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Distribution, Ecology and Potential
Impacts of the Chinese Mitten Crab
(*Eriocheir sinensis*) in San Francisco Bay

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Abstract

The arrival of the Chinese mitten crab to the San Francisco Bay-San Joaquin Delta (Bay-Delta) ecosystem has been a source of widespread concern. This crab has spread from its native range, in China, to coastal ecosystems throughout Europe and, most recently, into North America. The Chinese mitten crab population in California has exploded within the last decade to cover hundreds of miles of the Bay-Delta and its tributaries. The Chinese mitten crab is a large, catadromous crab, moving from freshwater habitats where it spends its juvenile years to saltwater habitats in order to reproduce. In other countries into which this species has been introduced, the abundance and behavior of the crab has caused detrimental impacts to fisheries and loss of bank stability in areas where it burrows.

Through a grant from the Water Resources Center, we set out to examine the ecology, distribution, and economic and ecological impacts of the Chinese mitten crab in the fresh and saline waters of San Francisco's South Bay. The Chinese mitten crab offers excellent opportunities to: 1) study the population dynamics of an invasive species; 2) examine differences and similarities for this organism between its native and new environments; and 3) use research findings to make recommendations for understanding and control of this organism.

We surveyed the tributaries and main body of South San Francisco Bay in order to examine the ecology and impacts of the Chinese mitten crab. We studied distribution and abundance of juvenile crabs by establishing 72 monitoring sites throughout the salinity gradient of several major South Bay tributaries. These sites were used in 1995, 1996 and 1999 to collect population and habitat data. Adult crabs in the South Bay were monitored using otter trawls over the same three-year period. Population parameters of mitten crabs, including size and sex ratios, were examined. We quantified habitat preferences of the mitten crab by examining stream characteristics including substrate type, vegetation type, and salinity. Gut contents were analyzed in order to examine dietary habits and dietary shifts with age, and frequent behavioral observations of crabs were made to confirm dietary and habitat preference data. In order to examine impacts to banks and levees, we examined burrowing by juvenile crabs and quantified sediment removal from burrowing by estimating burrow density and sediment removed per burrow. The potential impacts of Chinese mitten crab on two species of freshwater crayfish were studied using a combination of behavioral observations, laboratory experiments and surveys of the commercial crayfish industry.

We found mitten crabs to be broadly distributed throughout the freshwater tributaries of the South Bay, with the distribution spreading over the three years we monitored these sites. Adult mitten crabs were also found in the main body of the bay, with gravid (egg-carrying) females appearing between November and May of each year. Juvenile mitten crabs preferred intertidal sections of streams that had banks with high clay content and abundant vegetation overhanging or growing on the banks. Gut content analysis of mitten crabs revealed a high proportion of vegetative matter, with low amounts of invertebrates, regardless of the size of the crab or the habitat from which it was collected.

Abundance of Chinese mitten crab also increased over time, as seen by a continuous increase in burrow densities: densities reached a high of 18/ m² at one site in 1995 and 1996, and densities exceeded 30 burrows/ m² at two sites in 1999. Densities exceeding 30 burrows/ m² are considered to be damage-causing levels in other areas into which the crab has been introduced. Research into the impacts of Chinese mitten crabs on crayfish populations produced mixed results: based on behavioral observations, crabs and crayfish in the South Bay were found to co-occur; crayfish industry surveys revealed concern regarding potential competition of crayfish and mitten crabs; and experimental interactions suggested possible habitat competition between adults of crayfish and mitten crabs.

We present these findings in coordination with studies occurring in the North Bay, the Delta and throughout California which show that the Chinese mitten crab is quickly spreading throughout all of northern California, and has recently reached southern California through the state's aqueduct system. In addition, the sheer abundance of the crab has created significant impacts on the state's water projects. In particular, efforts to minimize impacts to fish from water project turbines and pumps have been seriously impeded by the crabs clogging these systems during their fall migration.

The results of our research include important findings for the spread of the organism, similarities and differences between its ecology here and in its native range, and impacts on physical and biological characteristics of San Francisco Bay. We have shown that the mitten crab population has exploded in the South Bay as well as throughout the Bay-Delta region. The highest densities of mitten crab burrows are currently restricted to intertidal segments of the banks and levees; however, at some locations within these areas, bank slumping and erosion already are significant. We believe that there is cause for concern for impacts on freshwater crayfish, although more research needs to be done to quantify these impacts.

Given the widespread distribution, abundance, and lack of specialized predators for the Chinese mitten crab, we believe complete control of this species would be extremely difficult and costly. A more effective strategy will be to focus control in specific regions where the crab is producing costly and damaging effects, such as the fish protection programs at state water projects. State and private parties have discussed commercialization of the mitten crab for consumption here or in Asia, and this option could provide an effective, though controversial, method of control. Our findings suggest that the mitten crab is here to stay as yet another member of San Francisco's evolving non-indigenous communities.

Key words: 0170, 0770, 0885, 2300, 0215, 0130, 0185, 0500, 1305, 1845

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Table of Contents

I. Introduction.....	1
II. Ecology and Impacts of the Chinese mitten crab.....	5
III. The Chinese mitten crab: distribution.....	10
IV. Methods to describe the distribution and ecology of the Chinese mitten crab and its impacts on the Bay-Delta ecosystem.....	13
V. Results.....	18
VI. Discussion.....	25
VII. Regional distribution and impacts of the Chinese mitten crab.....	31
VIII. Conclusions and recommendations.....	34
References.....	37
Figures.....	45
Tables and Appendices.....	

List of Figures

Figure 1. Native range of the Chinese mitten crab

Figure 2. European distribution of the Chinese mitten crab

Figure 3. Distribution of the Chinese mitten crab in the San Francisco Bay-Delta ecosystem, 1992-1998

Figure 4. The adult Chinese mitten crab

Figure 5. Abdomens of male and female Chinese mitten crabs

Figure 6. Life cycle of the Chinese mitten crab

Figure 7. Structure of the Chinese mitten crab burrow

Figure 8. Map of South Bay region where research was conducted

Figure 9a. Monitoring sites used for measuring Chinese mitten crab distribution

Figure 9b. Monitoring sites used for measuring Chinese mitten crab population density

Figure 10. South Bay distribution of Chinese mitten crab in 1995, 1996, and 1999

Figure 11. Two main types of modified stream channels in the South Bay

Figure 12. Average Chinese mitten crab burrow densities in South Bay tributaries

Figure 13. Percent gravid female Chinese mitten crabs captured by MSI trawls

Figure 14. Sex ratios of adult Chinese mitten crabs captured by MSI trawls

Figure 15. Average carapace widths of adult male and female Chinese mitten crabs captured by MSI trawls

Figure 16. Average size of South Bay juvenile Chinese mitten crabs

Figure 17. Rates of initiation of aggressive interactions between adult Chinese mitten crabs and adult signal crayfish

Figure 18. Effect of shelter on rates of aggressive interactions between adult Chinese mitten crabs and adult signal crayfish

Figure 19. Distribution of the Chinese mitten crab throughout the State Water Project of California.

Figure 20. Monitoring sites for the Delta Chinese mitten crab survey.

Figure 21. Estimated number of Chinese mitten crabs collected daily at the Tracy Fish Collection Facility, Tracy, CA, and daily low water temperatures.

Figure 22. Sex ratio of Chinese mitten crabs collected daily at the Tracy Fish Collection Facility

List of Tables and Appendices

Table 1. Summary statistics for adult Chinese mitten crabs captured by MSI trawls

Table 2. Summary statistics for Chinese mitten crab – signal crayfish behavioral experiments

Table 3. Juvenile mitten crab densities (crabs/m²) at monitoring sites throughout the Delta

Appendix 1. Survey sent to crayfish fishermen regarding effects of the Chinese mitten crab on crayfishing efforts

Appendix 2. Comparison between the ecology of the Chinese mitten crab and generalized attributes of successful invasive species

I. INTRODUCTION

The arrival of the Chinese mitten crab to the San Francisco Bay-San Joaquin Delta (Bay-Delta) ecosystem has been described as an issue of serious ecological and economic concern by both scientists and the popular media. First discovered in the southern portion of San Francisco Bay in the winter of 1992, the Chinese mitten crab, *Eriocheir sinensis*, soon spread throughout San Francisco Bay and its tributaries, giving this species the distinction of being among the most quickly and widely distributed of introduced aquatic species found in the Bay-Delta ecosystem. The mitten crab has had severe economic and ecological impacts in other countries into which it has been introduced. In the short time it has established in the Bay-Delta ecosystem, there is already evidence that this crab is effecting several ecological and economic processes. The recent introduction of this species and its widespread impacts makes the Chinese mitten crab a timely and important subject for the study of how invasive species are changing our ecosystems.

Although research has clarified some of the ecology of the Chinese mitten crab in its native range in Asia and in other countries into which it has been introduced, the ecology of the mitten crab is just beginning to be understood for its new home in the Bay-Delta ecosystem. The species composition, climate, hydrology, and the cultural and regulatory frameworks of the San Francisco Bay-Delta region are all quite different from other regions in which this crab has been studied. Through funding by a grant from the University of California's Water Resources Institute, we have studied several aspects of the mitten crab's ecology that are specific to the Bay-Delta ecosystem. This report will outline our research findings and supplement these findings with existing results from other regions and with information collected by contemporary projects underway to improve our understanding of the ecology and impacts of the Chinese mitten crab in California.

The objectives of this study have been to:

- 1) Quantify the distribution and abundance of the Chinese mitten crab in the freshwater, intertidal and saline habitats of South San Francisco Bay;
- 2) examine several aspects of the ecology of the Chinese mitten crab in its new environment: including habitat preference, diet, sex ratios and timing of migration and reproductive cycles;
- 3) determine ecological and economic impacts of the Chinese mitten crab, focusing on:
 - a) interactions of the mitten crab with two species of crayfish: the red swamp crayfish, *Procambarus clarkii*, and the commercially valuable signal crayfish, *Pacifastacus leniusculus*; and
 - b) threats to levee integrity caused by the burrowing habits of the mitten crab.

In this introductory section, we provide an overview of the ecology of the San Francisco Bay-Delta ecosystem. We discuss the history of biological invasions in this ecosystem and provide a brief discussion of the general ecology of biological invasions. In section II, we present a review of the ecology and impacts of the Chinese mitten crab as it is known for its native habitat and for other countries into which it has been introduced. Section III describes the world-wide distribution of the Chinese mitten crab, including its introductions into Europe and into North America. We present the methods, results and discussion of our research of the introduction of the Chinese mitten crab into South San Francisco Bay in sections IV, V and VI. In section VII,

we describe the distribution of the Chinese mitten crab throughout California, focusing on research and control efforts underway in the Sacramento-San Joaquin Delta (the Delta), the major tributary of North San Francisco Bay. Section VIII summarizes our research findings and discusses opportunities for control and application to other biological invasion research and management efforts.

The San-Francisco Bay-Delta Ecosystem

The San Francisco Bay-Delta ecosystem is comprised of 1,500 km² of aquatic habitat that drains a 153,000 km² watershed, equaling 40% of California's surface area (Nichols et al. 1986). This ecosystem supports a diverse assemblage of biota and human activities. The Bay-Delta ecosystem provides habitat to hundreds of native aquatic species, as well as providing water supply and riparian habitat for terrestrial species, waterfowl and migratory birds. Commercial and subsistence fishing and aquaculture are major industries in the San Francisco Bay and Delta. The Bay-Delta system supports one of the largest shipping industries in the Western hemisphere, containing four ports that host large volumes of national and international shipping traffic (Hall 1998). Up to 70% of the annual freshwater inflow of the Delta is diverted for consumption and irrigation (Boyle 1998). This water system supports an agricultural industry that provides nearly half of all the fresh fruits and vegetables for the U.S. and is one of the state's leading industries (Hall 1998).

The San Francisco Bay and Delta may be the most invaded aquatic ecosystem in the world (Cohen and Carlton 1995). Over 230 non-indigenous species have been identified in this ecosystem. At least 125 other species in the Bay are considered cryptogenic, meaning that they are of unknown origin. From 1851 to 1960, one new species established itself in the Bay-Delta ecosystem, on average, every 55 weeks; from 1961 to 1995, this figure rose to a new species establishing itself approximately every 14 weeks (Cohen and Carlton 1998). At this point, it is likely that the number of species of recent (within the past two centuries) foreign origin in the Bay-Delta ecosystem is approaching the number of species that have existed here since before the discovery of the Bay by Europeans (Cohen and Carlton 1998). An understanding of the process of biological invasions and the mechanisms by which these invasions occur is essential to determining how these organisms are affecting our ecosystems. Furthermore, an understanding of this process is critical for the Bay-Delta ecosystem, because this region contains a wealth of ecological and economic benefits that may be threatened by the increasing pressures of non-indigenous species.

Mechanisms and impacts of species invasions

Introductions of foreign organisms into new ecosystems have occurred since time began. The movement of species into new habitats is a major force in the evolution and distribution of species across the globe (Elton 1958). Humans, however, have accelerated this process by dramatically increasing the rate of movement of species and facilitating their movement across great distances to new regions and continents. Human methods of transport, including ships, planes, trucks and even walking, all have the potential to carry foreign organisms into new environments. As

regional and global transportation has increased over the past few centuries, the transport of species between ecosystems has greatly accelerated.

Non-indigenous species may be introduced but not have any substantial effect in their new environment. Most often, conditions in the new environment do not match the introduced organism's needs, and the species either does not establish as a reproducing population or does so in extremely low numbers (Locke et al. 1993). In a small number of cases, however, non-indigenous species do become established in their new environment. Of those species that become established, it is estimated that approximately 10% may become pests as defined by their economic, ecological or public health effects (Williamson 1996). The link between the transport of non-indigenous species and their establishment in a new ecosystem is poorly understood. As a leading scientist in biological invasion research has stated, "predictions of what species will invade, and where and when invasions will occur, remain one of the more elusive aspects of biological invasion science" (Carlton 1995). Factors involved in the establishment of non-indigenous species include suitability of habitat, available food sources, presence of reproductive partners if sexual reproduction is necessary, and presence of predators of the new species. The extent to which the recipient ecosystem has been disturbed by human activities, natural events, or by prior introductions of exotic species may also influence the environment's susceptibility to invasion. The relationship between habitat disturbance and biological invasion is defined by the effects of disturbance on weakening the health and integrity of an ecosystem and removing native species, which opens up niches for invading species to occupy. Although some studies have shown a correlation between habitat modification and increased invasion of exotic organisms (Leidy and Fielder 1985; Nichols 1994; Moyle and Light 1996), the specifics of these relationships are not well understood (Lozon and McIsaac 1997);

Susceptibility of aquatic ecosystems to invasion

Aquatic ecosystems are susceptible to high rates of invasion for several reasons. The interconnection of rivers, coastal zones, and oceans facilitates the rapid spread of introduced species. Many human activities have been implicated in the direct introduction of non-indigenous species into aquatic ecosystems. These activities include: aquaculture establishment; fish stocking; releases of species from breeding and rearing facilities; escapes or dumping of species from ornamental ponds and aquaria; introduction of species for biological control or profit; planting exotic vegetation for restoration and erosion control projects; importation with shipments of live seafood or bait; and transport of species in or on ships (Cohen and Carlton 1998). An estimated 400 non-native species currently exist in the Pacific, Atlantic and Gulf coasts of North America, in addition to hundreds of aquatic non-native species reported from around the world (Ruiz et al. 1997). Given that marine invertebrates are a relatively poorly researched and described group, these numbers are quite likely conservative estimates; there are undoubtedly many more non-native coastal and pelagic marine species that have not yet been described or recognized (Carlton 1995).

Hundreds of documented cases throughout the world illustrate that exotic species may have ecological and economic impacts in their new environment. In some cases, these impacts may be quite severe, such as the introduction of the zebra mussel, *Dreissena polymorpha*, into the Great

Lakes ecosystem of North America. According to the US Fish and Wildlife Service, this freshwater mussel will cause an estimated \$5 billion in damage to shipping and power plants by 2002, because of effects of the mussel including clogging of intake pipes and fouling of ships (Verrengia 1999). The mussel's high filtration capacity has caused a severe decline in phytoplankton abundance and has caused major changes to the Great Lakes food webs (Anonymous 1996).

Disturbance such as physical or chemical alteration of an aquatic habitat may, as discussed above, render the habitat more susceptible to biological invasion. The vast majority of aquatic systems in North America have been disturbed in one or more ways, by damming, canalization, dredging and major structural changes caused by urbanization or port development. The Bay-Delta ecosystem, which supports a major shipping industry, a vast network of water diversion and regulation projects, and several metropolitan areas certainly falls in the category of highly disturbed aquatic ecosystems, and this level of disturbance has been cited as one reason for the increased levels of establishment of introduced species in this ecosystem. In some areas of the Bay, 100% of the common species are introduced, creating "introduced communities" (Cohen and Carlton 1998).

Among the 234 introduced species of the Bay/Delta ecosystem that have been identified by Cohen and Carlton (1998), several established species are causing widespread ecological and/or economic impacts. In San Francisco Bay, the Asian clam, *Potamocorbula amarensis*, is causing drastic trophic changes. The clam was first observed in Suisun Bay, the upper arm of San Francisco Bay, in 1985. In less than a decade, the clam reached a density of over 10,000 individuals per square meter in some areas (Thompson 1998). The clam has a high filtration capacity and, like the zebra mussel has done in the Great Lakes, it has drastically reduced phytoplankton populations, altering the Bay's food chain (Alpine and Cloern 1992). It is believed that this clam, as a bottom-dweller, may be concentrating the toxic metal selenium that is then magnified through the food chain, affecting the health of the Bay's aquatic life as well as humans who fish from the Bay (Thompson 1998). Other species impacting the Bay include the European green crab, *Carcinus maenas*. This species has also invaded the Bay-Delta ecosystem. Blamed for the collapse of the Maine softshell crab industry after its introduction on the East coast, the occurrence of the green crab was first documented in San Francisco Bay in 1990 (Grosholz and Ruiz 1995). At a public hearing in Alameda, CA, on invasive species, an oyster aquaculturist testified that his oyster business loses an estimated \$25,000 to \$30,000 per year because of predation by the green crab (Finger 1998).

The Chinese mitten crab can now be added to the growing list of non-indigenous organisms that are changing the form and function of the Bay-Delta ecosystem. As we will describe in this report, the mitten crab population has exploded since its first sightings in 1992 to cover hundreds of miles of the Bay-Delta ecosystem (Figure 3). Studying this crab in the context of its new home in the Bay/Delta ecosystem is essential to an understanding of its role in the economy, ecology and health of the Bay area. In addition, research efforts described in this paper will contribute to our understanding of how non-indigenous organisms invade, establish and become successful in new environments.

