amphipods, isopods, tanaids, cumaceans and mysids), and the Atlantic mudsnail *Ilyanassa obsoleta*.

The recent discovery of the deposit-feeding Atlantic spionid *Marenzelleria viridis* in San Francisco Bay is of particular interest. *Marenzelleria* was transported by ballast water to western Europe in the 1980s and has since become one of the most common macrobenthic species in the North and Baltic Seas (Essink and Kleef, 1993; Bastrop et al., 1995). Preliminary studies reveal a variety of species interactions, in particular a significant positive relationship between increasing densities of *Marenzelleria* and increasing densities of *Corophium*, although the mechanism of this interaction is not known (Essink and Kleef, 1993).

As with the guild of filter feeders, the overall picture of the impact of introduced grazers and deposit feeders in the San Francisco Bay and Delta is not

known. Based upon Atlantic studies, however, it can be predicted that the mudsnail *Ilyanassa* is playing a significant—if not critical—role in altering the diversity, abundance, size distribution, and recruitment of many species on intertidal mudflats of San Francisco Bay. Millions of migrating mudsnails sweep large areas of mudflat clear of epibenthic diatoms (JTC, pers. obs., Barnstable Harbor, MA), and *Ilyanassa* has further been shown to be an opportunistic omnivore, consuming sponiid worms and littorinid snail egg cases (Brenchley & Carlton, 1983).

(e) Higher Level Carnivores and Omnivores

"... the arrival and establishment of the green crab signals another potentially exceptional level of ecosystem change in San Francisco Bay..."

—Cohen et al. (1995)

"... *Carcinus maenas* will significantly alter community structure, ecological interactions, and evolutionary processes in embayments of western North America"

—Grosholz & Ruiz (1995)

Introduced carnivorous and omnivorous crabs, snails, fish and terrestrial mammals undoubtedly have broad impacts throughout the San Francisco Bay and Delta ecosystem. Smaller introduced carnivores are now present (and often abundant) throughout the Bay. These include on soft sediments the recently introduced clam-eating slug *Philine auriformis* from New Zealand; on rocks and pilings the Atlantic barnacle-eating oyster drill *Urosalpinx cinerea*; and in hydroid masses on floats and navigation buoys the large Japanese isopod *Synidotea laevidorsalis*. We consider (here and in Section 5 below) three categories of carnivorous invaders in the estuary: the European green crab *Carcinus maenas*, introduced anadromous and warmwater gamefish, and introduced mammals.

The potential and observed roles of *Carcinus maenas*, first collected in California in 1989-1990 in the Estero Americano and in San Francisco Bay, have been addressed at length by Cohen et al. (1995) and by Grosholz & Ruiz (1995), the essence of whose findings have been quoted above. Cohen et al. (1995) noted that *Carcinus* consumes "an enormous variety of prey items," including organisms from five plant and protist phyla and 14 animal phyla. They predict that *Carcinus* will prey on many of the previously introduced species in San Francisco Bay—both epifaunal and infaunal taxa—with the clam *Potamocorbula* being a potential major prey item. *Carcinus*' habitat range includes marshes, rocky substrates and fouling communities, and the European and New England literature indicates broad and striking potential for this crab to become an important carnivore in these systems (Cohen et al., 1995). Grosholz & Ruiz (1995) report that *Carcinus* has already "significantly reduced densities" of the most abundant near-surface dwellers in Bodega Harbor, 75 km to the north of San Francisco. These taxa included the native bivalves *Transennella* spp., the cumacean *Cumella vulgaris* and the amphipod *Corophium* sp. In laboratory experiments, *Carcinus* captured and consumed Dungeness crab (*Cancer magister*) up to its own size.