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BIOLOGICAL STUDY

NONINDIGENOUS AQUATIC SPECIES IN A UNITED STATES ESTUARY:

A CASE STUDY OF THE BIOLOGICAL INVASIONS OF THE SAN FRANCISCO BAY AND DELTA

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EXECUTIVE SUMMARY

1. *The San Francisco Bay and Delta region is a highly invaded ecosystem.*

   - The San Francisco Estuary can now be recognized as the most invaded aquatic ecosystem in North America. Now recognized in the Estuary are 212 introduced species : 69 percent of these are invertebrates, 15 percent are fish and other vertebrates, 12 percent are vascular plants and 4 percent are protists.

   - In the period since 1850, the San Francisco Bay and Delta region has been invaded by an average of one new species every 36 weeks. Since 1970, the rate has been at least one new species every 24 weeks: the first collection records of over 50 non-native species in the Estuary since 1970 thus appear to reflect a significant new pulse of invasions.

   - In addition to the 212 recognized introductions, 123 species are considered as cryptogenic (not clearly native or introduced), and the total number of cryptogenic taxa in the Estuary might well be twice that. Thus simply reporting the documented introductions and assuming that all other species in a region are native—as virtually all previous studies have done—severely underestimates the impact of marine and aquatic invasions on a region's biota.

   - Nonindigenous aquatic animals and plants have had a profound impact on the ecology of this region. No shallow water habitat now remains uninvaded by exotic species and, in some regions, it is difficult to find any native species in abundance. In some regions of the Bay, 100% of the common species are introduced, creating "introduced communities." In locations ranging from freshwater sites in the Delta, through Suisun and San Pablo Bays and the shallower parts of the Central Bay to the South Bay, introduced species account for the majority of the species diversity.

2. *A vast amount of energy now passes through and is utilized by the nonindigenous biota of the Estuary. In the 1990s, introduced species dominate many of the Estuary's food webs.*

   - The major bloom-creating, dominant phytoplankton species are cryptogenic. Because of the poor state of taxonomic and biogeographic knowledge, it remains possible that many of the Estuary's major primary producers that provide the phytoplankton-derived energy for zooplankton and filter feeders, are in fact introduced.

   - Introduced species are abundant and dominant throughout the benthic and fouling communities of San Francisco Bay. These include 10 species of introduced bivalves, most of which are abundant to extremely abundant. Introduced filter-feeding polychaete worms and crustaceans may occur by the thousands per square meter. On sublittoral hard substrates, the Mediterranean mussel *Mytilus galloprovincialis* is abundant, while float fouling communities support large populations of introduced filter feeders, including bryozoans, sponges and seasquirts. The holistic role of the entire nonindigenous filter-feeding guild—including clams, mussels, bryozoans, barnacles, seasquirts, spionid worms, serpulid worms, 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 marsh mussel *Arcuatula demissa,* as a biogeochemical agent in the economy of Bay salt marshes is striking.

- Introduced clams are capable of filtering the entire volume of the South Bay and the northern estuarine regions (Suisun Bay) once a day: indeed, it now appears that the primary mechanism controlling phytoplankton biomass during summer and fall in South San Francisco Bay is "grazing" (filter feeding) by the introduced Japanese clams *Venerupis* and *Musculista* and the Atlantic clam *Gemma.* This remarkable process has a significant impact on the standing phytoplankton stock in the South Bay, and since this plankton is now utilized almost entirely by introduced filter feeders, passing the energy through a non-native benthic fraction of the biota may have fundamentally altered the energy available for native biota

- Drought year control of phytoplankton by introduced clams—resulting in the failure of the summer diatom bloom to appear in the northern reach of the Estuary—is a remarkable phenomenon. The introduced Atlantic soft-shell clams (*Mya*) alone were estimated to be capable at times of filtering all of the phytoplankton from the water column on the order of once per day. Phytoplankton blooms occurred only during higher flow years, when the populations of *Mya* and other introduced benthic filter feeders retreated downstream to saltier parts of the Estuary.

- Phytoplankton populations in the northern reaches of the Estuary may now be continuously and permanently controlled by introduced clams. Arriving by ballast water and first collected in the Estuary in 1986, by 1988 the Asian clam Potamocorbula reached and has since sustained average densities exceeding 2,000/m^2. Since the appearance of *Potamocorbula,* the summer diatom bloom has disappeared, presumably because of increased filter feeding by this new invasion. The *Potamocorbula* population in the northern reaches of the Estuary can filter the entire water column over the 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.

- Further, the Asian clam *Potamocorbula* feeds at multiple levels in the food chain, consuming bacterioplankton, phytoplankton, and zooplankton (copepods), and so may substantially reduce copepod populations both by depletion of the copepods' phytoplankton food source and by direct predation. In turn, under such conditions, the copepod-eating native opossum shrimp *Neomysis* may suffer a near-complete collapse in the northern reach. It was during one such pattern that mysid-eating juvenile striped bass suffered their lowest recorded abundance. This example and the linkages between introduced and native species may provide a direct and remarkable example of the potential impact of an introduced species on the Estuary's food webs.

- As with the guild of filter feeders, the overall picture of the impact of introduced surface-dwelling and shallow-burrowing grazers and deposit feeders in the Estuary is incompletely known. The Atlantic mudsnail *Ilyanassa* is likely playing a significant—if not the most important—role in altering the diversity, abundance, size distribution, and recruitment of many species on the intertidal mudflats of San Francisco Bay.

- The arrival and establishment in 1989-90 of the Atlantic green crab *Carcinus maenas* in San Francisco Bay signals a new level of trophic change and alteration. The green crab is a food and habitat generalist, capable of eating an extraordinarily wide variety of animals and plants, and capable of inhabiting marshes, rocky substrates, and fouling communities. European, South African, and recent Californian studies indicate a broad and striking potential for this crab to significantly alter the distribution, density, and abundance of prey species, and thus to profoundly alter community structure in the Bay.