II. ECOLOGY AND IMPACTS OF THE CHINESE MITTEN CRAB

Identification and taxonomy of the Chinese mitten crab

Identification

The Chinese mitten crab is usually identified by the dense patches of setae, or hair, found on the white-tipped chelae (claws) of larger juveniles and adults which gives this crab its name (Figure 4). Males and females both exhibit these hairy chelae, though the setae are generally fuller and cover a wider area of the chelae in the males (Zhao 1999; D. Rudnick, personal observation). The claws are approximately equal in size. The carapace is slightly wider than long and has four spines on its anterior lateral margins. The maximum carapace width of the adult mitten crab in California is approximately 80mm, although occasionally larger individuals are found (Siegfried 1999b). The crabs' pigmentation varies from a brownish orange, particularly among juvenile crabs, to a more greenish-brown seen in adult crabs and in newly molted crabs (Zhao 1999). The crab also exhibits a frontal notch between the eyes flanked by two small spines to either side of the notch; however, the spines and notch should not be considered morphologically conservative characteristics (see below). The legs of the mitten crab are generally twice as long as the width of the carapace, and, among older juveniles and adult crabs, the distal segments of the legs exhibit hairs along the lateral margins. After reaching a size exceeding approximately 10mm in carapace width, the male and female crabs can be differentiated by the shape of the abdomen, which in the female is rounded and occupies most of the area of the thorax; in the male, the abdomen is narrower and shaped like an inverted funnel (Figure 5).

Taxonomy

The Chinese mitten crab, *Eriocheir sinensis* H. Milne Edwards (Decapoda: Grapsidae: Varuninae), is one of two species of mitten crabs currently recognized within the genus *Eriocheir* which also includes *Eriocheir japonica* De Haan 1835 and its subspecies *E. japonicus hepuensis* Dai 1991 (Chan et al. 1995). Two species, *E. recta* and *E. leptognathus*, originally placed in this genus, have now been removed either because their designation as a species was considered invalid or because they have been reassigned to a new genus. *Eriocheir recta* was considered to be an additional crab within this genus, found in southern China and in Taiwan. In 1995, Chan et al. reassigned the mainland population of this crab as synonymous with *E. japonicus*, while the Taiwanese population was described as a new species, *E. formosa*, based on morphological differences. Most recently, Ng et al. (1999) reassigned *E. leptognathus* Rathbun 1914, to a separate genus, *Neoeriocheir*. Ng et al. also reassigned *E. formosa* to a new genus, *Platyeriocheir*, based on ontogenic and morphological differences. It is worth noting, however, that a genetic comparison of all these species that could provide evidence for their taxonomic relationships has not yet been reported. The morphological and genetic relationships within the *Eriocheir* genus and among associated groups are still unresolved, and not all mitten crab researchers use the taxonomic classification described above; thus the taxonomy of the Chinese mitten crab should be viewed as a work in progress.

There has been some debate among scientists as to whether *E. japonicus* and *E. sinensis* should be considered two subspecies of the same crab species. Li et al. (1993) confirmed that *japonicus* and *sinensis* are genetically identical and that hybrids between the two could easily be obtained.

These authors suggest that both crabs be grouped under the single species *E. japonicus*. Morphological differences between *Eriocheir* species are described, although whether these differences are a phenotypic expression of populations and hybrids, or true species-specific characteristics, is debatable. Li et al. (1993) described a mitten crab population with morphological traits intermediate to *sinensis* and *japonicus*, and suggested that morphological characteristics may be ecophenotypic, meaning that physical appearance is dictated by environmental conditions. Some morphological characteristics of the mitten crab are not conservative and thus may not provide good indicators, such as the use of the frontal carapace teeth, which change shape with the growth of the carapace and among populations of the species (Panning 1938; Li et al. 1993). Given the instability of the Chinese mitten crab's taxonomy, it is currently treated as a distinct species (Cohen & Carlton 1995). Given the morphological plasticity and genetic consistency of *Eriocheir*, it may be difficult to determine if Chinese mitten crabs in the Bay-Delta ecosystem are the products of a single or of multiple sources.

Life cycle

Mitten crabs begin their lives as marine pelagic zoeae. The crabs undergo 5 zoeal and 1 megalopal stages¹, and, under laboratory conditions, require an average of 15 days to reach the megalopal stage (Kim and Hwang 1995). In the megalopal stage, the crabs begin migrating inland towards fresh water. The megalopal crabs swim quickly, cueing towards a lower salinity to reach brackish water (Zhao 1999). Following the megalopal stage, the crabs settle to the substrate and continue their migration as juveniles. Juvenile mitten crabs undertake enormous journeys during their migration, and have been found as far as 1,250 km from the coast in freshwater streams (Dan et al. 1984). Juvenile crabs spend from one to five years feeding and growing in freshwater streams in China, with the vast majority maturing in one to two years, before beginning their migration downstream as adults (Hymanson 1999; Zhao 1999) (Figure 6).

According to European studies of this species, adult mitten crabs begin to migrate downstream in late fall and winter, with the males descending to brackish waters first, and the females following within a month of the males (Anger 1991). Zhao (1999) has described the chronological pattern of adult downstream migration in China as: small males, then small females, then large males and finally large females making their way downstream to reproduce. Although many reports indicate that adult mitten crabs require saline waters in order to produce viable larvae (Panning 1938; Anger 1991), it appears that maturation of the reproductive tissue may not necessarily be closely tied to salinity: for example, in China, aquacultured mitten crabs with mature gonads are harvested from freshwater environments (Hymanson 1999). Some mitten crabs mature in only one year in Asia and do not migrate out of the estuary; instead, they stay to rear in brackish waters (5-25‰) (Hymanson et al, 1999). Female mitten crabs carry from 250,000 to 1,000,000

¹ The zoea and the megalopa are the two larval stages of crabs, which are the earliest stages in a crab's life. The megalopal stage of crabs follows one or more zoeal stages. All larval stages are generally planktonic, i.e. passively living in the water column; settling to the bottom occurs when the crab makes the transition from a larva to a juvenile.

eggs attached to the pleopods (abdominal appendages) on the underside of their abdomen. In China, mitten crabs reproduce only once; most crabs reproduce in the fall but some hold over until the spring (Hymanson et al. 1999). Post-reproductive mitten crabs return to the coastal banks; the males die after mating and the females die after the eggs hatch (Zhao 1999).

Physiological requirements

The first zoeal stage of the mitten crab, which occurs in seawater, is strongly euryhaline². The larvae become increasingly stenohaline over subsequent zoeal stages, with a marine salinity optimum. The megalopa, which migrates to freshwater, is euryhaline, with an optimal growth response in brackish waters (5-25‰) (Anger 1991). It is probable that this pattern of developmental changes in larval tolerances coincides with the pattern of larval dispersal in the estuaries where the mitten crab eggs hatch and develop. Temperature and stage of larval development strongly influence salinity tolerance of mitten crab larvae. Larvae in laboratory experiments developed through metamorphosis at temperatures ranging from 12° to 18°C, and salinities from 15 to 32‰, but optimal growth depended on both the combination of temperatures and salinities used, and the stage of development of the crab. All larval stages of the Chinese mitten crab show a clear preference for warm water (15° to 18°C), and temperatures below 12°C do not allow any development beyond the first zoeal stage in the laboratory (Anger 1991).

Adult Chinese mitten crabs are extremely euryhaline. By hyper-regulating the ionic content of their body fluids, the crabs can quickly adapt from highly saline to low brackish and freshwater environments (Welcomme and Devos 1991). Adult mitten crabs exhibit a wide range of temperature tolerances; growth ceases only at temperatures below 7°C and above 30°C. Adult mitten crabs also are highly tolerant of dessication and are able to remain unsubmerged for several hours without mortality (Siegfried 1999b; Veldhuizen and Stanish 1999; D. Rudnick, personal observation).

Most of the life history information for the Chinese mitten crab comes from research conducted in China and Europe. Many aspects of the mitten crab's ecology, including its development and physiology, are similar in terms of environmental requirements across all habitats in which the crab is found. Some life history traits, however, do differ and these will be discussed further in our research results and discussion. In many cases, only laboratory experiments have been conducted on the life history of *E. sinensis* and this research should not necessarily be generalized across ecosystems in which the crab is now found.

Diet

The mitten crab is known to be predominantly omnivorous, although feeding habits may shift throughout the life cycle. Panning's (1938) statement that mitten crabs "eat whatever they can get" (p. 371) is probably an accurate description of the plasticity of this crab's eating habits. It is

² Euryhaline refers to the physiological ability of an organism to withstand a wide range of salinities; this is opposed to stenohaline, which refers to the condition of withstanding only a narrow range of salinity.

likely that the crab's eating habits are dominated by scavenging and detritivory. Fishermen in the San Francisco Bay area have reported that they have experienced substantial bait-stealing by the mitten crab; it has stolen indiscriminately, taking bait ranging from dead fish and shellfish to worms and even plastic lures (Hutchinson 1998). In countries into which the crab has been introduced, there have been concerns expressed by the fishing industry that the crab would attack and eat live fish. However, the probability of these relatively slow crustacea capturing healthy, free-swimming fish is low. Panning (1938) noted that he kept fish and mitten crabs in the same aquarium, with no harm to the fish. We have also kept mitten crabs and small fish in the same aquarium for several weeks, with no observed ill effects on either animal (D. Rudnick, personal observation). The crabs have, however, been known to feed on fish captured in fishing nets (Panning 1938). Dan et al. (1984) and Zhao (1999) have both found that in its native range in Asia the crab shifts toward a more carnivorous diet as it ages, incorporating items such as shrimp and other benthic invertebrates into its diet.

Burrowing

One of the best-known features of the juvenile Chinese mitten crab is its propensity for burrowing. After juvenile mitten crabs have migrated into brackish channels and creeks, they create burrows on the banks between the high and low tide lines that provide a refuge and protection from dessication. These burrows are generally built in banks with high clay or silt content, and are constructed by the crabs on a downward-sloping angle, retaining water when the tide recedes (Figure 7). In general, it is the smaller juveniles that construct and inhabit these burrows in intertidal areas; we have observed that the average size of crabs found in these burrows in South Bay tributaries is approximately 20mm carapace width (Figure 16).

In areas where crabs are particularly abundant, the burrows become tightly packed together and are often interconnected. The significant amount of sediment removed in areas with high densities of burrows can cause weakening of the bank, accelerate erosion and even cause banks to collapse (Panning, 1938; D. Rudnick, personal observation). The mitten crab was introduced into Germany at the turn of the century, and its high abundance in the coastal northern waterways caused extensive bank damage. Panning (1938) noted that the mitten crabs caused considerable damage to many banks and levees by causing the bank to cave in from such extensive sediment removal. This burrowing is of particular concern where waterways are controlled by human-made levees; weakening or destruction of such levees from extensive burrowing could pose serious threats to flood control and water supply efforts.

Public Health

The mitten crab as a host for the Oriental Lung Fluke

The Chinese mitten crab has been widely reported in both scientific literature and in the press to be an intermediate host for the Oriental lung fluke, *Paragonimus westermanii* (Leiper 1935; Chandler and Read 1961; U.S. Fish and Wildlife Service 1987; Cohen and Carlton 1995; Clark et al. 1998). The Oriental lung fluke is a parasite that uses a snail as its primary host, freshwater crayfish and crabs as intermediate hosts, and a variety of mammals, including humans, as final hosts in its life cycle (Chandler and Read 1961; Lapage 1963). Humans can become infected with

the parasite through ingestion. The fluke settles in the lungs and other parts of the body, and can cause significant bronchial or, in cases where it migrates into the brain and/or muscles, neurological illnesses. It is believed that no species of snail that is in the family of the primary host currently occurs in Europe, and no appropriate snail host has been found in the San Francisco Bay-Delta system (Clark et al. 1988; Veldhuizen and Stanish 1999); the fluke, however, has been reported to exist in other mammals throughout several parts of North America (Lapage 1963). A survey of 25 mitten crabs collected from San Francisco Bay did not find any flukes in the crabs (M. Torchin and A. Kuris, as cited in Cohen and Carlton 1995).

Recent information from China, however, contradicts the idea that the Chinese mitten crab presents a public health threat as a host of *P. westermanii*. Officials from the California Department of Water Resources visiting China during the summer of 1999 were informed by many sources there that the mitten crab is not a host for this parasite (Hymanson et al. 1999). Although Chinese sources agreed that many reports have been made of crabs infected with the fluke, they stated that no substantiating evidence has ever been provided. Several species within the genus *Sinopotamon*, which are in the group of crabs known as "Chinese creek crabs" and which live at higher elevations than the mitten crab, are known carriers of *P. westermanii* in Asia (Hymanson et al. 1999). Zhao (1999) confirmed that he has never heard of a single documented case of contraction of the lung fluke by humans from *E. sinensis*. Considering the discrepancies among published and oral reports, there does not yet seem to be a consensus as to whether the mitten crab is or can act as a host for the Oriental lung fluke.

Bioaccumulation of toxins in the mitten crab

As a benthic organism in San Francisco Bay, the Chinese mitten crab has the potential to bioaccumulate inorganic and organic contaminants that then may be passed up the food chain. This type of bioaccumulation is known to occur among crustacea (Baumard et al. 1998; Sastre et al. 1999) and has been documented in *E. sinensis* populations in Asia (Che and Cheung 1998). Research on bioaccumulation in the Chinese mitten crab in California has not yet been completed; however, California's Department of Health Services is planning to examine accumulation of common contaminants such as pesticides and heavy metals in *E. sinensis* (Loscutoff 1999).

III. DISTRIBUTION OF THE CHINESE MITTEN CRAB

Throughout its range, the Chinese mitten crab is catadromous, spending approximately 90% of its life in fresh water and migrating down to estuarine waters only to reproduce. The mitten crab therefore requires river systems that have some proximity to the ocean and associated estuarine habitats. Immediate access to the ocean, however, is not necessary: the mitten crab migrates an average of 500 km, and has been found as far as 1250 km, from the mouth of the Yangtse River in its native habitat in China (Dan et al. 1984). The Chinese mitten crab's native range includes Korea and China, extending from the West coast of Korea by the Yellow Sea to the Fukien province south of Shanghai (Panning 1938; Cohen and Carlton 1995) (Figure 1).

Invasion of the Chinese mitten crab into Europe

The Chinese mitten crab is found, at varying levels of abundance, throughout most of western, central and northern Europe (Figure 2). Perhaps the most well-known and thoroughly referenced case of invasion by the Chinese mitten crab is the documentation by Panning (1938) of the establishment of the crab in Germany. The first Chinese mitten crab found in Germany was a large male specimen discovered in the Aller River in 1912. Panning postulates that the most likely method of introduction was in the ballast water of ships traveling from central Asia. By the late 1920s, the crab was very common in the rivers around Hamburg, and by the early 1930s, the crab had become a serious pest throughout the major rivers and estuaries of western Germany. In the first 6 months of 1935, Panning (1938) reported capturing over 12,000 kg (3,444,680 individuals) at a dam on the Weser River in Germany. At this time, the infestation of mitten crabs was so intense that the crabs swarmed out of the rivers and were found walking down city streets and into houses! This high density of crabs also caused serious damage to fishing operations. The crabs attached themselves to the nets to feed on captured fish, they became entangled in net and cut netting with their claws in an effort to break free, and they were caught in such abundance in some fishing nets that their spines and legs caused substantial damage to the fish trapped with them (Panning 1938). After an unexplained dramatic reduction in abundance during the 1940s, the mitten crab population showed cyclic increases again in the 1950s, early 1970s, early 1980s and have been increasing again since 1993 (Gollasch 1999). Currently, the population is again very abundant in Germany; in the spring of 1998, 850kg (750,000 individuals) were caught by hand in the river Elbe in just two hours (Gollasch 1999).

Germany provided the base from which the Chinese mitten crab spread throughout much of central and northern Europe. The crab spread in the 1920s to Belgium, where it became a serious plague in the 1930s, and has begun to make a comeback again in the 1990s (Belgie Strandworkgroep 1999). In the Netherlands, the crab was common since the early 1930s, and the population became cyclically abundant every 10 years or so. During the 1980s, serious damage to fishing nets from the abundant crabs was reported from the Netherlands (Ingle 1986). It is believed the crab entered France from Belgium during the 1930s and spread throughout the river systems, becoming abundant in southern France by the 1960s. By 1959, the crab had spread to the Mediterranean coast, and was found in the Golfe de Gascogne, near Spain (Welcomme 1988). The crab has also been found Austria and occurs in the rivers of Czechoslovakia as far inland as Prague; it is likely that both populations spread from Germany into these countries. Recently, the

southernmost distribution of the crab was reported from Portugal, where the crab was reported by fishermen to be abundant during the late 1980s, and has been caught up to 80km inland (Cabral and Costa 1999).

The mitten crab also spread from Germany into the Baltic Sea and its surrounding countries: Denmark, Sweden, Finland and Poland reported capture of the crab beginning in the late 1920s and continuing to the present. All these countries, however, reported low numbers of crabs, with no findings of larvae and few findings of freshwater specimens (Haahtela 1963; Rassmussen 1987; Jazdzewski and Konopacka 1993). Researchers hypothesize that the crabs are found in low abundance because the salinity of the Baltic Sea is too low for the mitten crab to successfully reproduce; thus, the captures probably represent repeated introductions of crabs from shipping traffic and other human introductions (Rassmussen 1987).

North America

The first reported appearance of the Chinese mitten crab in North America was in a water-intake pipe in the Detroit River at Windsor, Ontario, Canada in October of 1965 (Nepszy and Leach 1973). Three specimens of *Eriocheir sinensis* were captured by commercial fishermen in Lake Erie in April and May of 1973 (Nepszy and Leach 1973). Between 1973 and 1994, a few additional adult crabs were taken from western Lake Erie (Cohen & Carlton 1995). It is believed that these crabs were probably introduced through ships' ballast water. The Great Lakes are too fresh for mitten crabs to successfully reproduce, so it is unlikely that these crabs were part of an established population, and no recurrences of the crab in this area have been reported. A single adult mitten crab was collected from the Mississippi River delta in 1987, with none reported since then (Cohen & Carlton 1995). The crab was also found in Hawaii in the 1950s, with no subsequent reports of occurrences (Edmondson 1959, as cited in Veldhuizen and Stanish 1999).

