

The twenty-eight species of introduced anadromous, freshwater or euryhaline fish in the estuary include many important carnivores now found throughout the upper estuary. In particular, carp, mosquitofish, catfish, green sunfish, bluegill, inland silverside, largemouth and smallmouth bass, and striped bass have been found to be among the most significant predators throughout the brackish and freshwater reaches of the Delta. Of particular concern is the extent to which these introduced fish have reduced populations or contributed to the local or global extinction of native California fish. Evidence for interference, reduction, and destruction of spawning and nursery sites of native species, and the extirpation of native fish from feeding grounds, has been found for introduced carp, catfish, green sunfish and bluegill.

3. SPATIAL PATTERNS OF COMPETITION

Little is known of pre-1850 Bay and Delta ecosystems by which to determine the diversity and density of the aboriginal aquatic biota, and thus assessments of whether introduced species replaced or displaced abundant native organisms are severely constrained. Stimpson (1857) implied (though he may have been speaking of echinoderms only) that the invertebrate fauna of the Bay was depauperate in both species and numbers of individuals, although it is possible that even by Stimpson's time the virtual elimination of a top level predator (the aboriginal Indian population) in the Bay Area had led to a top-down cascade of faunal changes; or that the elimination of a keystone species controlling habitat structure in the watershed (beaver), acting through effects on anadromous fish populations, could have similarly initiated a cascade effect (McEvoy, 1986). Nevertheless, despite the limitations on our knowledge of the Estuary's native fauna, it is clear that in certain habitats there were no native species in some taxonomic groups and trophic guilds.

Table 5 shows the patterns of spatial relationship between native and introduced invertebrates along the marine to freshwater gradient in the Estuary. These patterns suggest that at least for some invading species, resources were available that were not being comparably utilized by native taxa, perhaps facilitating the initial invasion and establishment of the exotic species. (The terms "open niche," "empty niche" or "vacant niche," sometimes applied to such situations, are misnomers. A "niche" refers to the living conditions of an existing species, not to imaginary ecologic space, open or otherwise; see Herbold & Moyle, 1986.)

The most common spatial pattern of invasion in the Estuary is for introduced species to occupy regions partially or wholly upstream of their apparent native counterpart species. These introduced and native counterparts may compete where their ranges in the Estuary overlap, but in many cases in at least part of its range, the introduced species is free from such competition. An example is the introduced Atlantic crab *Rhithropanopeus harrisi* which exists in the upper Bay and Delta at salinities below the 3 ppt tolerance limit of the native crab *Hemigrapsus oregonensis*. In turn, however, *Hemigrapsus*, through predation and possibly through competitive interactions, may limit *Rhithropanopeus*' downstream expansion (Jordan, 1989).

Table 5. Patterns of Invasion Along the Salinity Gradient in the San Francisco Estuary and the Adjoining Coast

Native species are listed in normal type. Invading species are listed in bold type.

Marine	Mesohaline	Oligohaline	Fresh
PATTERN: UPSTREAM INVADERS			
<u>Microcionid Sponges:</u>			
<i>Microciona microjoanna</i>	<i>Microciona prolifera</i>	None	None
<u>Halichondriid Sponges:</u>			
<i>Halichondria panicea</i>	<i>Halichondria bowerbanki</i>	None	None
<u>Acontiate Anemones:</u>			
<i>Metridium senile</i>	<i>Metridium senile?</i> <i>Diadumene franciscana</i> <i>Diadumene ?cincta</i> <i>Diadumene leucolena</i> <i>Diadumene lineata</i>	None	None
<u>Tubeworms (Serpulid Polychaetes):</u>			
<i>Serpula "vermicularis"</i>	<i>Ficopomatus enigmaticus</i>	<i>Ficopomatus enigmaticus</i>	None
<u>Flattened, Nestling Slipper Shells:</u>			
<i>Crepidula nuximaria</i> ^a <i>Crepidula perforans</i> ^a	<i>Crepidula plana</i>	None	None
<u>Convex Slipper Shells</u>			
<i>Crepidula adunca</i>	<i>Crepidula convexa</i>	None	None
<u>Muricid Snails:</u>			
<i>Ocenebra circumtexta</i> <i>Ocenebra lurida</i>	<i>Urosalpinx cinerea</i>	None	None
<u>Mussels in the Genus Mytilus:</u>			
<i>Mytilus californianus</i>	<i>Mytilus trossulus</i> <i>Mytilus galloprovincialis</i>	None	None
<u>Gem Clams:</u>			
<i>Transennella confusa</i> <i>Transennella tantilla</i>	<i>Transennella tantilla?</i> <i>Gemma gemma</i>	None	None
<u>Littleneck Clams:</u>			
<i>Protothaca staminea</i>	<i>Protothaca staminea</i> <i>Venerupis philippinarum</i>	None	None