- Nearly 30 species of introduced marine, brackish and freshwater fish are now important carnivores throughout the Bay and Delta. Eastern and central American fish -- carp, mosquitofish, catfish, green sunfish, bluegills, inland silverside, largemouth and smallmouth bass, and striped bass -- are among the most significant predators, competitors, and habitat disturbers throughout the brackish and freshwater reaches of the Delta, with often concomitant impacts on native fish communities. The introduced crayfish *Procambarus* and *Pacifastacus* may play an important role, when dense, in regulating their prey plant and animal populations.

- Native waterfowl in the Estuary consume some introduced aquatic plants (such as brass buttons) and native shorebirds feed extensively on introduced benthic invertebrates.

3. *Introduced species may be causing profound structural changes to some of the Estuary's habitats.*

   - The Atlantic salt-marsh cordgrass *Spartina alterniflora*, which has converted 100s of acres of mudflats in Willapa Bay, Washington, into grass islands, has become locally abundant in San Francisco Bay, and is competing with the native cordgrass. *Spartina alterniflora* has broad potential for ecosystem alteration. Its larger and more rigid stems, greater stem density, and higher root densities may decrease habitat for native wetland animals and infauna. Dense stands of *S. alterniflora* may cause changes in sediment dynamics, decreases in benthic algal production because of lower light levels below the cordgrass canopy, and loss of shorebird feeding habitat through colonization of mudflats.

   - The Australian-New Zealand boring isopod *Sphaeroma quoyanum* creates characteristic "*Sphaeroma* topography" on many Bay shores, with many linear meters of fringing mud banks riddled with its half-centimeter diameter holes. This isopod may arguably play a major, if not the chief, role in erosion of intertidal soft rock terraces along the shore of San Pablo Bay, due to their boring activity that weakens the rock and facilitates its removal by wave action. *Sphaeroma* has been burrowing into Bay shores for over a century, and it thus may be that in certain regions the land/water margin has retreated by a distance of at least several meters due to this isopod's boring activities.

4. *While no introduction in the Estuary has unambiguously caused the extinction of a native species, introductions have led to the complete habitat or regional extirpation of species, have contributed to the global extinction of a California freshwater fish, and are now strongly contributing to the further demise of endangered marsh birds and mammals.*

   - Introduced freshwater and anadromous fish have been directly implicated in the regional reduction and extinction, and the global extinction, of four native California fish. The bluegill, green sunfish, largemouth bass, striped bass, and black bass, through predation and through competition for food and breeding sites, have all been associated with the regional elimination of the native Sacramento perch from the Delta. The introduced inland silversides may be a significant predator on the larvae and eggs of the native Delta smelt. Expansion of the introduced smallmouth bass has been associated with the decline in the native hardhead. Predation by largemouth bass, smallmouth black bass and striped bass may have been a major factor in the global extinction of the thicktail chub in California.

   - The situation of the California clapper rail may serve as a model to assess how an endangered species may be affected by biological invasions. The rail suffers predation by introduced Norway rats and red fox; it may both feed on and be killed by introduced mussels; and it may find refuge in introduced cordgrass, although this same cordgrass may compete with native cordgrass, perhaps preferred by the rail. Other potential model study systems include introduced crayfish and their displacement of native crayfish; introduced gobies and their relationship to the tidewater goby; and the combined role that introduced green sunfish, bluegill, largemouth bass, and American bullfrog may have played in the dramatic decline of native red-legged and yellow-legged frogs.

5. *Though the economic impacts of introduced organisms in the San Francisco Estuary are substantial, they are poorly quantified.*

   - Although some of the fish intentionally introduced into the Estuary by government agencies supported substantial commercial food fisheries, these fisheries all declined after a time and are now closed. The signal crayfish, *Pacifastacus*, from Oregon, whose exact means of introduction is unclear, supports the Estuary's only remaining commercial food fishery based on an introduced species.

   - The striped bass sport fishery has resulted in a substantial transfer of funds from anglers to those who supply anglers' needs, variously estimated, between 1962 and 1992, between $7 million and $45 million per year. However, striped bass populations and the striped bass sport fishery have declined dramatically in recent years.

- Government introductions of organisms for sport fishing, as forage fish and for biocontrol have frequently not produced the intended benefits, and have sometimes had harmful "side effects," such as reducing the populations of economically important species.

- Few nonindigenous organisms that were introduced to the Estuary by other than government intent have produced economic benefits. The clams *Mya* and *Venerupis*, both accidentally introduced with oysters, have supported commercial harvesting in the Bay or elsewhere on the Pacific coast, and a small amount of recreational harvesting in the Bay (though these clams may have, to some extent, replaced edible native clams); the Asian clam *Corbicula* is commercially harvested for food and bait in California on a small scale; the Asian yellowfin goby is commercially harvested for bait; muskrat are trapped for furs; and the South African marsh plant brass buttons provides food for waterfowl. There do not appear to be any other significant economic benefits that derive from nongovernmental or accidental introductions to the Estuary.

- A single introduced organism, the shipworm *Teredo navalis*, caused $615 million (in 1992 dollars) of structural damage to maritime facilities in 3 years in the early part of the 20th century.

- The economic impacts of hull fouling and other ship fouling are clearly very large, but are not documented or quantified for the Estuary. Most of the fouling incurred in the Estuary is due to nonindigenous species. Indirect impacts due to the use of toxic anti-fouling coatings may also be substantial.

- Waterway fouling by introduced water hyacinth has become a problem in the Delta over the last fifteen years, with other introduced plants beginning to add to the problem in recent years. Hyacinth fouling has had significant economic impacts, including interference with navigation.