California

Adult Chinese mitten crabs, including gravid (egg-carrying) females, were first caught by commercial fish trawlers in San Francisco's South Bay in 1992 and in San Pablo Bay in 1994. There are no known records of the mitten crab in San Francisco Bay prior to these findings. The Chinese mitten crab was positively identified in California in 1994 by Robert Van Syoc of the California Academy of Sciences (Cohen and Carlton 1997). Within just a few years of the first sighting, the Chinese mitten crab became abundant and widely distributed throughout the Bay and Delta (Figure 3). Multiple press releases, popular press articles, and government and educational-institution research reports quickly focused attention on the presence of the Chinese mitten crab in California.

Mechanisms of introduction to California

The Chinese mitten crab most likely arrived in California by one or more of three processes: a natural introduction, such as migration or drift of larvae from native habitat; an unintentional introduction associated with such activities as the importation of cargo or ballast water; or the intentional introduction of the crab, for purposes including consumption or aquaculture establishment. Given the wide geographical separation of possible source populations such as China and Europe, combined with the preference of the mitten crab for coastal and freshwater

habitats, it is unlikely that the mitten crab arrived in North America from natural causes (Cohen and Carlton 1997). It is likely, however, that the crab became established unintentionally and/or intentionally as a result of human activities.

Ballast water (water carried in ships' holds for balance or weight compensation) and cargo holds of ships provide ample opportunity for organisms to find their way into new environments. The Bay-Delta ecosystem supports one of the largest shipping industries in the western hemisphere, including four large ports of call that receive several hundred million gallons of ballast water from ships arriving from foreign ports each year. Much of this traffic, and its ballast water, comes from the Pacific Rim (Carlton et al. 1985; Hall 1998). Ships regularly take on and release water at their ports of call, collecting and releasing living organisms as they pump water on or off the ship. Aquatic organisms can survive long voyages across the ocean in ships' ballast tanks: organisms have been found living in ballast water that has been retained on board ships for over a year (Chu et al. 1997). Chinese mitten crab larvae inhabit coastal areas where shipping traffic is concentrated; thus it is possible for ships to pick up these larvae with the water they pump on board and transport them to other continents. Ballast water has been cited as the most probable method of introduction of the Chinese mitten crabs into European countries (Panning 1938; Welcomme 1998), as well as into other parts of North America (Nepszky and Leach 1973).

Direct human transport is also a possible vector for the arrival of the Chinese mitten crab. In 1978, the late Dustin Chivers of the California Academy of Sciences observed that there were live mitten crabs available for import from Hong Kong and Macao firms (Cohen and Carlton 1997). In 1985, the California Department of Fish and Game (CDFG) found live mitten crabs for sale in Asian food markets in both San Francisco and Los Angeles. Mitten crabs hand-carried by passengers arriving on flights from Asia have been intercepted by U.S. Government Inspectors at San Francisco International Airport (Cohen and Carlton 1997). Concerns over importation and sales prompted banning of live imports in California in 1987 and for the US as a whole in by categorizing the Chinese mitten crab as an "injurious species" under federal law in 1989 (U.S. Fish and Wildlife Service 1989). It is evident that this crab is considered a desirable food item, at least among Asian communities, and proponents of its consumption continue to support harvesting and sale of the crab. In 1999, businessmen came before the CDFG Commission to propose establishing a commercial fishery of the Chinese mitten crab (Hieb 1999). As recently as spring of 1999, reports continue to be generated that, although illegal, sale of live crabs continues in venues such as farmers' markets (Veldhuizen 1999b). Given the evidence of commercial supply of and interest in the mitten crab, it is possible that the crab population was established by unintentional release of crabs imported for sale, or by intentional release of crabs for seeding or for aquaculture establishment.

IV. METHODS TO DESCRIBE THE DISTRIBUTION AND ECOLOGY OF THE CHINESE MITTEN CRAB AND ITS IMPACTS ON THE BAY-DELTA ECOSYSTEM

South Bay monitoring: physical and biological characteristics of South Bay streams

Surveys were conducted for Chinese mitten crabs in tidal channels and freshwater tributaries of southern San Francisco Bay, California, as far north as Oakland on the east side of the Bay and as far north as Palo Alto on the west side (Figures 8 and 9a). All of the sampled sloughs and creeks were confined in some way by levees. Many of the creeks on the west side of the Bay are concrete-lined flood control channels that provide little appropriate habitat for crabs. Most channels monitored throughout the South and East Bay, however, are lined with natural substrate and confined by set-back levees that allowed the river to occupy at least a restricted portion of its floodplain, and these types of channels do provide habitat for crabs.

Habitat conditions along South Bay sloughs change dramatically from the river mouth to its source. Areas near the Bay are tidally influenced, receiving brackish water from the Bay twice a day during high tides. Bank conditions change as well; substrate lining creeks and sloughs in these tidally influenced areas contain a high amount of clay. Bank vegetation in these areas is generally dominated by a single plant species, either alkali bulrush (*Scirpus robustus*) or pickleweed (*Salicornia virginica*), with additionally widespread patches of thistle, cow parsnip and a variety of other herbaceous plants and grasses. The majority of vegetative cover is found at the tops of banks, with the area between high and low tide devoid or nearly devoid of vegetation in these tidal areas. An exception is found in some creeks with low-grade banks; in these areas, bulrush extends to the low water line. Progressing upstream, vegetative cover diversifies to include shrubs and trees in those streams and creeks that are lined with natural substrate, and bank sediments in upstream areas contain a higher percentage of sand and gravel than mud.

Distribution and Abundance in the South Bay

Distribution

In order to examine mitten crab distribution, we monitored fifteen sites in tributaries of the South Bay in 1995, and the same 15 and 57 additional sites in 1996 and again in 1999 (Figure 9a). Sites were chosen to represent a wide range of salinities, habitat types and geographical locations throughout the South Bay watershed. At each site examined, the presence or absence of mitten crabs was established by burrow excavation, setting crab traps and visually inspecting the area for mitten crabs. Burrows were excavated by hand using trowels. The crab traps were made from rubber-coated wire mesh, were rectangular in shape and measured 60cm long x 15cm wide x 15cm high. Traps were baited with cat food and checked twenty-four hours after they were set. Visual inspection entailed daytime searches for mitten crabs in channel margins. We spent approximately one hour at each site before concluding that mitten crabs were likely absent from a site.

Abundance

We assessed densities of mitten crabs at four tidally influenced sites along the South Bay sloughs during July and August of 1995 and 1996 (Figure 9b). Two sites along Guadalupe River were

also sampled during September, October and November of 1995 and January of 1996. We sampled an additional site on Stevens Creek during May, June and July of 1999 in order to examine burrow densities. The three sites along Alameda Creek and Guadalupe River were not accessible for this sampling in 1999, because of high amounts of mud deposition prior to the field season making these sites inaccessible. Because most sites receive storm water runoff, high rainfall precluded sampling at all sites during the rainy season.

In order to assess mitten crab abundance, we randomly selected three cross-stream transects at each site on each sampling date. Sampling was always conducted within a four-hour period around low tide. Each transect was 5m in length and ran parallel to the stream channel along the exposed vertical banks; these transects encompassed the distance from the water line to the high tide mark along the bank. We did not excavate each burrow to count crabs because such extensive excavation would cause damage to the stream banks. We therefore used burrow density as a surrogate for mitten crab density, and assumed that one crab occurred in each burrow. We made frequent estimates of burrow occupancy by conducting small-scale excavation: burrow occupancy never fell below 80%. This one-crab-per-burrow estimate was appropriate given burrow structure for 1995 and 1996 surveys. More recently, however, burrow structure has become more complex as density has risen; single entrances lead to multiple burrows, some of which are interconnected. Future monitoring may necessitate a new estimator of number of crabs-per-burrow-entrance.

We determined adult mitten crab abundance from otter trawls conducted on a weekly basis year-round by the Marine Science Institute (MSI), Redwood City, CA. Mitten crab data was collected in spring of 1995, from October of 1995 to May of 1996, and from October of 1998 to May of 1999. The trawls were conducted in a series of 14 1000m² - transects that extended between the San Mateo-Hayward Bridge, southward to the Dumbarton Bridge (Figure 9a). Trawled crabs were frozen immediately upon vessel return, and analyzed on a quarterly basis. In addition to measuring crab abundance over time, we also collected information on sex, size, and gravidity (presence of fertilized eggs on the females).

Life History

Habitat parameters

Habitat parameters associated with the presence or absence of mitten crabs were measured at 61 of the 72 survey sites in the South Bay. Measurements were not made at most of the concrete-lined flood control channels because these areas were inaccessible and often devoid of water. At each measured site, we recorded water temperature, salinity, average water depth, substrate type and type of vegetation. Water temperature was measured in the shade with a thermometer, and salinity was measured using a hydrometer. We calculated water depth as the mean of four measurements taken with a meter stick along a transect. Bank substrates were classified according to their dominant component: clay; mud; sand; organic debris; or gravel/cobble. We also identified and recorded bank vegetation.

Population Parameters

Size and sex of mitten crabs were recorded in order to determine the growth and population structure of these crabs in the South Bay. In July and August of 1995 and 1996, we collected 30 juvenile crabs from each of the four different sites used for density measurements (Figure 9b). In addition, 30 crabs were also collected from one site each month that sampling could be safely done (avoiding high stormwater flow) from June 1995 to August 1996. Carapace width was measured at the widest part of width of the carapace, just posterior to the fourth antero-lateral spine (Figure 4), and was measured to the nearest millimeter with calipers. Sex was determined by the shape of the abdomen (Figure 5) for all crabs larger than 10 mm carapace width. In order to minimize changes to the population and accurately assess population size, most mitten crabs sampled in South Bay tributaries were measured on site and released, except those harvested for gut content analysis.

Diet

We conducted gut content analyses on over 150 crabs collected from upstream and downstream reaches of Guadalupe River, and from three additional South Bay sloughs, during July of 1996. Mitten crabs were collected on site, washed of mud and immediately preserved in 70% ethanol in the field. The gut contents of approximately twenty red swamp crayfish (*Procambarus clarkii*), a decapod crustacean that co-occurs with mitten crabs the South Bay, were also analyzed. Gut contents of crabs and crayfish were analyzed using a dissection microscope; contents were divided into categories including invertebrate matter, detritus and inorganic matter (sand and silt).

Behavioral Observations

In order to correlate data on distribution, habitat preferences and trophic status of juvenile mitten crabs, we conducted behavioral observations of crabs in their natural habitats. Because most of the areas that the juvenile crabs inhabit in the South Bay are shallow, active crabs can be easily seen in the creeks unless sediment load or tidal input is high. Observations of juveniles were made during the day and night in both upstream, non-tidal areas and in downstream, tidally influenced areas. We made observations at each of two sites during the day and again at night over a 24-hour period on five separate dates. Night-time observations were made within one hour of midnight and daytime observations were made within one hour of noon.

Ecological and Economic Impacts

Impacts on bank/levee integrity

As reported from European rivers, high densities of mitten crab burrows can cause extensive erosion and slumping in levees and earthen banks. In order to assess impacts of this introduced species to levees and channels of the San Francisco Bay area, we used burrow volume as a surrogate for volume of sediment removed. Burrow density was estimated using random transect methods described above; we estimated average burrow volume by collecting average burrow lengths and widths measured at 150 mitten crab burrows at four different sites. To calculate burrow volume, each burrow was assumed to be a cylinder of uniform width (radius=1/2 burrow entrance width, height = burrow length). We measured burrow width to the nearest centimeter, and burrow length by carefully excavating one side of the

burrow and leaving the other side intact. A tape measure was then laid along the intact half of the burrow, from entrance to end, to measure burrow length to the nearest centimeter.

Impacts on Co-occurring Species: Red Swamp and Signal Crayfish

A potential impact of great concern resulting from the introduction of the mitten crab into San Francisco Bay is the reduction in abundance of other species that occupy the same habitat (Anonymous 1999). The red swamp crayfish (*Procambarus clarkii*), common in the South Bay, and the signal crayfish (*Pacifasticus leniusculus*), common in the Delta, are two such species that may be affected by the introduction of the Chinese mitten crab. Although these species are themselves introduced, they have come to fill important ecological niches as detritivores and prey for a wide range of species. Crayfish also support a commercial fishery in the Sacramento Delta and other areas throughout California, and signal crayfish have been identified by government agencies as a species to be monitored for possible impacts from the Chinese mitten crab (Anonymous 1999).

Effects of Chinese mitten crabs on red swamp crayfish

The red swamp crayfish commonly occurs in South Bay sloughs and creeks and exhibits many of the same habitat preferences as the mitten crab. We studied the correlation between presence of mitten crabs and absence of crayfish at 36 of the 72 sites sampled for mitten crab presence/absence. We did not sample the remaining 36 sites because the habitat at these sites was not appropriate for supporting mitten crabs or crayfish. Crayfish presence was determined by visual inspection and by using baited traps.

Surveys to determine impact of the Chinese mitten crab on crayfish fisheries

In the winter of 1998/1999, we conducted formal and informal surveys of the Delta crayfish industry. Questionnaires were sent out to individuals and small companies that harvest crayfish on a regular basis from the Sacramento Delta area. Questions in the survey included whether fishermen were incidentally catching mitten crabs in crayfish traps, if they had observed any mitten crab/crayfish interactions, and whether they felt mitten crabs might be affecting crayfish populations (Appendix 1). Eight questionnaires were distributed in 1998/1999. After surveys were returned, we followed up with phone calls to those individuals who had provided contact information to answer and ask additional questions about the effects of the mitten crab on crayfishing.

Behavioral experiments to examine the interaction of Chinese mitten crabs and signal crayfish

To further determine whether the Chinese mitten crab is affecting crayfish populations, we conducted controlled laboratory experiments to examine the interaction between the two species. We specifically examined whether a dominance hierarchy existed between the two species, and whether the presence of shelter reduced aggressive interactions between the species. We designed the experiments to test two null hypotheses: first, that there is no dominance hierarchy between the two species, as measured by the difference in levels of initiation of aggressive behavior by Chinese mitten crabs towards signal crayfish or vice versa; and second, that the

presence of shelter does not have a significant effect on the level of aggression expressed by either species.

Experiments were conducted from October to December, 1998, at MSI in Redwood City, CA. Adult Chinese mitten crabs were collected from the US Bureau of Reclamation Fish Collection Facility in Tracy, CA, and brought directly to MSI. Adult signal crayfish were collected by baited trap from the Sacramento River in West Sacramento, CA, and brought directly to MSI. Mitten crabs and crayfish were provided with a combination of natural stone and constructed (from PVC and flowerpots) shelters. Mitten crabs were maintained on a diet of shrimp and squid, and crayfish were maintained on a diet of carrots, potatoes and squid. Mitten crabs and crayfish were individually identified using numbers painted onto the carapace with nail polish. Water temperatures in all aquaria were between 11° and 15°C for the crayfish, and between 14° and 17°C for the crabs.

Interactions were conducted in rectangular glass aquaria measuring 61cm x 30cm x 30cm. Gravel substrates were provided in each aquarium and temperature was maintained between 12° and 14°C. Experiments were conducted in natural light conditions during daylight hours. A total of 23 experiments were conducted. Prior to beginning each experiment, a mesh divider was placed in the center of each aquarium. In 21 experiments, one crab and one crayfish of the same sex were added, respectively, to the two separate compartments. In two interactions, two crayfish and one crab were added, respectively, to the two separate compartments to examine the effects on behavior of introducing multiple animals. The animals were allowed to acclimate for one hour, and then we removed the mesh separating the two animals and began recording the interactions. Each experiment was run for one hour. Individuals used in an experiment were not used for the following seven days, following the methods of Söderbäck (1991).

We also examined the effect of shelter on the behavioral interactions of mitten crabs and crayfish. In 16 of the 23 experiments, a natural stone shelter was first set up in one corner of the tank, and a crayfish or crab was added to this compartment; the other compartment was sectioned off by the divider, had no shelter, and housed the other species. After acclimation, the divider was removed and the behavior was recorded. Behavioral responses were categorized into the following categories, based on modifications of definitions given by Söderbäck (1991) and Bovbjerg (1953): *fight*, where the interacting individuals lock chela(e); *strike*, where one individual hits the other with its chela(e); *threat*, where one individual raises its chelae outstretched towards the other; *push*, where one individual pushes the other away using one or more of its walking legs; *avoidance*, where one individual retreats without overt aggression from the other; *retreat*, where one individual backs away from the other after it is faced with an aggressive action; and *ignore*, where the aggressive actions of one individual produce no noticeable response (such as strike or retreat) in the other individual.

V. RESULTS

Distribution and Abundance in the South Bay

Distribution

Mitten crabs were found at nine of the 15 sites we sampled during the summer of 1995 (Figure 10). Juvenile crabs were distributed up to eight miles inland from the Bay and the majority of these were confined mainly to tidally influenced areas. Of the 72 sites sampled in 1996, 20 were concrete lined channels and six were completely dry; thus 50 of the 72 sampled sites provided suitable habitat for crabs. Of these 50 sites, 34 sites contained mitten crabs. Three upstream sites that did not contain crabs during 1995 surveys were found to contain mitten crabs during the summer of 1996. In 1999, monitoring of sites during the summer months revealed a similar overall distribution, although crabs were additionally found during this season in a higher elevation tributary to Alameda Creek.

In 1995 and 1996, we did not find mitten crabs larger than 20mm carapace width in the South Bay sloughs that became concrete-lined channels less than one mile from the river mouth. No dead crabs or remains larger than 20mm in carapace width were found in these areas. This size limitation may occur because juveniles leave these areas to go back out into the Bay when suitable upstream habitat cannot be found. However, this pattern changed in ensuing years, because we found larger crabs, up to 35mm in length, in these sloughs in the summer of 1999. We found no crabs upstream of areas that were channelized and lined with concrete 1995 and 1996; in 1999, however, we observed crabs in areas upstream of concrete-lined portions of sloughs.

Abundance of juveniles

At the four South Bay slough sites examined for juvenile abundance in the summer of 1995, burrow densities ranged from 2 burrows/m² to 18 burrows/m² (Figure 12a). Burrow densities were highest during summer months (June-September) and lowest during the winter months (January and December) at three of the four sites sampled. The one site that did not show a decrease in burrow density during the winter, the upstream Guadalupe site (farther from the Bay), was the furthest upstream of the four sampled sites. The highest density of juvenile mitten crab burrows at the four sampled sites consistently occurred along the downstream Guadalupe River site (closer to the Bay) (up to 18/m²). In 1999, we found much higher burrow densities than found in 1995. Burrow densities at the two sites sampled in 1999 ranged from 18 burrows/m² to 39 burrows/m² during the summer months of 1999 (Figure 12b). At the Calabazas Creek site, burrow density showed a dramatic increase in four years: in 1995 the highest average burrow density recorded was 6 burrows/m²; but in 1999, burrow densities at Alameda Creek averaged 37 burrows/m² over the months of June and August (Figure 12).