Table 5. Patterns of Invasion Along the Salinity Gradient - continued

Marine	Mesohaline	Oligohaline	Fresh
<u>Macoma Clams:</u>			
<i>Macoma secta</i>	<i>Macoma nasuta</i>	<i>Macoma petalum</i>	None
<i>Macoma inquinata</i>	<i>Macoma petalum</i>		
<i>Macoma nasuta</i>			
<u>Shipworms:</u>			
<i>Bankia setacea</i>	<i>Teredo navalis</i>	None	None
<i>Lyrodus pedicellatus</i>			
<i>Teredo navalis</i>			
<u>Barnacles:</u>			
<i>Balanus crenatus</i>	<i>Balanus glandula</i>	<i>Balanus improvisus</i>	<i>Balanus improvisus</i> ^b
<i>Balanus glandula</i>	<i>Balanus improvisus</i>		
<u>Cirolanid Isopods:</u>			
<i>Cirolana harfordi</i>	<i>Eurylana arcuata</i>	None	None
<u>Hydroid-eating Idoteid Isopods:</u>			
<i>Synidotea bicuspidata</i>	<i>Synidotea</i>	None	None
<i>Synidotea ritteri</i>	<i>laevidorsalis</i>		
<u>Tanaids:</u>			
<i>Leptochelia dubia</i> ^c	<i>Sinelobus</i> sp.		
<u>Mud Crabs:</u>			
<i>Hemigrapsus nudus</i>	<i>Hemigrapsus</i>	<i>Rhithropanopeus</i>	<i>Rhithropanopeus</i> ^b
<i>Hemigrapsus oregonensis</i>	<i>oregonensis</i>	<i>harristi</i>	<i>harrisii</i>
<u>Entoprocts:</u>			
<i>Barentsia gracilis</i>	<i>Barentsia benedini</i>	None	<i>Umatella gracilis</i>
<u>Arborescent Bryozoans in the Genus Bugula:</u>			
<i>Bugula californica</i>	<i>Bugula neritina</i>	None	None
<i>Bugula pacifica</i>	<i>Bugula stolonifera</i>		
<i>Bugula neritina</i>			
<u>Phlebobranch Sea Squirts:</u>			
<i>Ascidia ceratodes</i>	<i>Ascidia</i> sp.	None	None
<i>Corella</i> sp.	<i>Ciona intestinalis</i>		
<i>Chelyosoma productum</i>	<i>Ciona savignyi</i>		
<u>Simple Stolidobranch Sea Squirts:</u>			
<i>Styela truncata</i>	<i>Styela montereyensis</i>	<i>Molgula manhattensis</i>	None
<i>Styela montereyensis</i>	<i>Styela clava</i>		
<i>Pyura haustor</i>	<i>Molgula manhattensis</i>		