- Perhaps the greatest economic impacts may derive from the destabilizing of the Estuary's biota due to the introduction and establishment of an average of one new species every 24 weeks. This phenomenal rate of species additions has contributed to the failure of water users and regulatory agencies to manage the Estuary so as to sustain healthy populations of anadromous and native fish, resulting in increasing limitations and threats of limitations on water diversions, wastewater discharges, channel dredging, levee maintenance, construction and other economic activities in and near the Estuary, with implications for the whole of California's economy.

RESEARCH NEEDS

Much remains unknown in terms of the phenomena, patterns, and processes of invasions in the Bay and Delta, and thus large gaps remain in the knowledge needed to establish effective management plans. The following are examples of important research needs and directions:

1. *Experimental Ecology of Invasions*

Only a few of the hundreds of invaders in the Estuary have been the subject of quantitative experimental studies elucidating their roles in the Estuary's ecosystem and their impacts on native biota. Such studies should receive the highest priority.

2. *Regional Shipping Study*

Urgently required is a San Francisco Bay Shipping Study which both updates the 1991 data base available and expands that data base to all Bay and Delta ports. A biological and ecological study of the nature of ballast water biota arriving in the Bay/Delta system is urgently required. Equally pressing is a study of the fouling organisms entering the Estuary on ships' hulls and in ships' seachests, in order to assess whether this mechanism is now becoming of increasing importance and in order to more adequately define the unique role of ballast water. A Regional Shipping Study would provide critical data for management plans.

3. *Intraregional Human-Mediated Dispersal Vectors*

Studies are required on the mechanisms and the temporal and spatial scales of the distribution of introduced species by human vectors after they have become established. Such studies will be of particular value in light of any future introductions of nuisance aquatic pests.

4. *Study of the Baitworm and Lobster Shipping Industries*

This study has identified a major, unregulated vector for exotic species invasions in the Bay: the constant release of invertebrate-laden seaweeds from New England in association with bait worm (and lobster) importation. In addition a new trade in exotic bait has commenced, centered around the importation of living Vietnamese nereid worms, and both the worms and their substrate deserve detailed study. These studies are urgently needed to address the attendant precautionary management issues at hand.

5. *Molecular Genetic Studies of Invaders*

The application of modern molecular genetic techniques has already revealed the cryptic presence of previously unrecognized invaders in the Bay: the Atlantic clam *Macoma petalum,* the Mediterranean mussel *Mytilus galloprovincialis,* and the Japanese jellyfish *Aurelia "aurita."* Molecular genetic studies of the Bay's new green crab (*Carcinus*) population may be of critical value in resolving the crab's geographic origins and thus the mechanism that brought it to California. Molecular genetic studies of worms of the genus *Glycera* and *Nereis* in the Bay may clarify if New

England populations have or are becoming established in the region as a result of ongoing inoculations via the bait worm industry. Molecular analysis of other invasions will doubtless reveal, as with *Macoma* and *Mytilus*, a number of heretofore unrecognized species.

6. *Increased Utilization of Exotic Species*

Fishery, bait, and other utilization studies should be conducted on developing or enlarging the scope of fisheries for introduced bivalves (such as *Mya*, *Venerupis*, and *Corbicula*), edible aquatic plants, smaller edible fish (such as *Acanthogobius*), and crabs (*Carcinus* and *Eriocheir*).

7. *Potential Zebra Mussel Invasion*

Studies are needed on the potential distribution, abundance and impacts of zebra mussels (*Dreissena polymorpha* and/or *D. bugensis*) in California, to support efforts to control their introduction and to design facilities (such as water intakes and fish screens) that will continue to function adequately should the mussels become established.

8. *Economic Impacts of Wood Borers and Fouling Organisms*

The economic impacts of wood-boring organisms (shipworms and gribbles) and of fouling organisms (on commercial vessels, on recreational craft, in ports and marinas, and in water conduits) are clearly very large in the San Francisco Estuary, but remain largely undocumented and entirely unquantified. A modern economic study of this phenomenon, including the economic costs and ecological impacts of control measures now in place or forecast, is critically needed.

9. *Economic, Ecological and Geological Impacts of Bioeroding Nonindigenous Species*

Largely qualitative data suggest that the economic, ecological, and geological impacts of the guild of burrowing organisms that have been historically and newly introduced have been or are forecast to potentially be extensive in the Estuary. Experimental, quantitative studies on the impacts of burrowing and bioeroding crustaceans and muskrats in the Estuary are clearly now needed to assess the extent of changes that have occurred or are now occurring, and to form the basis for predicting future alterations in the absence of control measures.

10. *Post-Invasion Control Mechanisms*

While primary attention must be paid to preventing future invasions, studies should begin on examining the broad suite of potential post-invasion control mechanisms, including biocontrol, physical containment, eradication, and related strategies. A Regional Control Mechanisms Workshop for past and anticipated invasions could set the foundation for future research directions.

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TABLES AND FIGURES

ACKNOWLEDGMENTS

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CHAPTER 1. INTRODUCTION

Over the past four centuries thousands of species of fresh water, brackish water and salt water animals and plants have been introduced to the United States (Elton, 1958; Carlton, 1979a, 1989, 1992b; Moyle, 1986; Hickman, 1993; Carlton & Geller, 1993). In some regions, such as the Hawaiian Islands, aboriginal introductions date back more than two millennia (Mooney & Drake, 1986). The taxonomic, habitat and trophic range of this vast nonindigenous biota is impressive—ranging from exotic flatworms (*Rectocephala exotica*) in the lily ponds of Washington, D. C., to Mexican crabs (*Platychirograpsus spectabilis*) in Florida rivers, to aquatic rodents such as the South American nutria (*Myocaster coypu*) in the southern United States.