Abundance of adults

Adult Chinese mitten crabs begin their downstream migration in the fall and breed through the winter and into spring. We therefore analyzed trawl data by dividing the dates into seasons that began in the fall of one year and ended in the summer of the next: for example, data was pooled so that spring of 1996 was analyzed as one reproductive season, and the following fall of 1996 was grouped with the spring of 1997. During the spring of 1995, a total of 66 crabs were

recorded by MSI trawls and trawls. The catch per unit effort (CPUE) for 1994/1995 trawls by MSI averaged 0.12 crabs/ trawl. In the beginning of 1996, 81 crabs were caught in MSI trawls. The CPUE for 1995/1996 was 125% that of 1995, at 0.16 crabs/trawl: in other words, crabs became about 25% easier to catch by trawl in fall 1995/spring 1996 than they were in spring 1995 (Table 1). In 1996/1997, however, the CPUE for crabs declined to 0.11. MSI Trawls for 1998/1999 yielded 117 crabs. The CPUE data is unavailable for 1998/1999 catches; however, if it is assumed that the number of trawls during 1998/1999 is similar to that of other years, then it is likely that CPUE was higher for 1998/1999 than previous years based on the higher number of crabs caught. It is difficult to compare data between the years, however, because regular collection and measurement of the crabs by MSI and us did not begin until February of 1995 and was not consistent thereafter.

Life History

Habitat and Population Parameters

We found mitten crabs throughout three different habitats in South San Francisco Bay: the main body of the Bay; tidal sloughs (tributaries influenced by tidal inflow); and freshwater creeks (tributaries upstream of tidal influence). Salinity among the three habitats was quite different, ranging from 15-35ppt in the body of the Bay, 1-15ppt in tidal sloughs, and <1ppt in freshwater creeks.

Adult mitten crabs and newly hatched mitten crab larvae occupy the open waters of the Bay. Adult mitten crabs reproduce, eggs hatch and larvae develop in the Bay. Because trawls were conducted year round, but adult crabs were collected only between October and May, and gravid females were found only between November and April (Figure 13), the premise that movement to saline waters for reproduction by mitten crabs in California, like their counterparts in other countries, occurs between late fall and late spring in saline environments is supported.

Within the reproductive season, trends in the data suggest that reproduction may have peaks or pulses: in 1996/1997, the highest percentage of gravid females was found in November and again in March of 1997. In 1998/1999, the peak in gravidity was found in November through February, with no noticeable spring peak as was found for 1997 (Figure 13). However, as indicated in Figure 14, some months of sampling yielded low numbers of female crabs (<3 per month), and so findings from low sample sizes should be treated cautiously in terms of examining trends in gravidity.

Sex ratio data collected for mitten crabs shows wide temporal and age-class variability. Adult mitten crabs collected in trawls from the Bay exhibited an overall male:female sex ratio of 44%. However, this overall ratio should not be viewed as a good estimate for the population sex ratio, as it is influenced by low sample sizes for some months and by a wide variation in sex ratios over the reproductive season (Figure 14; Table 1). The temporal variation does suggest a seasonal change in sex ratios. Males comprise the majority of adult mitten crabs trawled from the bay in the fall and early winter months of each year of data from 1995 to 1998/99. This sex ratio changed in 1996 and 1997, however, during the late winter/early spring, when more females were

collected (Figure 14). This trend in sex ratios may reflect a temporal sequence of migration according to sex, with the males migrating downstream first to the breeding grounds, and the females following the males, as has been discussed for this crab in other countries (Panning 1938; Zhao 1999).

Juvenile mitten crabs inhabit the tidal sloughs and lower reaches of freshwater creeks. Juveniles were found in both areas all year long, and were most common in areas of low salinity (<2-3ppt) that had steep, clay banks lined with bulrush. Water temperatures in these areas varied between 20° - 31°C during the summers of 1995, 1996 and 1999. Juveniles inhabiting the upper parts of freshwater creeks were older and larger than those inhabiting downstream and tidal areas. This pattern is consistent with the knowledge that Chinese mitten crabs migrate upstream to new areas during development. In freshwater creeks, juvenile mitten crabs were most abundant in shallow areas with slow moving water adjacent to deep pools with emergent macrophytes. Although mitten crabs were found upstream of riffles, no crabs were observed in riffle areas.

Growth

At the four sites sampled for mitten crab abundance in 1995 and 1996, crabs ranged in size from 5mm to 37mm carapace width. All four of these sites were within three miles of the Bay and all four were tidally influenced. The average size of juveniles ranged between 14 and 21mm carapace width during the summer of 1995 in intertidal areas sampled; similar size ranges were found in sites sampled during the summer of 1999 (Figure 16). As Chinese mitten crabs are capable of growing upwards of 30mm in a single season in order to reach reproductive maturity within a year, but may also take more than a year to reach maturity (Zhao 1999), we do not know if this size range of juveniles represents one or more year classes of crabs. However, juvenile crabs were present during the winter months that these sites were monitored, suggesting that juvenile mitten crabs remain in these habitats for more than one season before becoming sexually mature and migrating downstream to the body of the Bay.

Juvenile mitten crabs larger than 35mm carapace width and up to 80mm carapace width were found upstream of all four sampled sites during the summer of 1996 and again during the summer of 1999. Although crabs larger than 35mm carapace width migrated past all four sampling sites during fall migration back down to the Bay, crabs of this size were never found inhabiting burrows in tidally influenced sites during the summer or fall. These patterns in distribution of size classes indicate an inverse relationship between size and distance from the Bay, consistent with the understanding that these crabs migrate upstream as they age. It is possible that size differences along the stream continuum are caused by pulses of mitten crabs that are hatched during different times during the reproductive season. Larger mitten crabs found upstream may be hatched earlier in the season than their younger counterparts found at the same time of year but closer to the mouths of the tributaries.

Crabs collected from the South Bay in MSI trawls during the spring of 1995, fall 1995/spring 1996 and fall 1998/spring 1999 ranged in size from 27 to 78mm carapace width. The average size of females (40mm) was not significantly different from that of males (37mm) ($p=0.21$). Mean size of males and females was very consistent among months and between years (Figure 15).

Diet

Gut content analyses of juvenile mitten crabs revealed that the crabs eat mainly detritus. Invertebrate parts were found in only 2% of crab stomachs analyzed. No difference in diet was detected between mitten crabs inhabiting different habitats in the South Bay, i.e. the brackish river mouth compared to the tidal slough or freshwater creek. We note, however, that crabs held under laboratory conditions readily ate animal matter, including squid and shrimp, and we have observed mitten crabs eating dead fish in South Bay creeks (see below). We believe that, consistent with other reports (Panning 1938; Hymanson et al. 1999), the crabs are omnivorous and opportunistic in their diet. While other research indicates that the crab shifts towards carnivory as it ages (Dan et al. 1984), we did not detect this trend in our analysis.

Behavioral Observations

Field observations of juvenile mitten crabs during the summer of 1996 and 1999 revealed that mitten crabs were extremely active during the day and far less active during the night in South Bay sloughs and creeks. During the day, we observed mitten crabs foraging in the shallow stream margins among stands of emergent macrophytes. Mitten crabs were picking detritus off the substrate and picking algae off of rocks, wood and other objects in the stream. Nighttime observations during the summer of 1996 did not reveal any foraging.

During the day, mitten crabs typically foraged near a burrow or an object, such as a tire or a rock, that could serve as a refuge from predators such as wading birds and raccoons. We observed mitten crabs defending the area around their burrows or place of refuge, chasing away other crabs and crayfish from its area. We also observed that at several tidally influenced sites with soft substrates, prints of animals were abundant around the burrows and, in some cases, led directly up to the entrances of the burrows. We did not observe actual excavation of burrows, though a few burrows looked as though the animal had scratched around the entrance to the burrow. The prints of wading birds, raccoons and other small mammals were observed in these areas. Colleagues working in this area found what was probably raccoon scat in these areas containing pieces of mitten crab shell (Dudley 1999). It is likely that a wide range of birds and mammals inhabiting these habitats are predators of juvenile mitten crabs. Several predatory fish, including white sturgeon, striped bass, black bass, catfish, in addition to bullfrogs, loons and egrets, have been reported to prey on Chinese mitten crabs in the San Francisco Bay-Delta ecosystem (Veldhuizen and Stanish 1999).

Ecological and Economic Impacts

Impacts on bank/levee integrity

Burrows were found only in channels or levees in tidally influenced areas of South Bay tributaries that had substrates containing high percentages of clay and silt. In set-back levees, burrowing was almost always confined to the banks of the main channel, with occasional burrowing along the flatter embankment bordering the channel. Only at one site, on Alameda creek, were burrows observed extending out to the actual bank of the levee itself (D. Rudnick, personal observation).

Mitten crab burrows were only very dense in tidally influenced areas with steep banks. We observed mitten crab burrow densities ranging from $2/\text{m}^2$ - $18/\text{m}^2$ in 1995/1996, and from $18/\text{m}^2$ to $39/\text{m}^2$ in 1999 (Figure 12). We observed limited areas of bank collapse in areas with high densities of mitten crab burrows. Bank collapse often altered the morphology of the bank, changing the bank from a near vertical wall to a more reduced slope.

The average diameter of the mitten crab burrows measured during 1995 and 1996 was 3cm ($n=150$, $s.d.=1$), and average depth of the burrows was 20 cm ($n=150$, $s.d.=12$). The average volume of the burrows based on these measurements was 141cm^3 . Using the range of mitten crab densities found in the field ($4/\text{m}^2$ - $18/\text{m}^2$ for 1995/1996, and $18/\text{m}^2$ - $39/\text{m}^2$ for 1999 estimates) we estimated sediment removal caused by crab burrowing to range between 564cm^3 to $2,538\text{cm}^3$ per m^3 bank area for 1995 and 1996 densities, and from $2,538\text{cm}^3$ to $5,499\text{cm}^3$ per m^3 bank area for 1999 densities. This estimate does not include the secondary effect of increased erosion of banks weakened by burrows.

Impacts on co-occurring species: red swamp and signal crayfish

Effects of Chinese mitten crabs on the presence of red swamp crayfish

We found no correlation between the presence of mitten crabs and absence of crayfish during the summer 1996 survey. Of 36 sites sampled for both crayfish and crabs, 27 contained crayfish and 20 contained mitten crabs. All 20 of the sites that contained mitten crabs also contained crayfish. Monitoring, however, has not been conducted to look at potential changes in distribution of crayfish since 1996.

The guts of twenty red swamp crayfish sampled from the Guadalupe River during the summer of 1996 showed similar gut contents, composed mainly of detritus, to the guts analyzed for mitten crabs. No invertebrate parts were found in the sampled crayfish. No other obvious differences between the gut contents of crabs and crayfish could be detected, indicating that the diets of these two species are likely to overlap.

During August of 1999, we observed red swamp crayfish and Chinese mitten crabs simultaneously feeding on fish carcasses at a site along Calabazas Creek approximately four miles upstream from the mouth of the Creek. All individuals appeared to be adult or sub-adult in size. While both crayfish and crabs were feeding on the same group of fish carcasses, we observed that the crayfish nearly always backed away when feeding mitten crabs approached their section of the fish; however, mitten crabs did not change position when approached by crayfish. While anecdotal, this observation suggests that mitten crabs may exhibit dominance over crayfish in terms of access to food. The fact that both species were feeding simultaneously, however, suggested that the mitten crabs were not actively defending the food source from crayfish. It is possible that such dominance behavior would only have a significant effect on crayfish if food supplies were scarce.

Surveys to determine impact of the Chinese mitten crab on crayfish fisheries

Results from our surveys sent to commercial crayfishermen indicate that there is concern among members of this industry that mitten crabs are or soon will negatively impact crayfish populations.

Respondents indicated that they had brought up mitten crabs either on or in their crayfish traps, though no respondent reported high numbers of crabs (i.e. responses indicated <1 crab per 100 traps hauled). Respondents did not directly observe negative interactions occurring between the crayfish and mitten crabs they caught. A few respondents, both through the surveys and through personal communication, stated that they have seen a decline during 1997 and 1998 of their catch per unit effort for crayfish. Given the number of factors potentially affecting crayfish harvest (e.g., El Niño, pollution, habitat degradation), and the minimal years of data on crayfish harvest in the presence of mitten crabs, it is not currently possible to conclude whether the Chinese mitten crab is affecting crayfish harvests.

We received a low response rate from our surveys; only 3 out of 8 surveys sent out were returned. This low response rate may reflect a concern among crayfish fishermen about sharing information about where they are conducting fishing, as good harvest sites are prized and guarded in the industry (Hagen and Hagen 1998). Because it is illegal to possess live mitten crabs, there may be fear on the part of some crayfishers that reporting catch of mitten crabs, even though the catch is incidental, could make them liable for prosecution by government officials (Olds 1998). Although we assured survey participants of the confidentiality of all results, we believe that, if the survey is reissued, the importance of this research and the anonymity of the responses must be emphasized.

Behavioral experiments to examine the interaction of Chinese mitten crabs and Signal crayfish

For the purpose of analysis, we grouped the following behaviors together as expression of aggressive behavior: *push*, *threat*, *strike* and *fight*. We did not observe any predation by either species on the other over the course of these experiments.

Figure 17 shows the percent of aggressive behavior separated by sex for both signal crayfish and mitten crabs. The results do not show a significant difference between the number of aggressive actions initiated by male Chinese mitten crabs versus the number of aggressive actions initiated by male signal crayfish ($p=0.82$) (Figure 17 and Table 2). For female *Eriocheir* tested against female *Pacifasticus*, there was a large, though not statistically significant ($p=0.07$), difference in number of aggressive interactions initiated between the two. While the statistical power of the test was sufficient for male interactions ($>95\%$), based on the variance in and the low sample size of this pilot study for the female interactions, statistical power was too low to confirm our findings of no significant difference between females. We did find a significant difference between the sexes in the level of aggression exhibited; males of both crabs and crayfish exhibited a significantly higher rate of aggression than females of both species ($p<0.05$) (Figure 17 and Table 2).

The presence of shelter had a significant effect on reducing the rate of initiation of aggressive behaviors by male Chinese mitten crabs (Figure 18 and Table 2; $p<0.05$). Shelter did not, however, significantly affect the rate of aggressive interactions of females of either species or of male signal crayfish, although there was a large, non-significant decline in the occurrence of aggression exhibited by the male crayfish. Eleven aggressive interactions took place inside the shelter. In four of these interactions, the mitten crab was in the shelter and the crayfish attempted to enter the shelter; in the other seven interactions, the crayfish was in the shelter and the mitten crab attempted to enter the shelter. In all 11 interactions, the mitten crab gained or retained

control of the shelter; in four interactions in which the crayfish was in the shelter and was approached by the mitten crab, the mitten crab either forcibly ejected the crayfish from the shelter, or the crayfish retreated from the shelter after the mitten crab entered. In three interactions in which the crayfish was in the shelter, the mitten crab entered and remained in the shelter in front of the crayfish, pinning the crayfish against the back of the shelter until either the crab decided to move out or the experiment ended. In the four interactions in which the mitten crab was in the shelter and was approached by the crayfish, the mitten crab responded aggressively to the crayfish's approach and the crayfish retreated.

VI. DISCUSSION

Ecology

Distribution and Abundance

The distribution of Chinese mitten crabs in the South Bay tributaries presently appears to be restricted by: 1) the absence of water in intermittent streams during the summer months; and 2) the presence of concrete-lined flood control channels that do not provide suitable habitat for the crabs. Almost all of the freshwater and tidally influenced areas that were surveyed that provided habitat (i.e. not dry or lined with concrete) contained the crabs. It is also worth noting some of the changes in distribution observed between 1995/1996 and 1999. Whereas crabs were not found in any concrete-lined channels in the first two years of the survey, in 1999 we began to find crabs in concrete-lined channels. In addition, in 1999 we began to find larger crabs (>20mm carapace width) in tributaries which became concrete-lined close to their entrance into the Bay. These changes in distribution may indicate that more highly preferred habitats are becoming more scarce, possibly because of pressure from large mitten crab populations, leading crabs to use less ideal habitats that provide lower amounts of cover, vegetation and room for upstream migration. Currently, we are not finding crabs in the upper reaches of these tributaries, such as areas beyond reservoirs that feed the tributaries (Figure 10). It is possible, however, that the crabs do occur further upstream but they are present in numbers too low for us to be likely to observe them during monthly surveys.

If Chinese mitten crabs invade new ecosystems in California, the invasion will most likely be the result of human transportation of juveniles or adults to new areas and/or by using artificial channels that connect northern and southern watersheds in California. Most catadromous species have a larval retention mechanism to prevent larvae from being washed out into the ocean (Anger 1994). Mitten crabs most likely exhibit this type of retention mechanism as well (Anger 1991), making larval transport out of San Francisco Bay unlikely. The abundance of artificial channels that have been constructed for water transport between watersheds in California, such as the California Aqueduct, do, however, provide possible channels by which mitten crabs can enter new areas. Recently low numbers of mitten crabs have been reported in the aqueduct as far south as state water projects just north of Bakersfield, in southern California (Hieb 1999) (Figure 19). In addition to providing a population source for new ecosystems in California, the San Francisco Bay/Delta population can be considered a new source (e.g., via ballast water taken up in the Bay or humans deliberately transporting mitten crabs from the Bay-Delta into new areas) for the introduction of Chinese mitten crabs throughout North America as well as into other countries.

Because mitten crabs are a highly valued food item in Asian communities, fishing efforts are likely to increase over time. The Department of Fish and Game has conducted hearings to investigate the interest in and possibility of a commercial fishery for the Chinese mitten crab (Hieb 1999). Increases in the crab population and increases in the number of people fishing for the crabs makes accidental or intentional transport to new areas more of a possibility.

Reports from local citizens, fishermen and the California Department of Fish and Game indicate that adult mitten crabs are more common in South San Francisco Bay than in the North Bay and

Delta (Halat 1996; Hieb 1999). Given that the Chinese mitten crab was collected during the first few years only in the South Bay, it is probable that the mitten crab was introduced into the South Bay and spread from there. We are still in the early years of the invasion of this species; thus, it is possible that differences in abundance between the North and South Bay may be attributable to the fact that populations in the South Bay established earlier than North Bay populations. It is possible that environmental differences may also contribute to the differences in population levels between these areas.

From our data, it appears that mitten crabs have expanded in abundance and in distribution during the years we have conducted monitoring of the species. Reports submitted to the Department of Fish and Game support this finding. During the summer of 1995, only one report of a mitten crab in a South Bay slough was taken by a fish and game officer (Hieb 1999). In contrast, during the summer of 1996, at least ten reports of mitten crab sighting were reported by local citizens in San Jose (Halat 1996). This increase in reports, however, may not be solely a function of increased abundance, but may also be caused by an increased awareness of mitten crabs in the area. Data from MSI trawls between 1995 and 1999 also support the idea of population increases.