Table 5. Patterns of Invasion Along the Salinity Gradient - continued

Marine	Mesohaline	Oligohaline	Fresh
<u>Gobies</u>			
<i>Clevelandia ios</i>	<i>Clevelandia ios</i>	<i>Eucyclogobius newberryi</i> ^d	<i>Tridentiger bifasciatus</i>
<i>Coryphopterus nicholsii</i>	<i>Eucyclogobius newberryi</i> ^d	<i>Lepidogobius lepidus</i>	<i>Acanthogobius flavimanus</i>
	<i>Lepidogobius lepidus</i>	<i>Tridentiger bifasciatus</i>	
	<i>Tridentiger trigonocephalus</i>	<i>Acanthogobius flavimanus</i>	
	<i>Gillichthys mirabilis</i>		
	<i>Acanthogobius flavimanus</i>		
.....			
PATTERN: INSERTION INVADERS			
<u>Pileworms (Nereid Polychaetes):</u>			
<i>Nereis vexillosa</i>	<i>Nereis succinea</i>	<i>Nereis succinea</i>	<i>Hediste limnicola</i>
.....			
PATTERN: DOWNSTREAM INVADERS			
<u>Tube-dwelling Corophium Amphipods:</u>			
None	<i>Corophium acherusicum</i>	<i>Corophium spinicorne</i>	<i>Corophium spinicorne</i>
	<i>Corophium alienense</i>	<i>Corophium stimpsoni</i>	<i>Corophium stimpsoni</i>
	<i>Corophium insidiosum</i>	<i>Corophium acherusicum</i>	
	<i>Corophium heteroceratum</i>	<i>Corophium alienense</i>	
.....			
OTHER PATTERNS OF INVASION			
<u>Palaemonid Shrimp:</u>			
None	<i>Palaemon macrodactylus</i>	<i>Palaemon macrodactylus</i>	None
<u>Intertidal Mudsnailed:</u>			
None	<i>Cerithidea californica</i> ^e	None	None
	<i>Ilyanassa obsoleta</i> ^e		
<u>Intertidal Marsh Snails:</u>			
None	<i>Assiminea californica</i> ^f	<i>Assiminea californica</i> ^f	None
	<i>Ovatella myosotis</i> ^f	<i>Ovatella myosotis</i> ^f	

Table 5. Patterns of Invasion Along the Salinity Gradient - continued

Marine	Mesohaline	Oligohaline	Fresh
NO INVADERS (WITH POTENTIAL FOR INSERTION INVADERS)			
<u>Gnorimosphaeromid Isopods:</u>			
<i>Gnorimosphaeroma oregonense</i>	<i>Gnorimosphaeroma oregonense</i>	None ♂	<i>Gnorimosphaeroma insulare</i>
<u>Anisogammarid Amphipods:</u>			
<i>Anisogammarus confervicolus</i>	<i>Anisogammarus confervicolus</i>	None	<i>Anisogammarus ramellus</i>

- a *Crepidula nummaria* and *perforans* may not be separate species.
- b Regularly present but not reproducing.
- c Cryptogenic.
- d Formerly present, now extinct from the Estuary.
- e Race (1982) demonstrated that competitive and other interactions sort these snails along a salinity/elevation gradient by mid-summer
- f Berman & Carlton (1991) found little competitive interaction between these snails in Oregon marshes.
- g The introduced Japanese estuarine isopod, *Gnorimosphaeroma rayi*, is reported from Tomales Bay (north of San Francisco), but is not yet known from San Francisco Bay.

Other notable "upstream invaders" include the Atlantic barnacle *Balanus improvisus*, the most freshwater-tolerant barnacle in the world, whose range in the Estuary extends far upstream of the Bay's native barnacles; two Japanese gobies, *Acanthogobius flavimanus* and *Tridentiger bifasciatus*, which have become abundant in the upper Bay and Delta upstream of the native estuarine gobies, and have been transported south from the Delta in freshwater irrigation canals; the Australian serpulid worm *Ficopomatus enigmaticus*, the only tubeworm found in the brackish parts of the Bay and extending into quite low salinity water; and the shipworm *Teredo navalis*, which when it was introduced in the 1910s invaded upstream portions of the Estuary not previously entered by the Bay's existing native and exotic shipworms, and caused enormous damage to wooden maritime structures. In some cases, such as that of the freshwater entoproct *Urnatella gracilis*, the introduced species may live in such low salinity water that it never overlaps in range with its closest native, and more marine, counterparts.