The human role in changing the face of North America, in terms of the abundance and diversity of the animals and plants of lakes, rivers, estuaries, marshes, and coastlines, has been demonstratively profound:

- Sea lampreys (*Petromyzon marinus*) invaded the Great Lakes, destroying extensive native fisheries; the Eurasian carp (*Cyprinus carpio*), released in New York in 1831, is now a national pest; Nevada's Ash Meadows killifish (*Empetrichthys merriami*) became extinct at the hands of introduced mosquitofish, mollies, crayfish, and bullfrogs; and scores of exotic fish species now dominate aquatic habitats from Florida to New York and from the Atlantic drainage to California.
- Asian clams (*Corbicula fluminea*) spread across all of North America in only 40 years, moving from west to east—from the Columbia River to California and then quickly across the southern United States to the Atlantic seaboard, a dramatic and startling invasion of this canal- and pipe-fouling clam (McMahon, 1982). Fifty years later, European zebra mussels (*Dreissena polymorpha* and *Dreissena bugensis*) are similarly spreading across North America—this time from east to west, from the Great Lakes to the Mississippi and into Oklahoma.
- Alien plants—including the spectacularly successful purple loosestrife (*Lythrum salicaria*), Eurasian watermilfoil (*Myriophyllum spicatum*) and water chestnut (*Trapa natans*)—are now the dominant, and at times the only, vegetation, for hundreds of square miles of aquatic and marsh habitats in North America.

Despite these many invasions, there are with rare exception no syntheses of the spatial and temporal patterns, mechanisms or impacts of these nonindigenous aquatic and estuarine organisms. For the great majority of invasions, records are scattered among thousands of scientific papers and buried in general monographs, student theses, government reports, consultant studies and anecdotal accounts. While a comprehensive review of freshwater and marine invasions would be extraordinarily useful, an initial approach to understanding the ecological and economic impacts of nonindigenous animals and plants in U. S. aquatic and marine environments may be attained through case studies: the assessment of the role of invasions in defined geographic regions, focusing on historical and modern-day dispersal pathways, on the biological, ecological and economic consequences of invasions, and on prospects for future invasions.

We present here such a regional study, focusing on one of the largest freshwater and estuarine ecosystems of the United States: the San Francisco Bay and Delta region, a region known to have sustained numerous invasions for over a century.

(A) PRIOR STATE OF KNOWLEDGE

At the time of our study there was no synthesis available of the diversity and impacts of the nonindigenous aquatic and estuarine species of the San Francisco Bay and Delta region, an area that extends from the inland port cities of the Central Valley to the coastal waters of the Pacific Ocean at the Golden Gate.

This region includes examples of most of the common aquatic habitats found throughout the warm and cool temperate climates of the United States and, as such, represents an ideal theater for assessing the diversity and range of effects of aquatic invasions. Within the Bay-Delta Region are fresh, brackish, and salt water marshes, sandflats and mudflats, rocky shores, benthic sublittoral habitats of a wide sediment range, eelgrass beds, emergent aquatic macrophyte communities, planktonic, nektonic, and neustonic communities, extensive fouling assemblages, and communities of burrowing and boring organisms in clays and wood. Also represented is a vast range of habitat disturbance regimes. Over a 140-year period of substantial human commercial and other activities—since about 1850—a minimum of more than 200 plants, protists and animals from the aquatic and coastal habitats of eastern North America, Europe, Asia, Australia, and South America have invaded these ecosystems.

Prior lists or descriptions of the introduced freshwater, anadromous and estuarine fish fauna in the San Francisco Bay-Delta region were provided by Moyle (1976b) and McGinnis (1984); of freshwater mollusks by Hanna (1966) and Taylor (1981); of marine mollusks by Nichols et al. (1986); and of introduced marine and estuarine invertebrates by Carlton (1975, 1979a,b), supplemented by Carlton et al. (1990). Silva (1979) and Josselyn & West (1985) noted some introductions of marine and brackish seaweeds, but no comprehensive assessment of possibly introduced seaweeds had been made. Atwater et al. (1979) provided a list of introduced vascular plants in San Francisco Bay salt marshes, but appear not to have distinguished between aquatic plants that are characteristically found within marshes and essentially terrestrial plants that are occasionally found at the edges of or within marshes. During our study the Bay-Delta Oversight Committee of the California Department of Water Resources produced a briefing paper summarizing some of the previously published information on introduced fish, wildlife and plants of the Bay-Delta region (BDOC, 1994), and Orsi (1995) published a list of introduced estuarine copepods and mysids.

No information had been compiled on possible introductions among freshwater invertebrates (including species of freshwater sponges, jellyfish, flatworms, oligochaete and polychaete worms, snails, clams, crustaceans, insects and bryozoans), freshwater macroalgae, or fresh, brackish or salt water phytoplankton. Protozoan introductions had been similarly neglected.

Based on the information available prior to our study, and on consideration of extant lists of aquatic or marine introductions in other regions (Leppäkoski, 1984; den Hartog, 1987; Mills et al., 1993, 1995; Jansson, 1994), we had estimated that the number of aquatic and estuarine introductions in the Bay-Delta system could exceed 150 invertebrate species, 20 fish species, 10 algal species, and 100 vascular plant species.

(B) CONTRIBUTIONS OF THE PRESENT STUDY

The present work is the first regional case study in the United States of the diversity and ecological and economic impacts of nonindigenous species in aquatic and estuarine habitats. Previous studies (Mills et al., 1993, for the Great Lakes; Mills et al., 1996, for the Hudson River) have largely concentrated on species check-lists with a minimal review of ecological or economic effects of the exotic biota. We intend the present study to be a comprehensive synthesis which may serve as a comparative model for other regional studies in U. S. waters.

The present study also sets forth detailed and clear criteria for determining which species are present and established within the study zone. Prior regional surveys of aquatic introductions have implied but rarely defined these criteria, a situation that impedes ready quantitative comparisons between regions. We include (Chapter 5) a supplemental list of vascular plant species based upon criteria which we judge to approximate the criteria in prior regional surveys of aquatic introductions in the USA, in order to facilitate such comparisons.