Mitten crabs are not extremely abundant in all areas along South Bay tidal sloughs; areas of high mitten crab abundance are patchy and are most often limited to sloughs with vertical or near-vertical banks. In areas where mitten crabs are very abundant in the South Bay, space does appear to be a limiting factor. In such areas, the burrows frequently run into one another and in several instances we have observed one entrance leading to three or more burrows. The decrease in density of burrows over winter months at three of four sampling sites is probably the result of a combination of: 1) crabs moving to the Bay for reproduction; 2) crabs leaving for upstream areas to continue development; and 3) deterioration of burrows because of environmental factors including high water events that wash away burrows and sediment collapses that remove burrows. Although it seems that several species opportunistically prey upon mitten crabs, no local predator is known to specialize on these crabs, and their continued abundance indicates that natural control of the population is unlikely at this time.

The numbers of adult crabs trawled by MSI in the South Bay are low considering the abundance of juveniles we have documented. These low numbers may be reflective of an accurate sample of adult mitten crabs in the South Bay. It is also possible, however, that trawls are not capturing a representative sample of the adult population. Reasons may include trawls being taken in sub-optimal locations to sample the majority of the crabs (e.g., adults are remaining adjacent to the tributaries they migrate from, and are thus not abundant in the open waters of the South Bay; or adults are congregating farther north in the bay than trawls occur) or because the trawling method is not an efficient way for capturing crabs (e.g., the crabs can move out of the way of the otter trawl before it can capture them). In the future, it will be useful to sample areas near the mouths of South Bay tributaries in order to discover whether crabs are indeed remaining closer to the shores of the Bay. At this time, otter trawling is the most comprehensive method available and is compatible with the efforts of MSI to collect additional biological data, so we do not foresee that this method of collection will be eliminated the future.

Life History

Age-dependent changes in habitat preferences of mitten crabs in the South Bay correspond to the life history pattern of this species. From our data of adults trawled from the body of the Bay, it appears that adult male mitten crabs descend to the breeding grounds in mid- to late fall and are followed by the adult females. The pattern of egg-hatching for the Bay population, based on when gravid females are found, appears to be similar to reports of eggs hatching in spring in Europe (Anger 1991). As larval development and metamorphosis, at least in the laboratory, takes place over a few weeks (Anger 1991; Montú et al. 1996), the eggs are probably being released from adults in the mid to late spring. The newly metamorphosed juveniles (<5mm carapace width) appear to arrive in freshwater areas in the South Bay during the early summer. It is likely that newly settled juveniles then migrate upstream from the Bay until they find a suitable area to settle and begin growth. This reasoning is based on our findings that the smallest juveniles are most abundant in tidally influenced areas, while larger juveniles are found in tidally influenced areas upstream into freshwater areas. As juveniles grow and require more resources, they may be prompted to move further upstream into non-tidal areas where crabs are less abundant and competition for resources is reduced.

The smallest reproductively active adult mitten crabs collected from the Bay were approximately 35mm in carapace width (MSI data, unpublished). We have found mitten crabs of this size burrowing in tidal areas. It is possible that some crabs never leave tidal areas, and complete their growth and development without moving upstream; such crabs would leave tidal areas and move downstream during the winter. The majority of mitten crabs, however, are probably moving upstream into freshwater habitats in order to further develop and grow. It has been reported that mitten crabs take between 1 and 5 years to develop in their native range and in other countries into which they have been introduced (Hymanson et al. 1999). It should be noted, however, that little published information regarding the life span and time to reproduction is available for the mitten crab outside of its native range. In China, approximately 5% of crabs develop within one year, the majority (60%) develop in two to three years, and the rest take longer than three years to develop (Hymanson et al. 1996). Given the wide range of sizes of mitten crabs we found at any one time in tidally influenced, freshwater and saline environments of the South Bay, it is possible that these different size crabs belong to multiple year classes that are developing at different rates. Zhao (1999) has also suggested that there may be two types of Chinese mitten crabs in the Bay: one type, predominant in the South Bay, matures within about a year and is relatively small; the larger race develops in 2 years, and is predominantly found in the North Bay and Delta. At this time, the differentiation between populations and the source of this variation remain unproven conjectures.

Gut content analysis of juvenile mitten crabs indicate that the juveniles are mainly detritivores. Traps baited with rock fish, cat food, tuna or anchovies were not attractive to juvenile mitten crabs in the field. Juvenile crabs held in aquaria in the laboratory, however, ate both algae provided from a local creek and dead shrimp, and field observations recorded mitten crabs feeding on dead fish. Reports of bait stealing by mitten crabs from recreational anglers suggest that the crabs will prey upon any type of food, animal or vegetable, presented to them (Hutchinson 1998).

Our behavioral observations of the activity patterns of mitten crabs are not in complete agreement with reports from the literature. The crabs we observed were quite active during the day, foraging and defending their burrows. Asian and European literature, however, indicates that mitten crabs in those countries may be more active in the night and early morning hours (Panning 1938; Dan et al. 1984). Although we did not observe any crab activity at night, it is possible that crabs migrate during that time.

Ecological and Economic Impacts

Impacts on banks and levees

We found mitten crab burrows almost exclusively in tidally influenced areas of South Bay tributaries. Although crabs sometimes inhabit burrows in freshwater areas, these burrows are almost always on the stream bottom rather than along the banks. As a result, damage to stream banks in the San Francisco Bay and Delta should be confined to tidally influenced areas. Densities of mitten crab burrows are very high in South Bay tidal sloughs, and are higher than 30/m² in some areas. Peters and Panning (1933) reported 30 burrows/m² to be a damage - causing density of mitten crabs along German stream banks, leading to bank collapses and erosion.

Mitten crabs that burrow are, on average, less than 40mm carapace width; larger mitten crabs usually do not burrow but take cover under objects on the substrate or in deep pools. Although it is smaller crabs that are burrowing, large numbers of these crabs have the potential to cause bank damage over time. Burrowing removes sediment from the bank, weakening the overall structure. In addition, mitten crab burrows are designed to hold water at low tide. Water retained in the burrows increases the pore pressure on the banks, increasing the potential for bank slumping. Our observation of slumping in high burrow-density areas suggests that the burrows may indeed be causing bank slumping to occur. By increasing pore pressure and removing sediment, mitten crab burrows also make bank areas more susceptible to natural erosive forces such as rain and tidal events.

Most of the South Bay tidal channels where mitten crabs burrow are set-back levees (Figure 7). The distance between the levee and the banks of the main channel in which the crabs are burrowing is often 10 meters or more. This set-back structure means that the levees are relatively well protected from burrowing at the channel margins. Over time, however, extensive burrowing could reduce this distance and threatened levee integrity. At this time, few mitten crabs have been observed burrowing into the actual levees in the South Bay.

Impacts on co-occurring species

One of the major ecological concerns related to the establishment of the Chinese mitten crab in the San Francisco Bay and Delta is the potential impact of the crabs on co-existing organisms. We have found that, at this time, mitten crabs are the most visually abundant macrocrustacean in the tidal channels and freshwater streams of the South Bay. The red swamp crayfish overlaps with mitten crabs in habitat and dietary preference in the South Bay. At present, it does not appear that mitten crabs have affected the presence of crayfish in the South Bay. Further testing, including controlled field and laboratory experiments, are needed in order to examine direct and

indirect effects, including competition for food and shelter, between the two species. Because mitten crabs are visually much more abundant, aggressive and active than the red swamp crayfish, we do believe direct or interference competition from the mitten crab on crayfish is possible.

Results of behavioral experiments did not allow us to reject the hypothesis of no dominance hierarchy between mitten crabs and signal crayfish. In the case of interactions between females, however, we did not have the statistical power in this series of experiments to determine a difference in level of aggression. We believe that additional experimental studies are necessary to improve confidence in these findings. We did not conduct studies between varying sizes of crabs and crayfish because of the time of year during which studies were conducted (large juveniles and adults were more abundant at this time of year and were readily available using our trapping methods) and because of our interest in limiting the initial number of variables in these experiments. Given that both adult mitten crabs and crayfish have a multiple-year lifespan, it is quite feasible that different size classes of these species interact under natural conditions, and the possibility for aggressive interactions between these size classes needs to be examined.

Experiments designed to test relationships between Chinese mitten crabs and other species should seriously consider the effects of sex on behavior. The significant difference in level of aggression between males and females of both crabs and crayfish reveals that male and female study subjects should not be lumped together for the purpose of analysis. These findings suggest that several different dynamics could occur under natural conditions, depending on the sex of species that interact. Combined with the possibility of different behaviors arising when different size classes interact, the real-world effects of crayfish-crab interactions are potentially extremely complex. Conjectures about simple dominance orders between the species are not appropriate based on our findings.

The presence of shelter was correlated with a significant reduction in male mitten crab aggressive behavior initiated towards male crayfish, and a non-significant but large reduction in the rate of aggressive behavior initiated by male crayfish. We suggest that these reductions in aggressive behavior occurred because one animal simply was not visible to the other, and thus may not have provoked an interaction. The implications of these findings include that: when sufficient shelter is available for crabs and crayfish, the rate of competition may be lower; conversely, areas with low available shelter, including open streams with little vegetative or bank cover, or areas where mitten crab or crayfish populations are dense may have higher levels of competition. If shelter is a limiting environmental factor, and direct competition for shelter does occur, our findings suggest that the mitten crab will be a dominant competitor for habitat over the crayfish. The lack of observed predation suggests that these two species may not seek each other as prey, but that the potential for competition may still occur because of the overlap of habitat. Although we did not experimentally test for food competition, our field behavioral studies and gut content analysis suggests that food preferences overlap between mitten crab and crayfish species, and could also lead to competition between the species.

Mitten crabs are likely to effect other Bay species as well. In the North Bay and Delta, mitten crabs are likely to interact with the signal crayfish, in addition to other benthic invertebrates including the Harris mud crab, *Rithropanopeus harrissi*. The mitten crab has also become

established in tributaries of San Pablo Bay (between North San Francisco Bay and the Delta) that provide habitat for the endangered California freshwater shrimp, *Syncaris pacifica*. The crab's opportunistic foraging habitats could include such shrimp as a prey item.

The signal crayfish is a commercially important crustacean in the delta, drawing in about \$4 million/year for the crayfish industry in this area (Hieb 1999). Our formal and informal surveys indicate that crayfishermen are concerned about potential impacts of the mitten crab on the signal crayfish industry, and that they have in some instances incidentally harvested them in their traps. The crab has also been a nuisance to commercial bay shrimp trawlers. Shrimp trawlers have found it time consuming to remove crabs from their nets, which may be caught in numbers as high as hundreds per trawl in the South Bay, and the shrimp industry is concerned about damage to both their nets and catch from the mitten crabs (Veldhuizen and Stanish 1999).

VII. REGIONAL DISTRIBUTION OF THE CHINESE MITTEN CRAB

Our research indicates that mitten crabs are well-established in South San Francisco Bay and its tributaries. The Chinese mitten crab is also particularly prevalent in the North Bay and the water systems that feed it: Suisun Marsh; the Sacramento-San Joaquin Delta (the Delta); and their tributaries (Figure 20). Over the past 5 years, the crab has become distributed throughout hundreds of miles of tributaries feeding the Bay and Delta (Figure 3).

Distribution of the Chinese mitten crab in North Bay tributaries

Mitten crabs were observed in Suisun Marsh and the Sacramento Delta beginning in 1996. In that year, 45 mitten crabs were collected from a combination of otter trawls and samples taken from fish collection facilities and at the Contra Costa power plant at Antioch (Hieb 1997). The appearance of the crabs prompted the California Department of Fish and Game to begin a survey of the crabs in 1997. Four stations in Suisun Marsh and 11 in the Delta were chosen for monitoring crab abundance and distribution; three additional stations in the Delta were added in 1998 (Holmes and Osmondson 1999) (Figure 20). Stations were monitored in July and August of 1997 and 1998. At each station, the site was surveyed at minus low tide, when the maximum bank area was exposed. Surveyors searched for mitten crabs along a 5m transect, excavating all burrows between high and low tide marks, and searching all debris, rootwads, overhanging vegetation and ponded water for mitten crabs (Veldhuizen 1997, Holmes and Osmondson 1999). In order to determine if there is a correlation between crab abundance and salinity, researchers surveyed mitten crab abundance along a salinity gradient from 3.9‰ downstream in Suisun Marsh to 0.1‰ upstream in the Delta. Also in 1998, researchers examined the use of floating aquatic vegetation by juvenile mitten crabs in order to determine whether floating vegetation provided a refuge for young crabs (Holmes and Osmondson 1999). A 1m² dip net was used to sample the vegetation, and the roots, stems and leaves were searched for crabs.

In both 1997 and 1998, mitten crab densities were higher in Suisun Marsh than in its tributary, the Delta (Table 3). Mitten crab densities actually decreased at three of four Suisun Marsh stations between 1997 and 1998. Between 1997 and 1998, however, Suisun Slough experienced a two-fold increase in density, from 1.46 crabs/m² to 3.04 crabs/m². In the Delta, mitten crabs were found at four stations in 1997 and at three stations in 1998.

Salinity gradient surveys revealed that, in 1998, the average density of juvenile mitten crabs was higher downstream of the Delta than in the Delta. In general, size increased along the gradient from downstream to upstream (Holmes and Osmondson 1999). This size distribution agrees with our South Bay findings that size increases along a waterway as salinity decreases, suggesting that younger crabs tend to use brackish waters and migrate into fresher water as they grow older.

It is unclear at this time whether the lower densities of mitten crabs in the North Bay than are seen in the South Bay are reflective of differences in population sizes or if they are influenced by sampling techniques. In the North Bay, burrow densities are far lower than burrow densities in the South Bay (Hieb 1999). Sampling mitten crabs using burrow excavation and bank search techniques in the North Bay may yield lower numbers than similar efforts in the South Bay because these sampling efforts may not account for crabs using other parts of the ecosystem in the

North Bay, such as the substrate of open waterways or vegetation. Vegetative cover, particularly submerged and floating aquatic vegetation, is denser in the Delta than in other parts of the Bay ecosystem, such as in Suisun Marsh and the sloughs of the South Bay; the crabs may be using this vegetation as refuge more frequently than they do in other areas of the Bay (Veldhuizen 1999). As discussed above, however, lower densities in the North Bay than in the South Bay could be a reflection of true population size differences, possibly resulting from mitten crabs having been present in the South Bay and its tributaries for a longer period of time.

Distribution outside of the Bay and Delta

Mitten crabs are also expanding their range outside of the North and South Bay. As of 1998, the distribution of the Chinese mitten crab extended north of Colusa in the Sacramento River drainage, and east past Sacramento and Stockton (Figure 3). The crabs have been making their way south through the California Aqueduct, and as of February of 1999, have been sighted as far south as the Cross Valley Canal State Water Project, a few hundred miles north of Los Angeles (Anonymous 1998) (Figure 19). Currently, the crabs are not abundant at these outer ranges; however, these numbers could rise if densities in the Bay area continue to increase, inducing crabs to migrate farther to seek food and shelter.

Impacts on Fish Collection Facilities

The impact of mitten crabs on state and federal fish collection facilities is one of the most visible and well-known effects of this species in its new environment. Several state and federal agencies maintain pumping facilities throughout California that generate power and/or control water flow. Fish and other aquatic life, however, can suffer high rates of mortality by becoming sucked into turbines and pumps. State and federal agencies are required to minimize these impacts as part of their responsibility for managing these water projects. Often, protection is achieved by creating a screen that guides fish out of the channel just prior to the pumping station and into a collection area; this system is collectively referred to as a "fish collection facility". Fish are either channeled around the pumping station, or they are put into a truck and released on the other side of the pumping facility.

The Chinese mitten crab threatens the function of these fish collection facilities and, in some areas, has already seriously impacted such facilities. As mitten crabs migrate downstream in the fall, they can become entrained with the fish in these collecting facilities. When the mitten crabs are abundant, they clog the collection facilities, and their sharp spines and legs damage and even kill many of the fish entrained with them. Separating fish from such large numbers of mitten crabs is extremely difficult and time consuming. For example, at the Tracy Fish Collection Facility (TFCF) in Tracy, CA, fish salvage operations nearly ceased as the number of mitten crabs entrained in the facility increased. Although there were only a few mitten crabs found in the fish screens at TFCF in 1996, by 1997 the number exploded to tens of thousands. In the summer and fall of 1998, 775,000 crabs passed through the facility (Figure 21). At its peak, over 30,000 crabs were entrained in the fish collection facility in a single day. As the numbers of mitten crabs increased, so too did the length of time over which they were captured in the fish facilities. In 1996 crabs were present only during a few months in the fall, but by 1998 they were captured nearly year-round. The clogging of TFCF by mitten crabs lead to the deaths of estimated

thousands of fish that would normally have been saved by the facility; the exact numbers of fish deaths are impossible to quantify (Siegfried 1999b).

In order to remove them from the fish collection facilities and waterways in 1997 and 1998, crabs were collected in large bins, put onto trucks and buried off-site. The effects of trapping these crabs on fish salvage was not quantified, but qualitative observations indicated that large numbers of fish were lost because of removal techniques that also captured the fish along with the crabs (Siegfried 1999). In 1998, the U.S. Bureau of Reclamation began work on a prototype for a travelling screen, which is a type of conveyor-belt apparatus that was originally designed to remove debris from the collection facility. This unit was tested for removal of mitten crabs and was shown to be capable of removing 90% of crabs from the collection area. This unit was put into place at the facility in the fall of 1999 (Siegfried 1999b). Simultaneously, however, and for unknown reasons, the mitten crab population arriving at the fish collection facilities was far smaller than that in 1998; the problems experienced at the facility were greatly reduced by this lower migration. It is unknown whether this population reduction was a single year event or a signal of a downward trend in the North Bay/Delta population of mitten crabs.

While the travelling screen will greatly enhance the separation of fish from crabs and improve fish salvage capabilities, the disposal of mitten crabs is still a problem for collection managers. Because the mitten crab is listed as a federally injurious species, facility managers are restricted from selling or transferring live mitten crabs to any corporation or other agency. Managers have so far chosen to bury the crabs, but critics have lamented that this procedure creates a considerable waste of protein (Sams 1998). The Bureau has recently contracted with a waste management company to remove the crabs for conversion to fertilizer (Siegfried 1999).