A second spatial pattern, rarer and perhaps more difficult for an exotic species to successfully achieve, is that of an "insertion invader." An example was described by Oglesby (1965), who pointed out that among nereid worms the introduced brackish water worm *Nereis succinea* occupies a geographic position in the estuary between the range of the native marine worm *Nereis vexillosa* and the range of the native freshwater worm *Hediste limnicola*. He argued that *succinea*, being more finely and narrowly adapted to the brackish water ecotone, may outcompete the

more broadly adapted *vexillosa* and *limnicola* within this zone.

A third spatial pattern in the Estuary, uncommon and somewhat unexpected, is the "downstream invader" mode exhibited by the introduced amphipods in the tube-building genus *Corophium*. John Chapman has suggested that the native *Corophium* species may have been adapted to a specific flow and sedimentation regime, and that the dramatic human alteration of these parameters (due to hydraulic mining, soil-eroding agricultural practices, construction and roadbuilding, and the leveeing of channels on the one hand, and dam construction and water diversions on the other) that has occurred since the mid-19th century may have facilitated the invasion of the Estuary by at least three species of more marine-adapted *Corophium*.

Other spatial patterns of native-invader competition are also represented in the Estuary:

- In the case of the brackish-water, fouling-inhabiting Korean shrimp *Palaemon macrodactylus*, there are no apparent native counterparts, upstream or downstream, and thus no obvious competitors.
- The native marsh snail *Assiminea californica* and the Atlantic marsh snail *Ovatella myosotis*, occur in the same marsh areas and appear to be counterparts, but studies in Oregon on these two snails found little evidence of any competitive interactions between them (Berman & Carlton, 1991; while in the Estuary these snails apparently co-occur over their whole elevational range, in Oregon they co-occur only in the lower part of *Ovatella*'s elevational range).
- The introduced Atlantic snail *Ilyanassa obsoleta* now occupies the Bay mudflat areas formerly occupied by the native snail *Cerithidea californica*. Each spring the two populations of these snails collide, and by mid-summer the exotic *Ilyanassa* restricts the native *Cerithidea* to high-marsh salt pannes (an environment too high in salinity for *Ilyanassa* and thus providing a habitat refuge for *Cerithidea*) through egg-string predation and direct competitive interference (Race, 1982).

Along with competition, other interactions between native and introduced species may also occur, potentially leading to changes in community or habitat structure, or to the replacement, displacement or local elimination of the native taxa. Examples are reviewed in the sections below.

4. COMPETITIVE INTERACTIONS AND HABITAT ALTERATIONS

At the end of the 20th century, exotic species play a major role in structuring or altering aquatic environments.

We have considered above the evidence for dramatic alterations in the food webs and energy flow in the San Francisco Bay and Delta ecosystem due to individual species and species guilds. With such evidence in hand, it is easy to overlook the fact that for many abundant species in the Bay and Delta, little or nothing is known about their ecological roles—trophic or otherwise—in the

ecosystem. For such common introduced species as the marsh plants brass buttons (*Cotula coronopifolia*) and peppergrass (*Lepidium latifolium*), many of the freshwater fish, the mat-forming mussel *Musculista*, the bed-forming mussel *Mytilus galloprovincialis*, the soft-shell clam *Mya*, the littleneck clam *Venerupis*, and many of the introduced polychaetes, crustaceans, hydroids, sea anemones, tunicates and bryozoans, little or nothing is known of their competitive and potentially regulatory interactions with native species and with each other.

Certain observations and experimental data are available, however, both in the Bay and elsewhere, to gain some insight into the additional extensive community-level modifications that have taken or may be taking place through competitive and other interactions of nonindigenous species.