The present study is also the first regional survey of introductions to include a listing (although preliminary) of cryptogenic species—species which are neither demonstrably native or introduced (Chapter 4). As discussed by Carlton (1996a), the development of such lists is a necessary first step in correcting prior tendencies to profoundly underestimate the potential extent of biological invasions and in providing a more complete basis for understanding the sources, characteristics and frequency of success of biological invaders.

Both older (Elton, 1958) and newer (e. g. Mooney & Drake, 1986; Drake et al., 1989) reviews of biological invasions propose a number of theoretical models to explain the success of animal and plant invasions in regions where they did not evolve. However, for most such studies, comprehensive data sets on the diversity of invasions, temporal patterns of invasion, and ecological impacts have not been available by which to test the applicability or robustness of invasion theory. The present study provides an extensive review of an introduced biota exceeding 200 taxa in a defined geographic region, and thus provides a rare data set with which to test invasion models.

CHAPTER 2. METHODS

(A) DEFINITIONS

1. STUDY ZONE

The study zone for this report is defined as the estuarine and aquatic habitats that are within the normal range of tidal influence in San Francisco Bay, the Sacramento-San Joaquin Delta and tributaries, and referred to herein as the San Francisco Estuary or the Estuary (Fig. 1). The primary data set (Chapter 3 and Table 1) contains all demonstrably nonindigenous organisms that are characteristically found in estuarine or aquatic habitats (including marshes, mudflats, etc.), and for which there is significant evidence supporting their establishment within the study zone.

2. PRIMARY DATA SET: INTRODUCED SPECIES IN THE SAN FRANCISCO ESTUARY

Inclusion in the primary data set thus requires evidence demonstrating that the organism in question is (1) not native to the Estuary, and (2) currently established in the Estuary.

We define native organisms as those organisms present aboriginally, which for the Bay-Delta region means prior to 1769 when the first European explorers entered the area. The types of evidence that we utilized to determine the native versus introduced status of aquatic and estuarine organisms, as discussed by Carlton (1979a) and Chapman & Carlton (1991, 1994), include:

- global systematic evidence (involving taxonomic information from both morphology and molecular genetics) and biogeographic evidence, including the global distribution of closely related species;
- the existence of identifiable mechanisms of human-mediated transport;
- historical evidence of presence or absence;
- archaeological evidence of presence or absence;
- paleontological evidence of presence or absence;
- the extent to which distribution can be explained by natural dispersal mechanisms;
- rapid or sudden changes in abundance or distribution;
- highly restricted or anomalously disjunct distributions (in comparison to distributions of known native organisms);
- occurrence in assemblages with other known introduced species; and
- for parasites or commensals, occurrence on introduced organisms.

We define established organisms as those organisms present and reproducing "in the wild" whose numbers, distribution and persistence over time suggest that, barring unforeseen catastrophic events or successful eradication efforts, they will continue to be present in the future. "In the wild" implies reproduction and persistence of the population without direct human intervention or assistance (such

Figure 1. The San Francisco Estuary

as reproductive assistance via hatcheries or periodic renewal of the population through the importation of spat), but may include dependence on human-altered or created habitats, such as water bodies warmed by the cooling-water effluent from power plants, pilings, floating docks, and salt ponds or other manipulated, semi-enclosed lagoons. The types of evidence that we used to assess establishment include:

- population size;
- persistence of the population over time;
- distribution (broad or restricted) of the population, and trends in distribution;
- for species dependent on sexual reproduction, the presence of both males and females, and the presence of ovigerous females; and
- the age structure of the population as an indicator of successful reproduction.

3. OTHER DATA SETS

Beyond the primary data set, we considered and compiled information on several additional categories of organisms, including:

- cryptogenic organisms, that is, organisms in the Estuary that are neither demonstrably native nor introduced (Table 2);
- nonindigenous organisms that have been reported from or were intentionally introduced to the Estuary, but which did not become established or for which there is inadequate evidence regarding their establishment (Table 8 and Appendix 2);
- nonindigenous organisms which are established in aquatic environments tributary to or adjacent to the Estuary, and which may in the future extend their range into the Estuary (Table 9);
- nonindigenous organisms which are not characteristically found in estuarine or aquatic habitats but which have been occasionally reported from or may make occasional use of the Estuary (Appendix 1).

Probably the largest and most difficult "gray zone" between the primary data set and organisms in these additional categories involves those nonindigenous plants reported from coastal or freshwater wetlands for which specific information on occurrence within the tidal boundaries of the Estuary is not available. Although previous regional studies of aquatic invasions (Mills et al., 1993, 1995) have included many such gray-zone plants, we limited inclusion in our primary data set to those that both: (a) have habitat descriptions indicating that they are primarily marsh plants, and not primarily terrestrial or moist ground plants occasionally found in or near marshes; and (b) have been reported specifically from the Delta, and not just from the Central Valley or the Bay Area generally. Similar questions arose, though less commonly, with other types of organisms, to which we applied similar logic.

Those candidate organisms which are not listed in Table 1 because of criterion (a), are instead listed in Appendix 1. Adding the plants in Appendix 1 to the organisms in Table 1 would produce a list of nonindigenous organisms for the Estuary comparable those produced for the Great Lakes (Mills et al., 1993) and the Hudson River (Mills et al., 1995), as discussed further in Chapter 5. Candidate organisms which failed to meet criterion (b) are listed in Table 9. Even following these restrictive criteria, we may have included in Table 1 some plants that are found in the Delta region in marshes or diked ponds, but not in tidal waters.

(B) DATA SOURCES AND PRESENTATION

Initial lists of taxa in the above-described categories were compiled from the prior studies discussed in the introduction and from a review of the regional biological and systematic literature including regional monographic studies, keys, field guides and checklists; from published (mainly in the gray literature) and unpublished species lists generated by public agencies and private consultants; and from discussions with taxonomists, field biologists, refuge managers and consultants familiar with the region.