The entrainment of mitten crabs at TFCF has been beneficial in at least a few ways; the facility has provided an excellent source for estimation of population size, and has provided insight into aspects of the ecology of the mitten crab. For example, population estimates made over the last few years at TFCF using 10-minute counts and estimates made from collection bins of crabs have confirmed the exponential population growth rate for this species (Figure 21). The dramatic numbers have also raised public awareness about the serious problem these crabs are creating for water management facilities (Sams 1998; Vogel 1998 and 1998b). By recording data on abundance and sex of crabs, TFCF has shown a clear male bias in sex ratio for crabs migrating through the facility throughout the fall migration season (Figure 22). By recording daily temperatures and comparing temperature with crab numbers, the facility has shown a correlation between a drop in water temperature and the initiation of downstream migration of crabs (Figure 21). This information enhances our knowledge about the ecology of the mitten crab and provides a foundation for future research to determine environmental cues for the crab's behavior. Such research may lead to answers for how to control the mitten crab population.

VIII. CONCLUSIONS AND RECOMMENDATIONS

In many respects, the Chinese mitten crab is ideally suited to invading such aquatic ecosystems as the San Francisco Bay-Delta ecosystem (Appendix 2). Our research has found that juvenile crabs are broadly and densely distributed throughout the tributaries of South San Francisco Bay. We have also found that adult mitten crabs are spawning in the open waters of the South Bay. The crabs' reproductive season occurs from early winter to late spring, with variation throughout the past three years in terms of peak gravidity during this season. The mitten crab population appears to be continuing to expand throughout the freshwater habitats of the South Bay, as well as throughout the Bay-Delta ecosystem, and has now reached into southern California.

There are several potential and realized impacts from the establishment of this species. Impacts to banks and levees are substantial, though localized, to intertidal portions of tributaries containing steep banks, high mud content and dense vegetative cover. These habitat characteristics describe portions of several South Bay sloughs, so there is cause for concern for the integrity of these channel banks. Low burrow densities in the North Bay and Delta suggest that burrowing activities do not pose an immediate threat to banks and levees in these regions. The broad, opportunistic diet of the mitten crab suggests that it could be a competitor for food with other detritivorous species, such as freshwater crayfish. The mitten crab could also compete for shelter or space with crayfish and other benthic invertebrate species. Our initial surveys of the crayfishing community and experimental interactions between adult mitten crabs and signal crayfish support such concerns. The opportunistic diet and wide range of the mitten crab also suggest that it could prey upon sensitive species. We believe mitten crab predation on free-swimming fish is unlikely except in situations where fish are confined, such as in commercial fisheries, sport angling, or in state water project collection facilities.

The extensive distribution and enormous abundance of this species, combined with its opportunistic dietary habits and plasticity of behavior, suggests that widespread control of the Chinese mitten crab would be a difficult and costly undertaking. Eradication of the population at its current size is not feasible. Lessons from Europe, however, do suggest that for unknown reasons the Chinese mitten crab population commonly undergoes oscillatory cycles of abundance; it may be extremely abundant for 10 or 15 years, and then suddenly decline for a decade or more at a time. We may witness similar population cycles in the Bay-Delta ecosystem. At this time, however, it is not possible to accurately predict the length or timing of such cycles, and we believe control efforts can be immediately applied to systems that are suffering acute damage from mitten crabs, such as fish collection facilities and commercial fisheries. More diffuse impacts from mitten crabs, including bait-stealing from sport anglers, and weakening of banks and levees from burrowing, are symptoms of the overall abundance of this population and will be more difficult to ameliorate.

The Chinese mitten crab has become an established member of the non-indigenous communities of the San Francisco Bay-Delta ecosystem. We believe that the ecological niche filled by this new invader is similar in some respects to that of other detritivorous benthic invertebrates like freshwater crayfish and intertidal crab species. However, the abundance of this crab, its propensity to migrate in huge pulses, and its distribution throughout a range of salinities are

creating many changes throughout the saline and freshwater habitats of this ecosystem. The economic and ecological costs of this crab, both realized and potential, are a clear lesson that the effects of introducing non-native species to new environments cannot be underestimated. The prevention of further introductions capable of causing such widespread economic and ecological effects should be a local, national and global priority.

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Ecological Project, Richmond, California, 26 August.



Figure 1. Native breeding range of the Chinese mitten crab. Range indicated by stippled shaded areas, extending from the north along the west coast of Korea, south to Hong Kong. Full migratory range extends up tributaries east of shaded area. Zhao(1999) and Hymanson (1999) note that the full range of the mitten crab has recently increased dramatically beyond its historical range depicted here: the crab has been introduced to Vietnam, extending its range considerably south. The successful aquaculture of the Chinese mitten crab throughout Asia has spurred seeding of the crab in rice fields and ponds throughout China: 26 of 30 provinces in China, including inland provinces of western China, currently participate in Chinese mitten crab aquaculture (Zhao 1999).

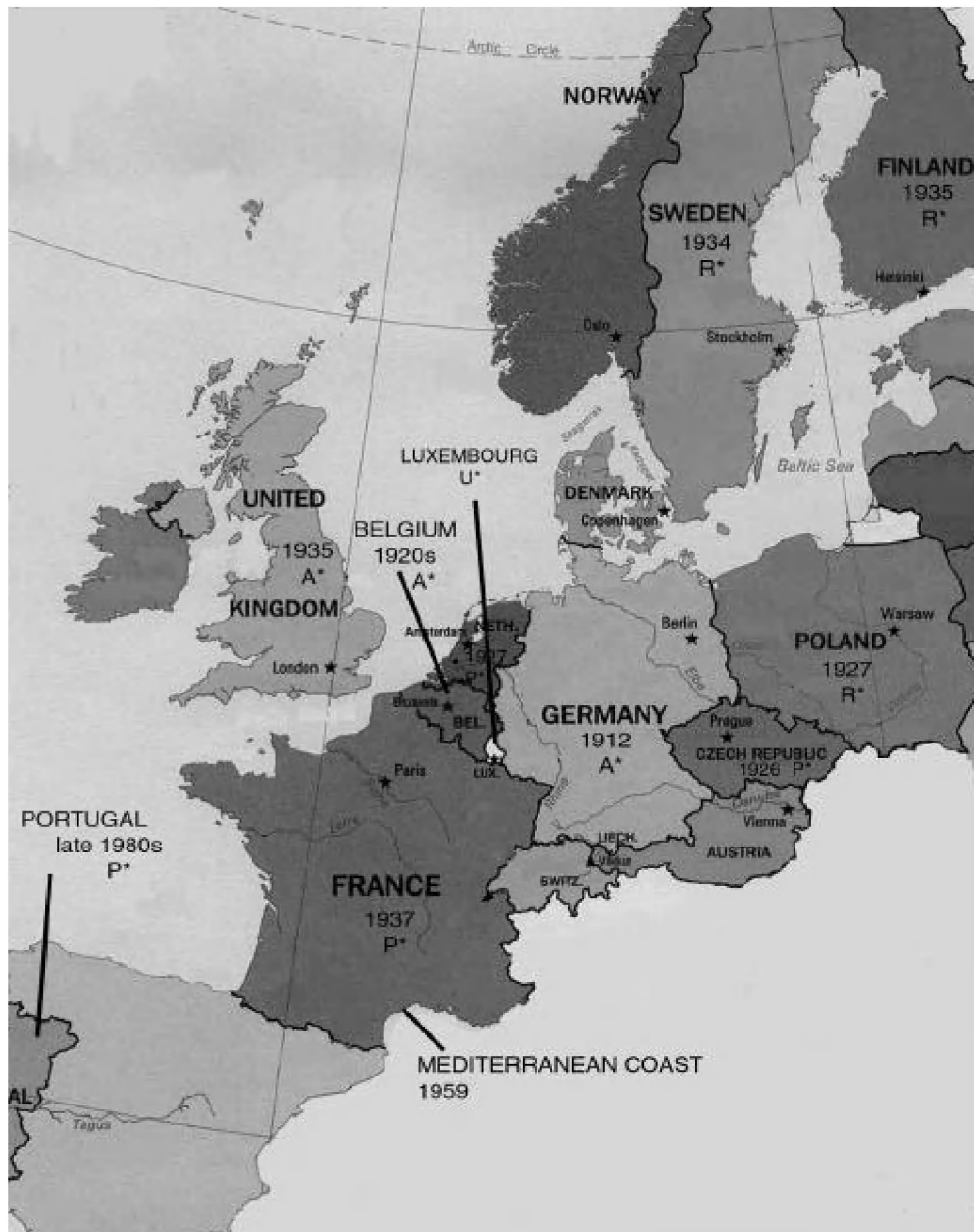


Figure 2. European distribution of the Chinese mitten crab. Dates refer to the first year of sighting of the mitten crab in that country as reported in the scientific literature. Letters refer to abundance of mitten crab, as follows: A*= currently present and abundant or undergoing a population explosion; P*= currently present but not reported to be in abundance; R*= currently present but rare or in low numbers; U*= undetermined population status: no literature could be found on current population.

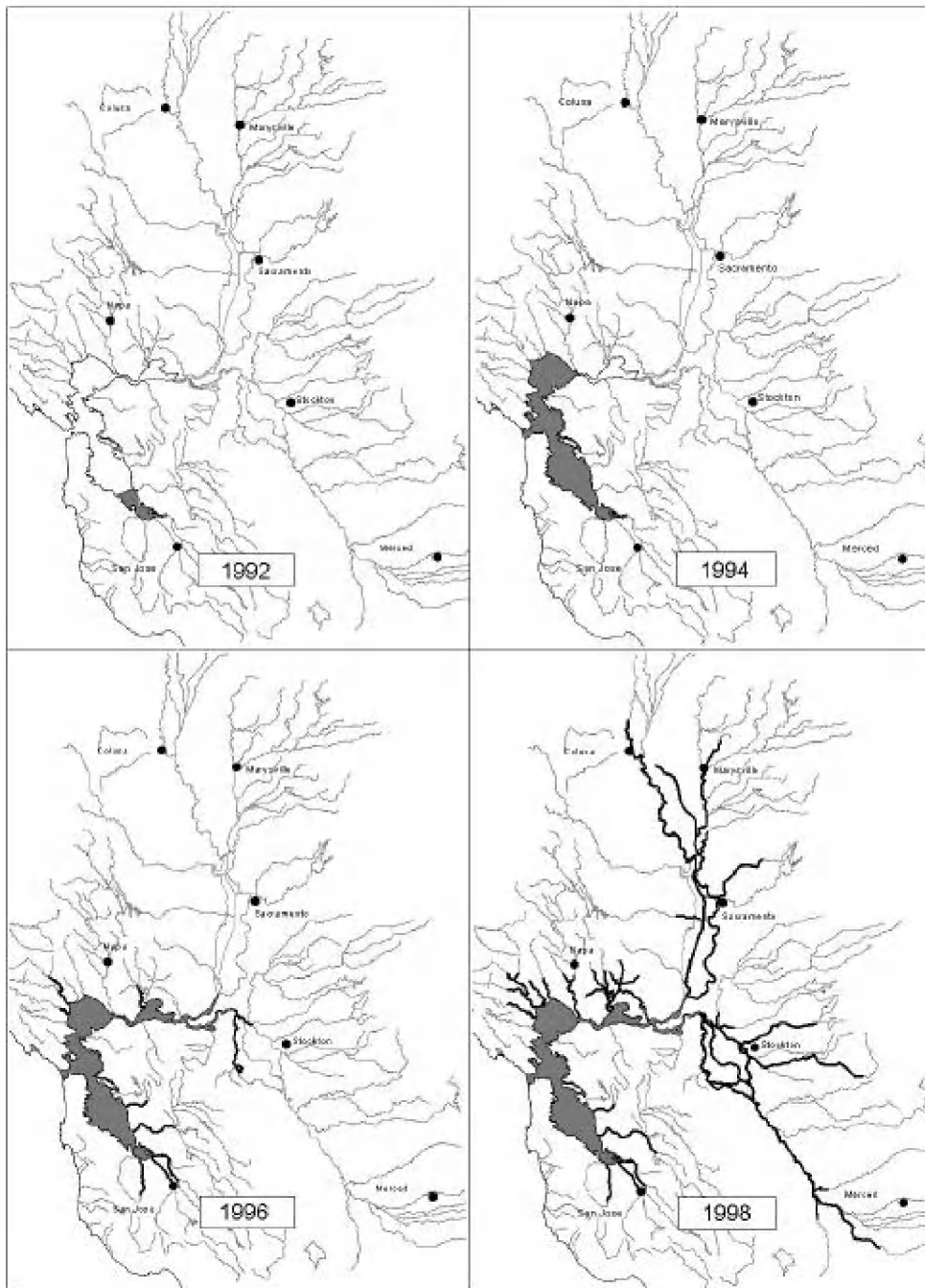


Figure 3. Distribution of the Chinese mitten crab in the San Francisco Bay-Delta ecosystem in 1992, 1994, 1996 and 1998. Shaded waters and streams represent presence of the crab. Reprinted with permission from the California Department of Fish and Game.

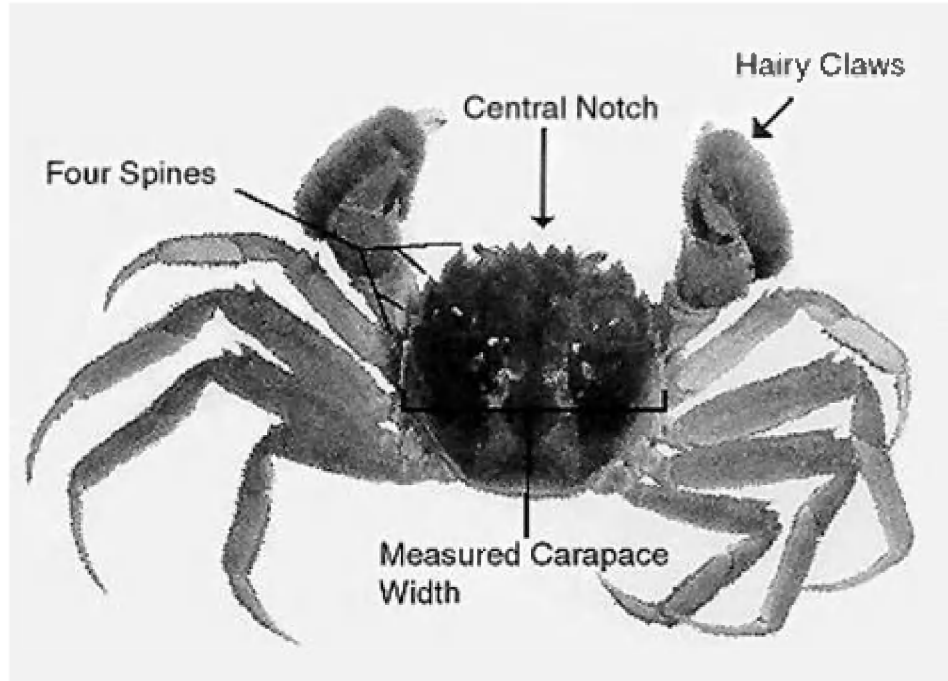


Figure 4. Adult Chinese mitten crab, *Eriocheir sinensis*. Typical identifying characteristics are highlighted: the central notch between the eyes, flanked by two small spines to either side of the notch; the hair (setae) on the claws, and the four spines of the carapace, beginning behind each eye and extending approximately half way along the lateral margins of the carapace. In addition, the subadult and adult Chinese mitten crab is identified as orange-brown to green-brown in color. It has been suggested by Zhao (1999) that the subadult crab is orange-brown and, at sexual maturity, turns green-brown in color. The carapace is rounded and relatively smooth, with a small horizontal furrow, or depression, in the center of the carapace flanked by two curved vertical furrows to either side (visible as lighter-colored areas in the center of the carapace in the above image). We used the measured carapace width, shown above, to determine the size of crabs: this measurement is taken at the widest point of the carapace, just posterior to the 4th lateral spine.

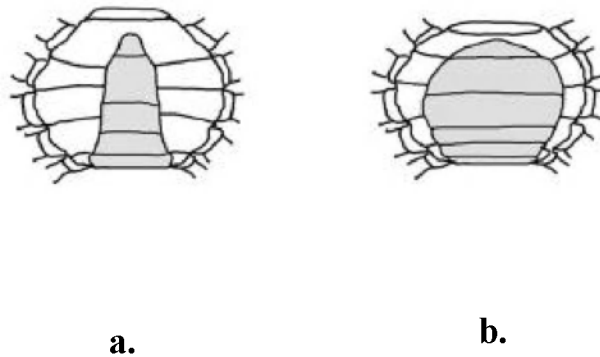


Figure 5. Abdomens of male and female Chinese mitten crabs. a) Abdomen of male Chinese mitten crab; b) abdomen of female Chinese mitten crab. The female mitten crab abdomen is broad and fills the majority of the underside of the crab, whereas the male abdomen is narrower and is shaped like an inverted funnel. Male and female abdomens are discernable when the crab is $>10\text{mm}$ carapace width; juvenile male and female mitten crabs smaller than this size have abdomens that are often not differentiable in shape.