(a) Soft-Bottom Communities

In subtidal and intertidal soft-bottom communities, dense beds (> 2,000 individuals/m²) of *Potamocorbula amurensis* appear to have mechanisms that prevent the successful establishment of other organisms, native or introduced. These mechanisms may include predation on the larvae of these organisms, more efficient filter feeding (Nichols et al. 1990) and direct spatial competition.

In the only experimental studies done to date in San Francisco Bay on the interactions between benthic native and introduced invertebrates, Race (1982) has shown experimentally that the introduced mudsnail *Ilyanassa obsoleta* restricts the native mudsnail *Cerithidea californica* to upper intertidal, high salinity habitat through egg predation and direct interference.

(b) Fouling Communities

Competitive interactions in Bay and Delta fouling communities can be inferred from studies of the same or similar species in other systems; the absence of such work in San Francisco Bay is notable. Working in nearby Bodega Harbor, Standing (1976) experimentally demonstrated that the hydroid *Obelia "dichotoma"*, also present in San Francisco Bay, decreases the settlement rate of barnacles but increases the settlement rate of ascidians. By interfering with barnacle recruitment, ascidian settlement is enhanced, and dense aggregations of ascidians support a diverse associated community. Working in North Carolina, Sutherland (1977, 1978) found that the bryozoan *Schizoporella* sp. (identified as *S. unicornis* but perhaps not that species) and the seasquirt *Styela plicata* (introduced from the Pacific to the Atlantic, although this was not known to Sutherland) have a stabilizing role in community structure: when dense, these two dominant species exclude other species from invading, resulting in patches with fewer species and less change over time. On a greater time scale, however, *Styela* destabilizes the fouling community through annual "sloughing off" of the large summer individuals, taking the associated fouling community with it. Both *Styela* species and *Schizoporella unicornis* are common in San Francisco Bay. Sutherland's observations may further aid in explaining the apparent replacement of mussel beds (*Mytilus edulis*) in parts of New England by the introduced Asian seasquirt *Styela clava*, a species common throughout the Bay's fouling communities.

(c) Marsh Communities

Competitive interactions in Bay marsh systems are poorly known. At local sites, the introduced peppergrass *Lepidium latifolium* may compete with native pickleweed *Salicornia virginica*, and may also play a role in displacing rare native marsh plants such as *Lillaeopsis masoni* (Trumbo, 1994). At a site in San Pablo Bay, the introduced chenopod *Salsola soda* also appears to be competing with *Salicornia*. Despite existing populations of the native *Spartina foliosa*, three species of the cordgrass *Spartina* have been intentionally planted in San Francisco Bay salt marshes (Spicher and Josselyn, 1985). One of these, *Spartina alterniflora*, which has converted 100s of acres of mudflats in Willapa Bay, Washington into cordgrass islands, has become abundant in parts of San Francisco Bay and may be 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 substantially alter habitat for native wetland animals and infauna. Dense stands of *S. alterniflora* may change sediment dynamics, reduce benthic algal production because of lower light levels below the cordgrass canopy, and reduce shorebird feeding habitat through colonization of mudflats (Callaway, 1990; Callaway & Josselyn, 1992). In British estuaries, the invasion of mudflats by *Spartina anglica* has produced adverse effects on shorebirds (Goss-Custard & Moser, 1990).

(d) Freshwater Systems

The Delta today hosts large populations of exotic species: the Asian clam *Corbicula* can form dense beds many meters in extent, the eastern American worm *Manayunkia* can occur in sediments in densities of 2,000 to 5,000/m², introduced crayfish and fish are frequently the only crayfish or fish species encountered, and meadows of floating or rooted aquatic plants may dominate areas of formerly open water.

The introduced crayfish *Orconectes*, *Procambarus* and *Pacifastacus*, when dense, are capable of extensive local habitat alteration through burrowing activities and presumably play an important role in regulating their prey plant and animal populations. Some introduced bottom-feeding fish are similarly capable of structurally altering habitats; carp, for example, dig up the bottom, destroying rooted vegetation and rendering potentially productive areas unsuitable for use as spawning or nursery areas by other fish species.