Further information on the species thus identified was developed through a review of the pertinent current and historical biological literature, museum records and specimen collections, and interviews with biologists. We also undertook limited field work in order to check the presence or distribution of certain species, and to check for the presence of previously unreported species in some rarely sampled habitats. This information was used to develop the following species lists:

- Table 1, listing introduced species in the Estuary;
- Table 2, listing cryptogenic species in the Estuary;
- Table 8, listing species recently recorded from the Estuary but whose establishment is uncertain;
- Table 9 and Appendix 3, listing introduced species in adjacent aquatic habitats;
- Appendix 1, listing terrestrial species that may occasionally be found in the Estuary;
- Appendix 2, listing older inoculations of nonindigenous species that did not become established; and
- Appendix 4, listing introduced species in the northeastern Pacific known only from the Estuary.

For each species listed in Table 1 we determined where possible:

- the date of first collection or observation or planting in the Estuary, in California and in northeastern Pacific waters or coastal states or provinces; and where this was unavailable, the date of the first written account of the organism in the area;
- the native range of the species;
- the immediate geographic source of the introduction;
- the transport mechanism;
- the organism's current taxonomic status, most frequently utilized synonyms, and common names; and
- its current spatial distribution and abundance in the Estuary.

We included common names from Turgeon et al. (1988) and Carlton (1992) for mollusks, Cairns et al. (1991) for coelenterates, Williams et al. (1989) for decapods, Gosner (1978) for other invertebrates, Robins et al. (1991) for fish and Hickman (1983) for higher plants.

The data are presented in the species descriptions in Chapter 3 and summarized (in large part) in Table 1. Some of these data are also provided for the species listed in Tables 8 and 9 and the appendices. We also reviewed the available information on the ecological roles and economic impacts of individual introduced species and of introduced species assemblages. This information is summarized in the species descriptions in Chapter 3 and discussed in Chapter 6.

(C) ANALYSIS

The primary data set in Chapter 3 and Table 1 was quantitatively analyzed with regard to taxonomic groups, native regions, timing and transport mechanisms. The results are presented in Chapter 5.

1. TAXONOMY

The numbers of species per taxonomic group were tabulated at two levels of aggregation. A first tabulation was done at the taxonomic levels of order (for vertebrates), phylum (for invertebrates), subkingdom (for plants) and kingdom (for protozoans). A second, more highly-aggregated, tabulation was done at the levels of class (vertebrates), a traditional, non-phyletic grouping (invertebrates), and kingdom (plants and protozoans).

2. NATIVE REGION

The numbers of species per native region were tabulated with regard to eleven marine regions and five continental regions. The marine regions consist of the eastern and western portions of the North and South Atlantic oceans and the North and South Pacific oceans, the Indian Ocean, the Mediterranean Sea, and the Black and Caspian Seas. The Western South Pacific region consists primarily of waters around Australia and New Zealand. The five continental regions consist of North America, South America, Eurasia, Africa, and Australia/New Zealand. Where an organism's native range included more than one region, that organism's count was split proportionally.

3. TIMING

We analyzed the timing of introductions in terms of both the date of first record in the Estuary, and the date of first record in the northeastern Pacific. The numbers of species were tabulated in four 30-year periods with the first beginning in 1850 and the last ending in 1969, and one 26-year period (1970-1995). In the few cases where an organism's date of first record was a period that spanned parts of two tabulation periods, that organism's count was proportionally divided between the periods.

We distinguished two different types of dates of first record. The first and preferred type is the date of initial planting or first observation or collection of the species in the area. Where this was unavailable, we reported the earliest date available (date of writing, submission or publication) of the first written account of the species in the area. In Table 1, dates of first written account are preceded by the symbol '≤', meaning that the date of first planting, observation or collection was on or before (in some cases, perhaps a considerable time before) the indicated date. Dates of first written account were excluded from the quantitative analysis.

We also excluded from the analysis those dates of first record that we judged to be a clear artifact of collecting bias, or a fortuitous discovery of a species in a restricted habitat or locality, and whose inclusion would have contributed to a misleading picture of the temporal pattern of invasions in the Estuary. This is discussed further in Chapter 5 under "Results." These dates are marked by asterisks (*) in Table 1.

4. TRANSPORT MECHANISMS

We analyzed the stocks of organisms that have been introduced to the Estuary in terms of the transport mechanisms (also called "transport vectors," "means of introduction" and "dispersal mechanisms") that brought them to the northeastern Pacific. We utilized thirteen categories of mechanisms, as defined in Table 1 and discussed in Chapter 5 under "Results." Where multiple possible transport mechanisms were determined for an organism, that organism's count was divided proportionally among the possible mechanisms.

CHAPTER 3. INTRODUCED SPECIES IN THE ESTUARY

PLANTS

SEAWEEDS

Chlorophyta

Bryopsis sp. [CODIALES]

Silva (1979) reported an unidentified species of *Bryopsis* which only reproduces asexually in the Bay and which he described as exhibiting weedy behavior: developing explosively and frequently being cast ashore in large quantities, creating a nuisance as it decomposes. It has been observed in the Bay since at least 1951, from Alameda to Richmond on the East Bay shore and at Coyote Point. Bryopsis occurs in ship fouling (pers. obs.) and, in concert with the other introduced seaweeds, we tentatively suggest ship fouling as the mechanism of introduction.

Codium fragile tomentosoides (Suringar, 1867) Hariot, 1889 [CODIALES]

DEAD MAN'S FINGERS, SPUTNIK WEED, OYSTER THIEF

Codium fragile is native to the northern Pacific, and is found in North America on exposed coasts from Alaska to Baja California (Abbot & Hollenberg, 1976). The weedy subspecies *C. f. tomentosoides* is native to Japan (where it is eaten) and was introduced to Europe in the nineteenth century and to New York, probably as ship fouling, around 1956, subsequently spreading north to Maine and south to North Carolina (Carlton & Scanlon, 1985; includes discussion of coastal transport mechanisms). It was first collected in San Francisco Bay in 1977, probably introduced as ship fouling (Carlton et al., 1990), and as of 1985 not reported from any other site in the northeastern Pacific (Carlton & Scanlon, 1985).