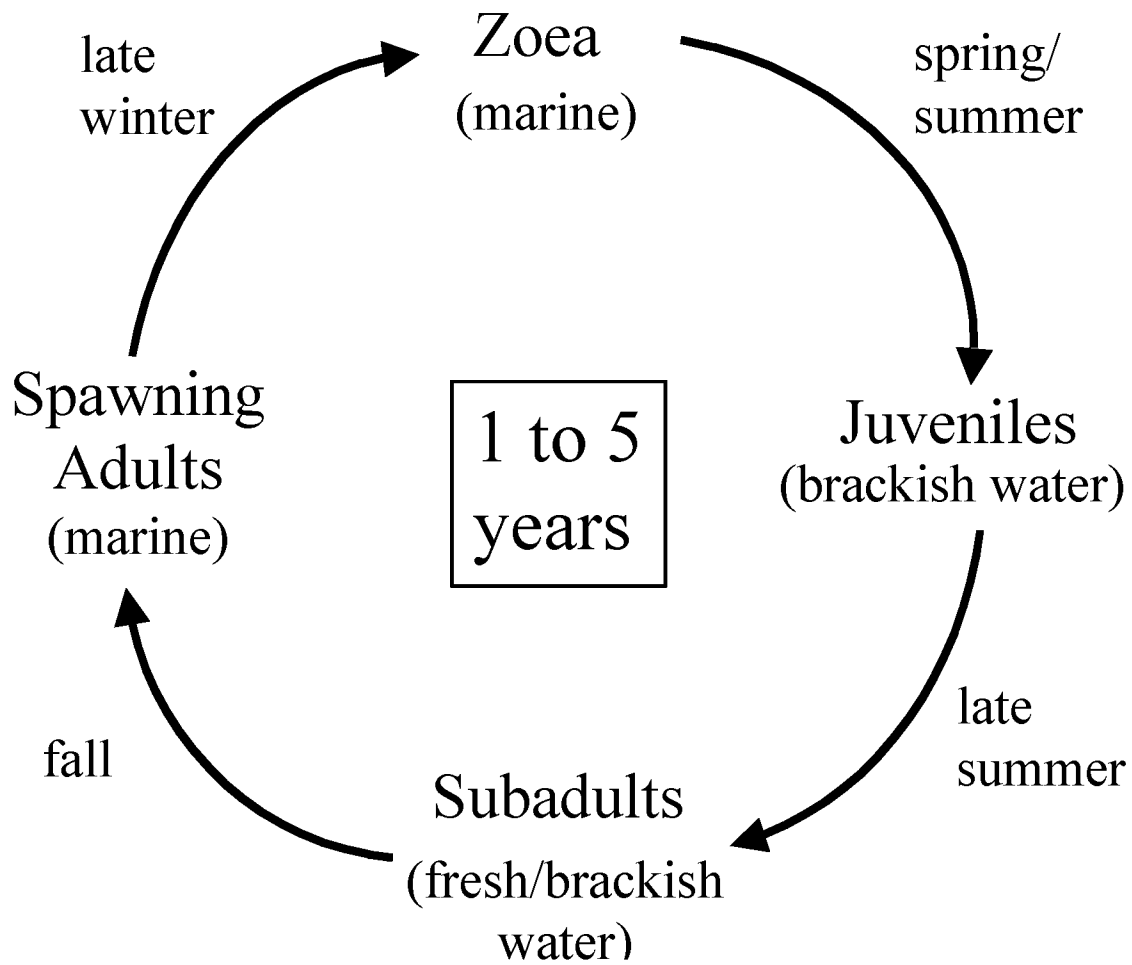


Figure 6. Life cycle of the Chinese mitten crab. Although the majority of crabs are believed to complete the cycle from zoea to reproductive adult in one to two years, mitten crabs may take up to 5 years to develop to maturity. Although some crabs appear to spend their entire juvenile and subadult lives in brackish waters, the majority of crabs spend their subadult life in freshwater lakes or streams.

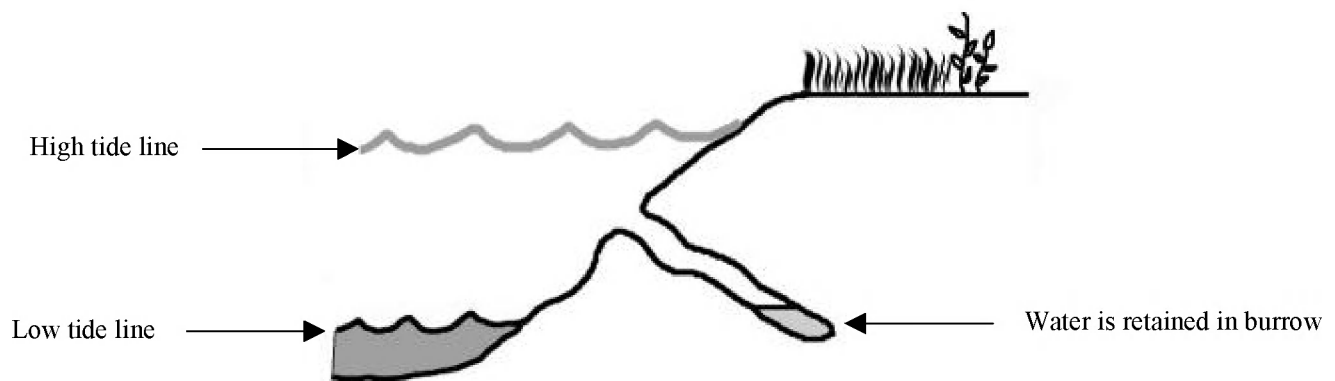


Figure 7. Structure of a Chinese mitten crab burrow. Burrows are generally built between the high and low tide lines in tidally influenced streams. Burrows average 7cm in length and are oriented on a downward-sloping angle from the entrance. This angle allows retention of water at the bottom of the burrow, protecting the crab from dessication when the tide recedes.

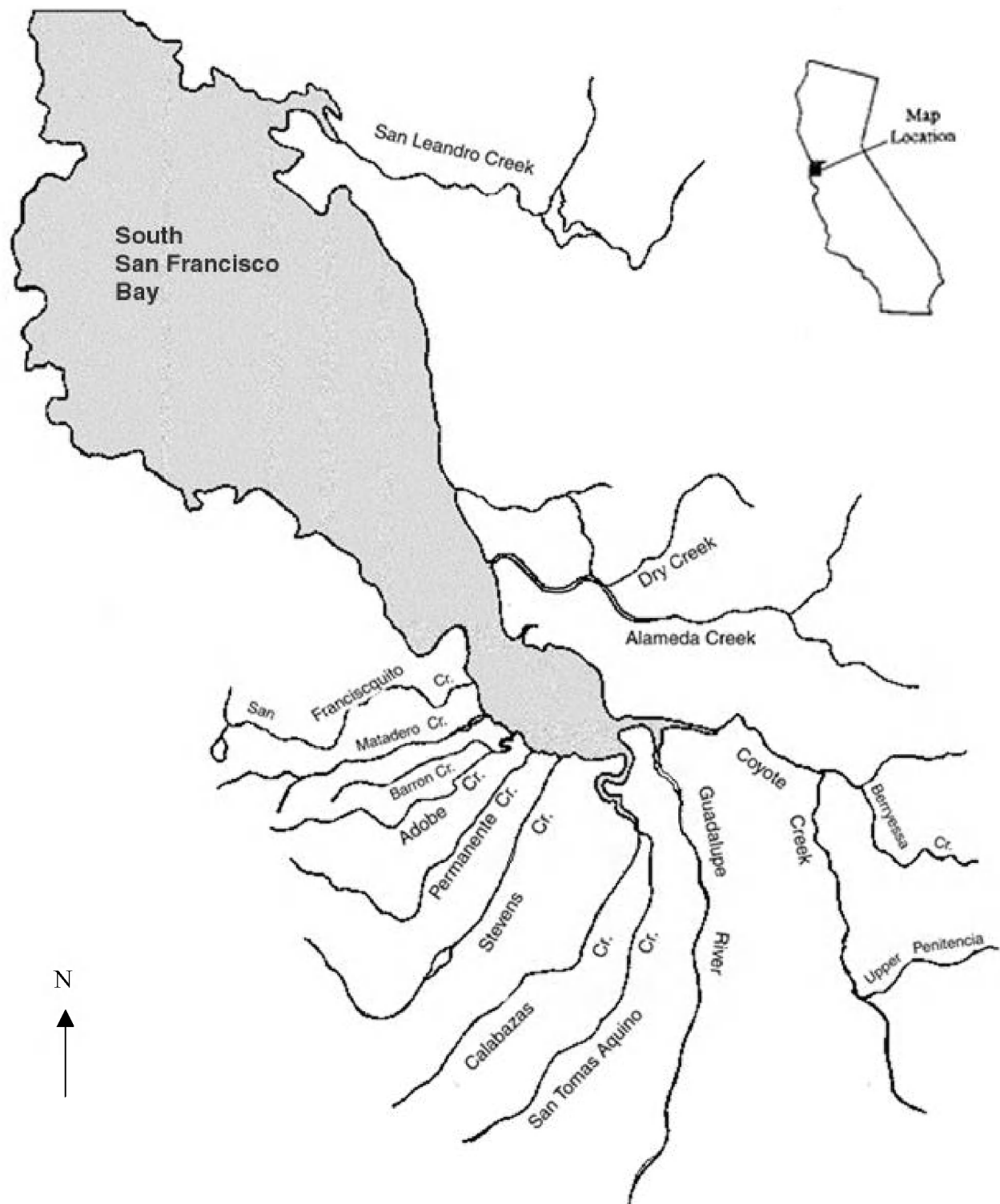


Figure 8. Freshwater tributaries of the South Bay used for project research. A few smaller and unnamed tributaries that were periodically monitored are not included in this map.

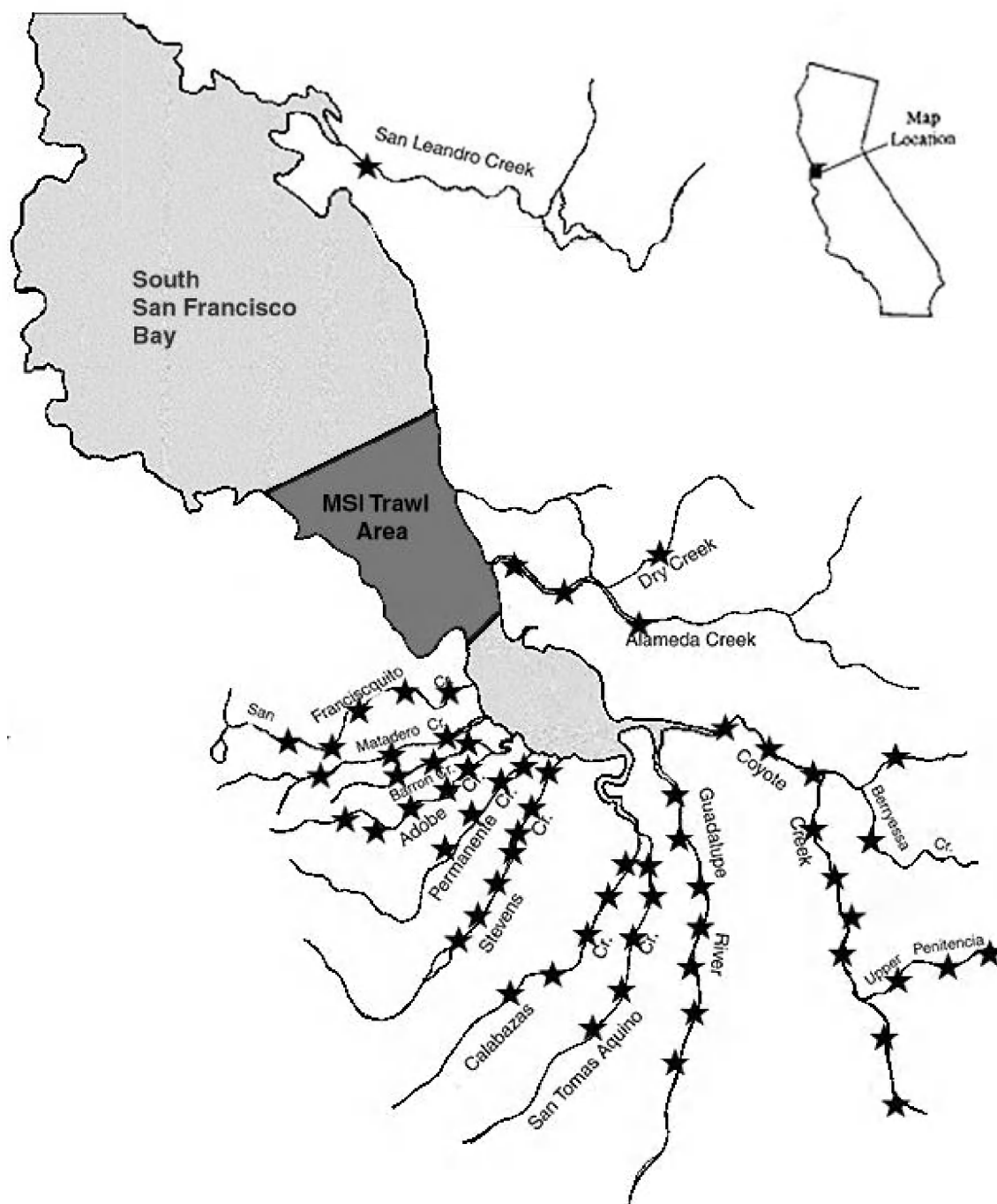


Figure 9a. Locations of monitoring sites used in 1995, 1996 and 1999 surveys. Approximately 10 additional sites are located on small and unnamed tributaries of these creeks (not shown). Darker shaded area indicates approximate location of Marine Science Institute trawls for adult Chinese mitten crabs.

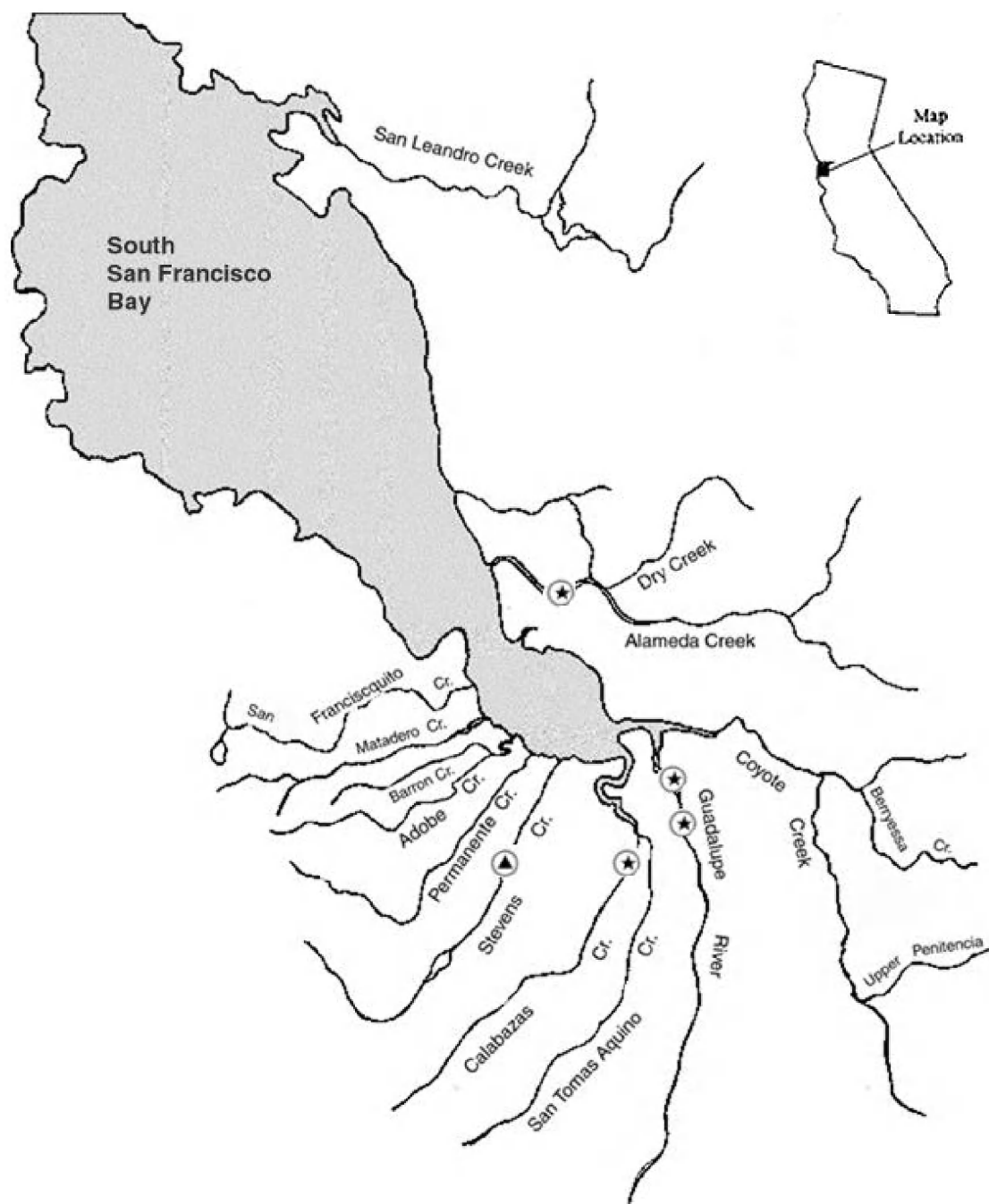


Figure 9b. Sites used for measuring Chinese mitten crab population densities. Five-meter transects of burrow densities and excavations to determine burrow occupancy rates were conducted at these sites. Circled stars indicate sites used in 1995-1996; circled triangle indicates additional site used in 1999.