Several introduced freshwater plants can become locally abundant. These include the aquarium plant *Egeria* (= *Elodea*), which has been responsible for clogging channels and boat berths, and the water hyacinth (*Eichhornia crassipes*), which manifests itself as a nuisance plant by blocking waterways, interfering with vessel operations, and fouling pumps. Both of these plants alter conditions of shading and cover and, in the case of water hyacinth, may become dense enough in places to interfere with fish migration (CDBW, 1994).

(e) Bio-eroders: Is the Bay Margin Disappearing?

Some evidence exists that bio-erosion of the Bay and Delta land margins may be occurring at the "hands" of burrowers and borers among the exotic fauna. The introduced crayfish *Procambarus clarkii* excavates burrows 5 cm in diameter and as much as 100 cm deep in Delta levees and banks. Muskrats similarly create extensive burrow systems in the Delta. The recently introduced Chinese mitten crab *Eriocheir* is known to form extensive excavations along river banks.

However, the most numerous bio-eroder around the Bay margins is the New Zealand boring isopod *Sphaeroma quoyanum*. Carlton (1979b) has described portions of certain eastern and northern bay shores, characterized by many linear meters of fringing mud banks riddled with the one-half centimeter holes of this isopod, as "sphaeroma topography," a phenomenon illustrated by Barrows (1919) and Hannon (1976). Higgins (1956) concluded that this isopod plays "a major, if not the chief, role in erosion" of intertidal sandstone and tuff terraces along the south shore of San Pablo Bay, due to boring activity that weakens the rock and facilitates its removal by wave action. Hannon (1976) reported one estimate that *Sphaeroma* could "remove up to 10 meters of dike in one year", a number that appears excessive. Nevertheless, *Sphaeroma* has been burrowing into bay shores for over a century, and it would not be surprising to learn that the land/water margin has retreated at certain sites by a distance of at least several meters due to this isopod's activities.

Exceedingly valuable would be observational and experimental studies in the Estuary that focus on the erosion rates of crayfish, muskrats, isopods and, if they become abundant along channel, stream and river banks, Chinese mitten crabs.

5. THE REGIONAL AND GLOBAL EXTIRPATION OF NATIVE SPECIES

No estuarine or aquatic introduction in the San Francisco Bay region has solely or indisputably led to the extinction of a native species. Short of this, however, invasions in the Bay have led to the complete habitat or regional extirpation of species, have contributed to one global extinction of a California freshwater fish, and are now strongly contributing to the further demise of endangered marsh birds and mammals.

(a) Introduced Fish and the Extirpation of Native Fish

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 introduced striped bass, largemouth and smallmouth bass, bluegill and green sunfish, through predation or 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 silverside 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 a decline in the native hardhead. Predation by striped bass, largemouth and smallmouth bass may have been a major factor in the global extinction of the thicktail chub.

(b) Invaders and the Endangered California Clapper Rail: Eaten by Rats and Foxes: Trapped by Marsh Mussels: Habitat Altered by Plant Invasions

The California clapper rail may serve as an example of how populations of an already endangered species may be further threatened by biological invasions. Despite the interest in clapper rails in San Francisco Bay, however, there has been little quantitative investigation of the impact of introduced species, suggesting fruitful avenues for investigation.

Norway rats, established in many areas of California by the mid-1880s, have long been recognized as significant predators on clapper rail, starting with early observations such as the following (de Groot, 1927):

"the clapper rail has no more deadly enemy than this sinister fellow. No rail dares nest on a marsh area which has been dyked, for as surely as she does this vicious enemy will track her down and destroy the eggs. Many nests have I found bearing mute evidence of the fact that some luckless rail had gambled her skill at nest-hiding against the cunning of the Norway rat, only to have her home destroyed."