In San Francisco Bay *C. f. tomentosoides* is common intertidally and subtidally attached to rocks, seawalls, piers and floating docks. Josselyn & West (1985) report it as common (found 60-100% of the time) at Coyote Point, and frequent (30-60%) at Redwood City, Palo Alto. In 1993-94 we found it on floating docks in the East Bay from Richmond to San Leandro and at Pier 39 in San Francisco.

Phaeophyta

Sargassum muticum (Yendo, 1907) Fensholt, 1955 [FUCALES]

Sargassum muticum is a Japanese species which was first collected in North

America in 1944 in British Columbia, apparently introduced in shipments of Japanese oyster spat (*Crassostrea gigas*), and subsequently spread both north and south into protected waters. It was reported from Coos Bay in 1947, Crescent City in 1963 and Santa Catalina Island in 1970, and is now found at scattered sites from Alaska to Baja California (Abbott & Hollenberg, 1976; Silva, 1979). It was introduced to Europe in the early 1970s, apparently also in shipments of Japanese oyster spat (Druehl, 1973; Critchley, 1983; Danek, 1984).

S. muticum was first observed in San Francisco Bay by Silva on the riprap at the entrance to the Berkeley Marina in 1973. It has been reported on the pilings of the Golden Gate Bridge, in the San Francisco Yacht Harbor, on the inside breakwater at Fort Baker, at Angel Island, Sausalito and the Tiburon Peninsula, on the east side of Yerba Buena Island, at Crown Beach in Alameda, and from Albany and Richmond (Silva, 1979; Danek, 1984). Josselyn & West (1985) found it commonly (60-100% of the time) at Tiburon Peninsula and infrequently (5-30%) at Twin Sisters.

In San Francisco Bay *S. muticum* appears to be restricted to low intertidal areas with hard substrate and moderate to high salinity. Germlings grow at salinities down to 10 ppt (to 20 ppt according to Norton (1977)), but maximum survival is at 25-30 ppt salinity. Low salinities and storms eliminated the Tiburon population in the winter and spring of 1983 (Danek, 1984). *S. muticum* was more abundant at Crown Beach, Alameda during the drought years of 1990-91 than it is at present (pers. obs.).

Both lateral branches and fertile fronds of *S. muticum* break off regularly and float and disperse by currents and wind drift, surviving afloat for up to 3 months, and can initiate new populations (Danek, 1984). Danek (1984) reports that "in Britain *S. muticum* has become the dominant species at low tide levels, and is a successful competitor against indigenous species such as *Cystoseira* and *Laminaria*...it forms large floating mats (Fletcher & Fletcher, 1975) causing problems for fishermen and small boat navigation." An eradication program in England was "largely unsuccessful" (Silva, 1979). In Canada, Druehl (1973) considers it to be replacing populations of *Zostera* in some places, and Dudley & Collins (1995) report that it has become a dominant intertidal species in the Channel Islands and Santa Barbara area. However, Silva (1979) states that "there is no evidence that *S. muticum* is displacing the native biota of San Francisco Bay."

<u>Rhodophyta</u>

Callithamnion byssoides Arnott [CERAMIALES]

Callithamnion byssoides is native to the northwestern Atlantic from Nova Scotia to Florida (Taylor, 1957). It was not listed in Silva's (1979) review of Central Bay benthic algae, but Josselyn & West (1985) found it attached to rocks "near MLLW throughout the northern and southern reaches of the bay" in collections between 1978 and 1983. They report it as frequent (found 30-60% of the time) at Redwood City, Palo Alto and China Camp, and infrequent (5-30%) at Tiburon Peninsula, Point

Pinole and Crockett. *Callithamnion* species are common fouling species (WHOI, 1952). *C. byssoides* may have been transported to San Francisco Bay as ship fouling, or possibly with the algae used to pack New England bait worms or lobster.

Polysiphonia denudata (Dillwyn) Kützing [CERAMIALES]

Polysiphonia denudata is native to the Atlantic coast from Prince Edward Island to Florida and the tropics, commonly occurring in tide pools and in shallow bays attached to rocks, shells and wharves (Taylor, 1957). It was not listed by Silva (1979) in his review of Central Bay benthic algae, but Josselyn & West (1985) reported it as a "common drift algae during summer months, especially in South San Francisco Bay" (citing Cloern, pers. comm.), and as drift or epiphytic in both San Pablo Bay and South Bay in collections between 1978 and 1983. They further suggest that "the extensive decaying mats observed by Nichols (1979) in Palo Alto during the summer of 1975" may have been *P. denudata*. We (JTC) observed a sometimes abundant *Polysiphonia*, which we presume to have been *P. denudata*, in Lake Merritt, Oakland in 1963-64.

Polysiphonia species are common fouling species or artificial structures, including ships (WHOI, 1952; Fletcher et al., 1984), and a species of *Polysiphonia* was the organism most tolerant of copper- and mercury-based anti-fouling compounds in tests in Florida (Weiss, 1947), suggesting that *P. denudata* probably arrived in San Francisco Bay as hull fouling, although introduction by ballast water is possible. Josselyn & West (1985) reported *P. denudata* as frequent (30-60% of the time) at Point Pinole, and infrequent (5-30%) at stations on the western shore of the South Bay, on the Marin shore, and at Crockett. It apparently reproduces asexually in San Francisco Bay, and is not reported from other Pacific coast estuaries (M. Josselyn, pers. comm., 1985).