Predation on both rail eggs and rail chicks is considered to be high, with as many as a third of rail eggs said to be taken by rats (Josselyn, 1983; BODC, 1994). The cordgrass zones of salt marshes support the highest clapper rail densities by providing cover and/or isolation from rats, raptors and feral predators (Josselyn, 1983), and thus the expansion of these zones by the introduced Atlantic cordgrass *Spartina alterniflora* could benefit rails. Alternatively, competitive replacement of native cordgrass by *S. alterniflora* could reduce preferred cover for the rails.

Although present inland in California since the 1870s, the red fox has appeared on the margins of San Francisco Bay, adding another critical clapper rail predator to the ecosystem a century after the appearance of the Norway rat. In California the red fox has preyed on the eggs and sometimes the young or adults, and disrupted nests or colonies, of the clapper rail (as well as other birds, including least tern, snowy plover, Caspian tern, black-necked stilt and avocet) (Forester & Takekawa, 1991; Takekawa, 1993; BDOC, 1994).

Reduction in clapper rail populations by exotic species through processes other than direct predation may also have occurred. De Groot (1927) reported, under the heading of "the invisible foe," the following concerning the relationship of adult rails to the Atlantic ribbed marsh mussel *Arcuatula demissa*:

"This apparently harmless little mussel has been another of the rail's most relentless enemies, and the number of rail deaths attributable to its activities is incredible...Countless millions of these small mussels cover the edges and sometimes the entire bottoms of the gutters and creeks of the west Bay marshes. Up under the banks, where the rail so commonly feed and hide when the tide is out, these death traps are found in great numbers...Along comes a rail gingerly pecking into the

soft mud (and it) rams (its) beak into the open mussel and in an instant the trap is sprung and the rail is helplessly and hopelessly trapped... shaking and scraping and pulling are all in vain...(and) the poor rail eventually (dies) by starvation"

De Groot further believed that "at least seventy-five percent" of the adult rails of the Redwood marsh area in the South Bay had lost toes by entrapment in mussel shells. He argued that this led to the loss of juvenile birds as well:

"But while the adult rail generally escapes with merely the loss of a toe or two, young birds must meet death frequently...(there is) some basis for stating that probably one or two chicks in every brood, if not more, meet an untimely end in this manner..."

More recent observers note that clapper rails in the Bay are frequently missing one or more toes (Moffitt, 1941; Josselyn, 1983; Takekawa, 1993) and Josselyn (1983, p.69) includes a photograph of an adult clapper rail missing one toe and with an *Arcuatula* clamped to another.

Unfortunately, accurate quantification of rail:mussel interactions is lacking, and thus the impact (implied by de Groot to be approaching one-third brood mortality at the valves of the mussel) on clapper rails remains unknown. That the rail/mussel interaction may not be all one sided, however, is suggested by Moffitt's (1941) study of rail feeding, wherein he found in a sample of 18 birds that 66 percent of the animal food of the rail (and 57 percent of the total food) consisted of *Arcuatula*.

(c) Other Examples of Reductions and Extirpations

Around the Bay and Delta, reduction and elimination of populations of other native species have occurred or appear to be in progress as the result of interactions with introduced species. Unfortunately, as with impacts on the clapper rail, and with the sole exception of impacts on native snails, no quantified data appear to be available. It has thus been suggested or observed that:

- the introduced Atlantic mudsnail *Ilyanassa* has displaced from mudflats to saltmarsh pannes and reduced the population of the native mudsnail *Cerithidea*;
- introduced green sunfish, bluegill, largemouth bass and the introduced American bullfrog may have contributed to the decline of native red-legged and yellow-legged frogs in the Bay and Delta region, largely through predation;
- introduced red fox, through predation, reduce or limit the recovery of populations of the endangered salt-marsh harvest mouse;
- introduced crayfish have displaced some native crayfish species and threaten others;
- introduced peppergrass (*Lepidium latifolium*) may displace rare native marsh plants, such as *Lillaeopsis masoni*.