VASCULAR PLANTS

Dicotyledones

Chenopodium macrospermum J. D. Hooker var. *halophilum* (Philippi) Standley [CHENOPODIACEAE]

SYNONYMS: *Chenopodium macrospermum* J. D. Hooker var. *farinosum* (Watson) Howell

Probably native to South America, this plant is found in wet places and marshes at low elevations between Orange County and Washington state, including the coastal California (Munz, 1959) the San Francisco Bay Area and the Delta (Hickman, 1993).

Cotula coronopifolia Linnaeus, 1753 [ASTERACEAE]

BRASS BUTTONS

Brass buttons is a native of South Africa that has become established along the Pacific coast from California to British Columbia, and is reported as adventive in New England (Peck, 1941; Muenscher, 1944; Steward et al., 1963). In 1878, Lockington (1878) reported it as an introduced plant common in wet places on the San Francisco peninsula. As it was likely to have spread to the Bay's littoral zone by around that time, we have taken 1878 as the date of first observation in the Estuary. It was probably introduced in ships' ballast (as suggested by Spicher & Josselyn, 1985).

In California brass buttons has variously been reported as common in salt and freshwater marshes along the coast (Robbins et al., 1941; Mason, 1957; Munz 1959; Hickman, 1993), as present in San Francisco Bay saltmarshes (Jepson, 1951), as common in wet places near high-tide levels in the tidal marshes around Suisun Bay (Atwater et al., 1979), and as uncommon in the Delta (Madrone Assoc., 1980; Herbold & Moyle, 1989). A 1981 aerial survey of Suisun Marsh classified 3,800 acres, or 5% of the area surveyed, as *Cotula* habitat (Wernette, 1986), and in 1989 it was found at 18 of 48 sites. Along with alkali bulrush, saltgrass or fat hen, brass buttons comprised the principal vegetation at two sites in each of 1987, 1988 and 1989 (Herrgesell, 1990). Waterfowl frequently graze on brass button seeds, and the diked, brackish marshes around Suisun Bay are managed in part to promote its growth (Josselyn, 1983).

Lepidium latifolium Linnaeus [BRASSICACEAE]

BROADLEAF PEPPERGRASS, PERENNIAL PEPPERWEED, TALL WHITETOP

Broadleaf peppergrass is a native of Eurasia, where it is reported from Norway to North Africa and east to the Himalayan region. It has been introduced to many parts of the United States, Mexico and Australia, and is found on beaches, tidal shores, saline soils and roadsides throughout most of California (Hickman, 1993; Young & Turner, 1995; May, 1995). Suggested mechanisms of transport to North America along the New England coast prior to 1924 include transport in gluestock (animal bones) shipped from Europe, the seeds adhering to scraps of tissue or burlap sacking (Morse, 1924, cited in May, 1995); with material shipped to a dye and licorice works (Eames, 1935, cited in May, 1995); and clinging to the wool of sheep (Rollins, 1993, cited in May, 1995).

Broadleaf peppergrass was discovered in Montana in 1935, and in California near Oakdale, Stanislaus County in 1936, possibly having been transported with beet seed (May, 1995). By 1941 it was reported from San Joaquin and Yolo counties on the edge of the Delta (Robbins et al., 1941). Herbarium specimens exist from Grizzly Island (collected in 1960), Antioch Dunes (1977) and the Bay shoreline at Martinez and Point Pinole (1978). It was reported as common in the tidal marshes of the San Francisco

Estuary (Atwater et al., 1979), and uncommon in the Delta (Madrone Assoc., 1980; Herbold & Moyle, 1989). Recently it has been reported as invasive and spreading in shallow ponds and adjacent moist uplands in the Central Valley wildlife refuges, and in high tidal marsh areas and diked seasonal wetlands in Suisun Marsh (where hundreds of acres on Grizzly Island are affected) and throughout the Bay (Trumbo, 1994; Dudley & Collins, 1995; Malamud-Roam, pers. comm., 1994; May, 1995).

Broadleaf peppergrass produces large amounts of seed, can reproduce asexually by spread of rhizome sections, and is tolerant of a broad range of environmental conditions (Trumbo, 1994; May, 1995). It often becomes established on disturbed, bare soils, and was also observed in pickleweed (*Salicornia*) plains and among *Scirpus* spp. (May, 1995). May (1995) reports that it may be intolerant of frequent or prolonged flooding, and our observations suggest that it is limited to the upper edge, or often above the upper edge, of tidal inundation.

Trumbo (1994) suggests that at Suisun Marsh peppergrass first got established in agricultural areas, then as farms closed during the 1950s expanded rapidly "unchecked by frequent cultivations and crop competition" and invaded wildlife areas of the marsh. He claims that it competes with pickleweed, thereby reducing habitat for the endangered saltmarsh harvest mouse, and that its dense growth is unsuitable for use as nesting cover by waterfowl, although May (1995) reports that waterfowl nests have been observed in monotypic stands of peppergrass. BDOC (1994) states that it may outcompete and displace certain rare native marsh plants, such as *Lilaeopsis masoni* and *Cordylanthus mollis mollis*. CDFG has tested burning, discing and herbicide treatments as control measures for pepper grass, which is ranked as a "B"-level plant pest by the California Department of Food and Agriculture (BDOC, 1994).

Limosella subulata Ives, 1817 [SCROPHULARIACEAE]

AWL-LEAVED MUDWORT

Limosella subulata is native to Europe or the east coast of North America, and found in southern British Columbia and in fifteen western states. It is reported from muddy and sandy intertidal flats in the Delta (Muenscher, 1944; Munz, 1959; Atwater et al., 1979; Herbold & Moyle, 1989; Hickman, 1993).

Lythrum salicaria Linnaeus [LYTHRACEAE]

PURPLE LOOSESTRIFE

Native to Europe, purple loosestrife is invasive worldwide. It was introduced to North America by the early 1880s, either as seeds in solid ballast or in the wool of sheep, or as a cultivated plant. It can grow in monospecific stands, competes with