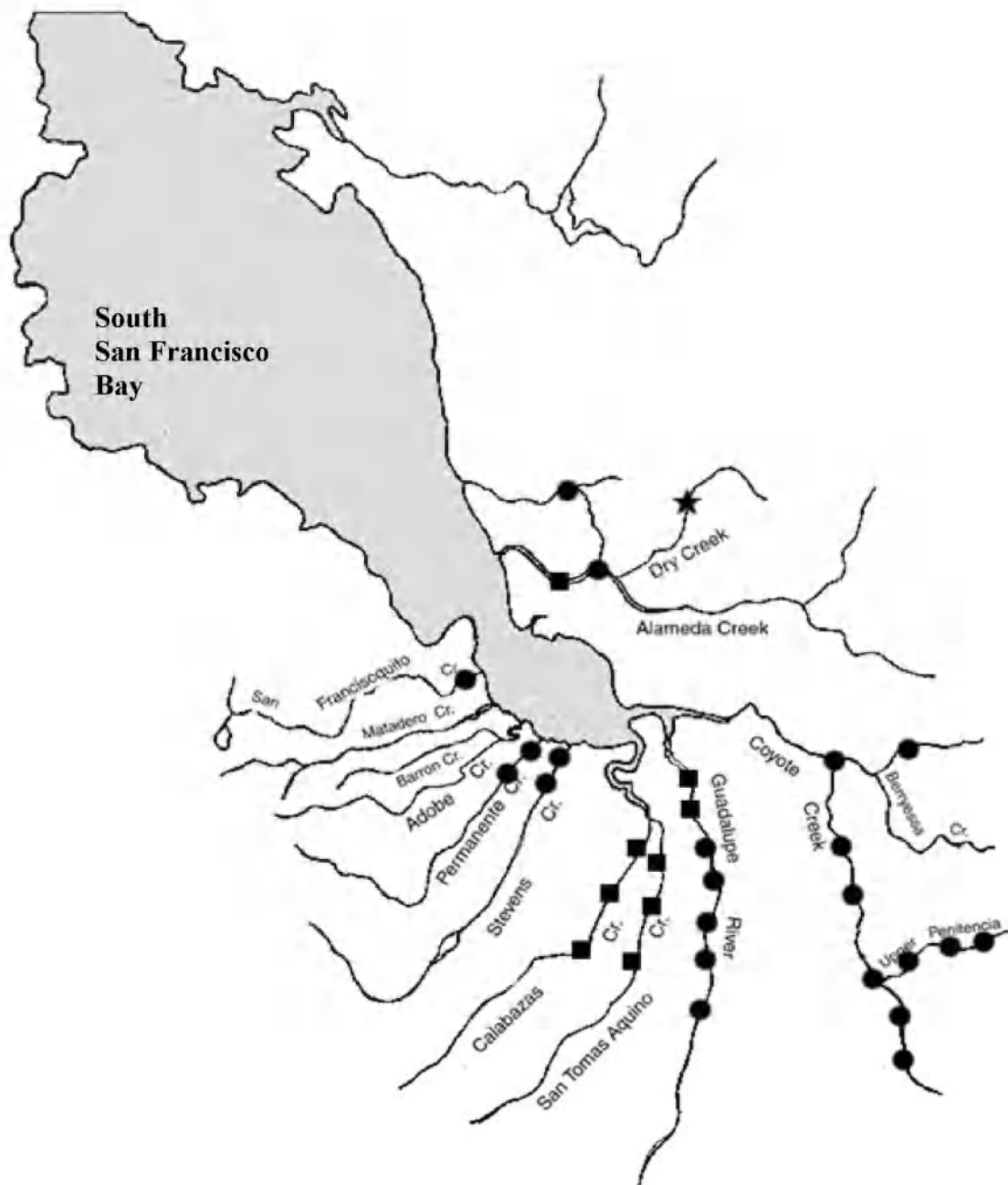


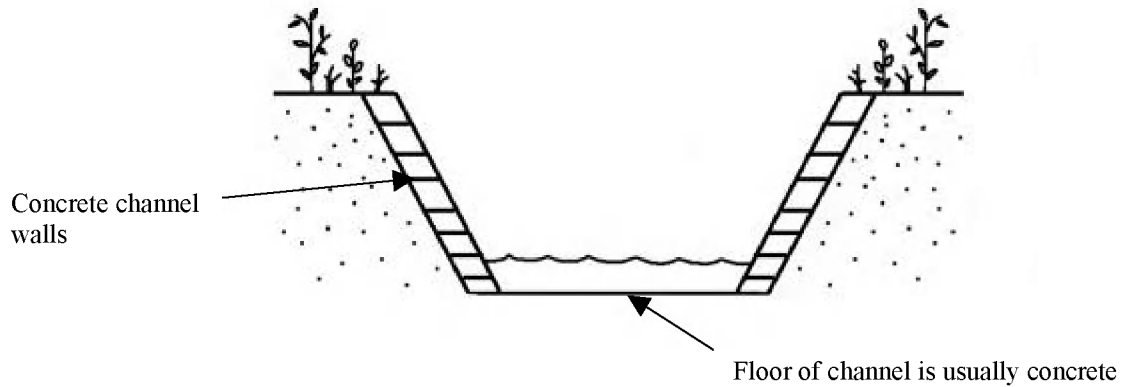
Figure 10. Distribution of Chinese mitten crabs in 1995, 1996 and 1999.

● = 1995 sightings

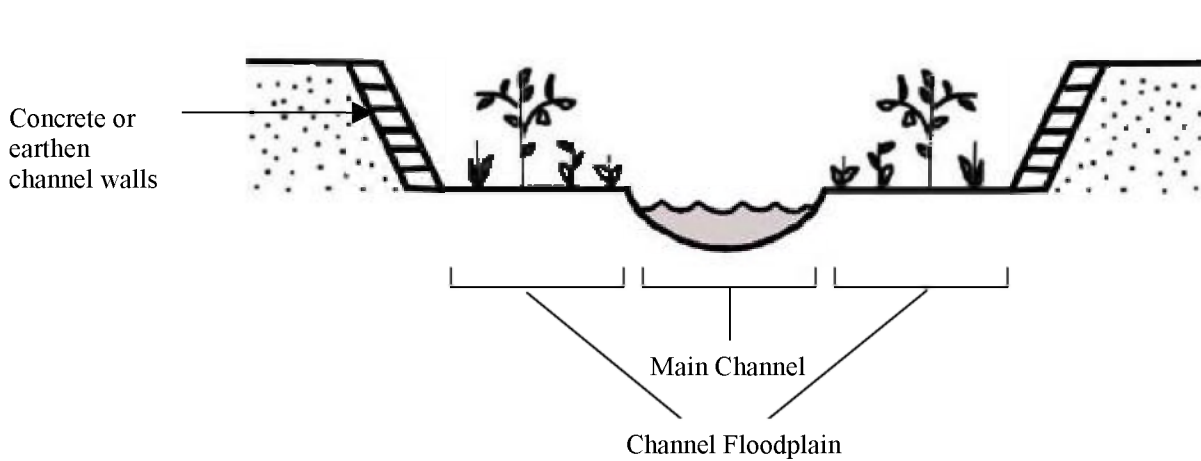
■ = additional areas where mitten crabs were sighted in 1996

★ = additional areas where mitten crabs were sighted in 1999

All areas where crabs were present in year surveyed were again present at those sites in subsequent years: i.e., all 1995 sites again contained crabs in 1996 and 1999.



a) Concrete-lined Flood Control Channel



b) Set-back Levee

Figure 11. The two main types of modified stream channels in the South Bay. a) Concrete-lined flood control channels provide little or no opportunity for shelter or foraging by mitten crabs; b) set-back levees provide earthen banks and aquatic and bank vegetation that can be used by mitten crabs.

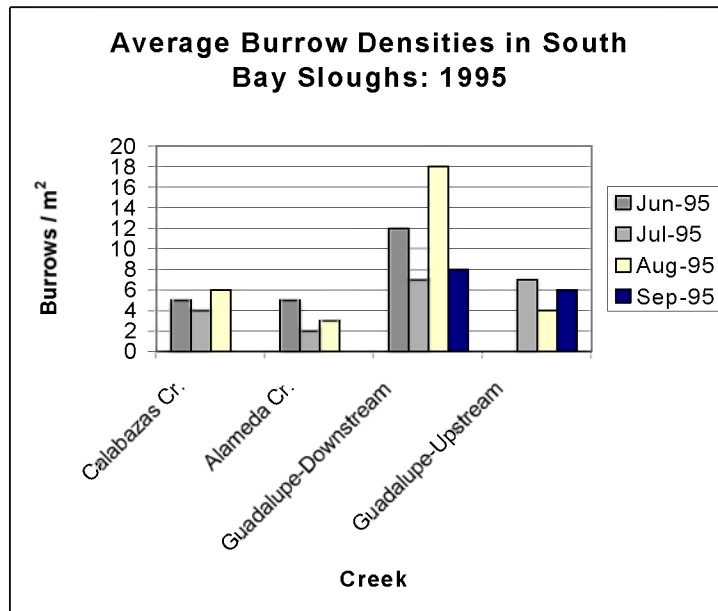


Figure 12a. Average Burrow Densities calculated from averages of three 5m transects taken at each of four sites along South Bay Sloughs, Santa Clara County, CA, in 1995. Densities are given in number of burrows/m².

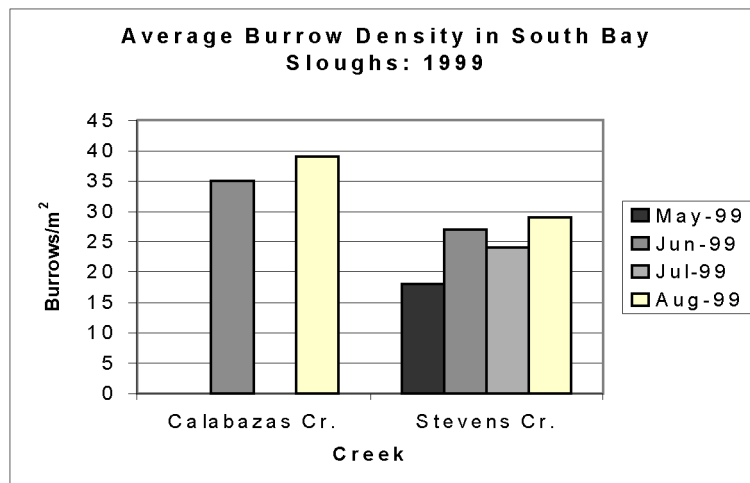
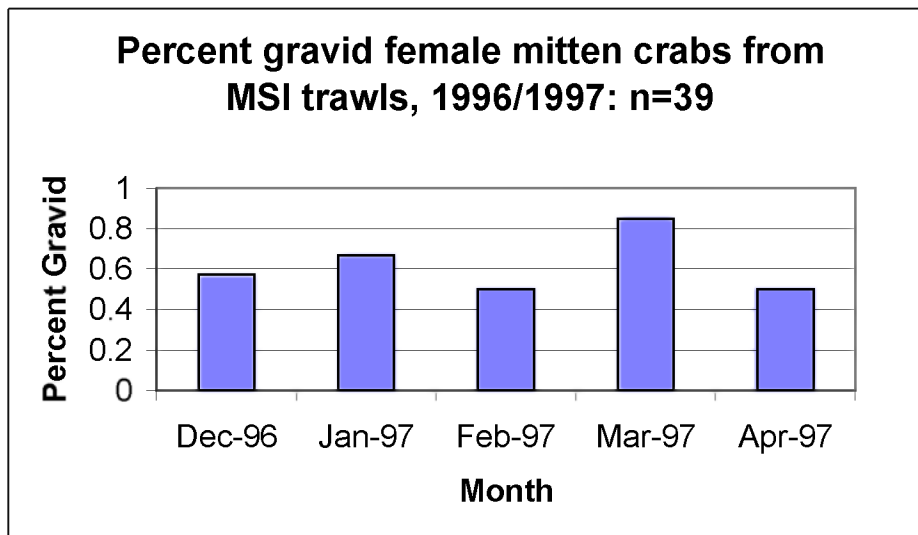
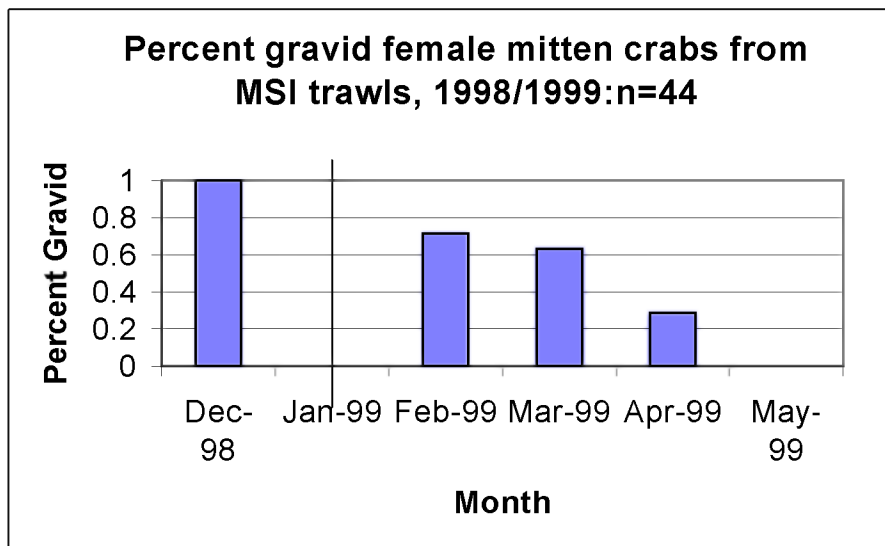


Figure 12b. Average Burrow Densities calculated from averages of three 5m transects taken at each of two sites along South Bay Sloughs, Santa Clara County, CA, in 1999 (Except for June 1999 at Calabazas Creek when two transects were taken at this site). Densities are given in number of burrows/m².

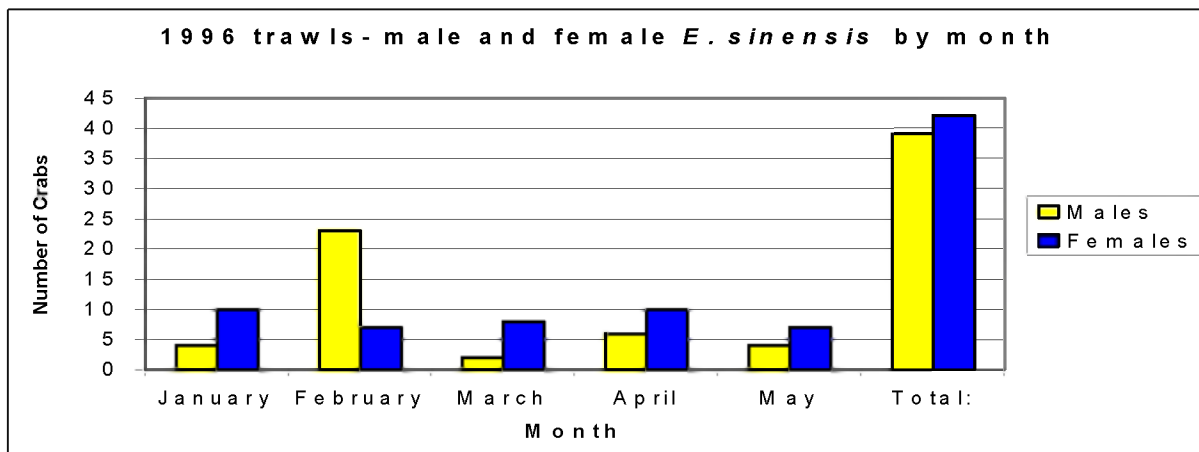


a)

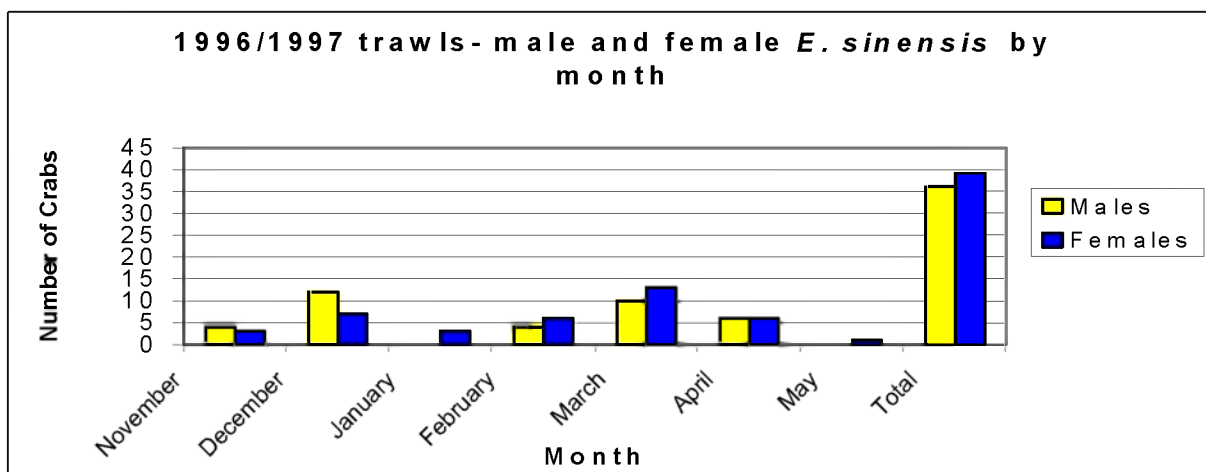


b)

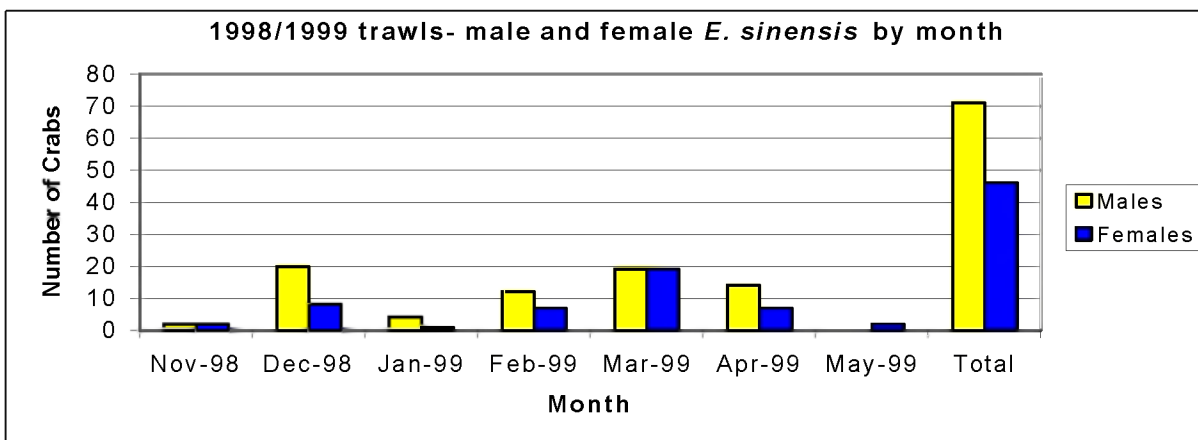
Figure 13. Percent gravid female mitten crabs from MSI trawls, South San Francisco Bay, CA, 1996/1997 and 1997/1998. All months during which >3 females were found are represented. Months for which sample size <3 are not reported: November of 1996 and 1998 both had a sample size of <3 ; the vertical line through January of 1998 indicates that sample size was too small to be included. Trawls during all other months did not collect female mitten crabs.



a)

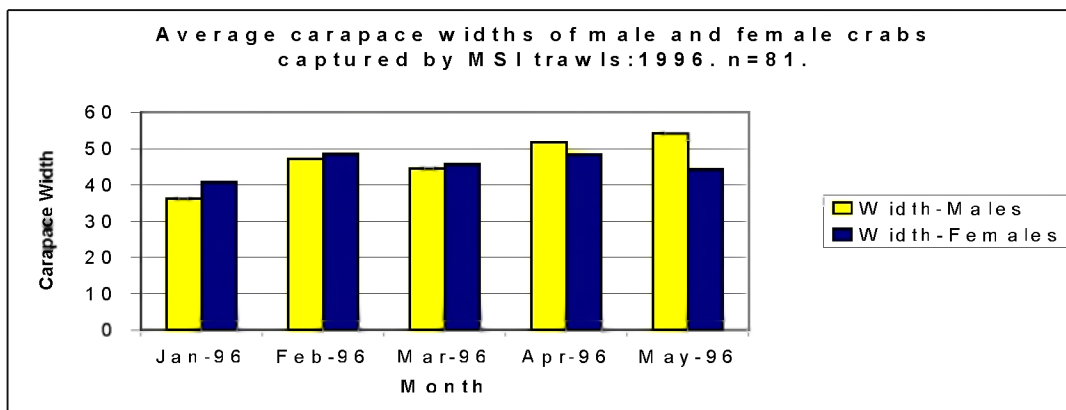


b)

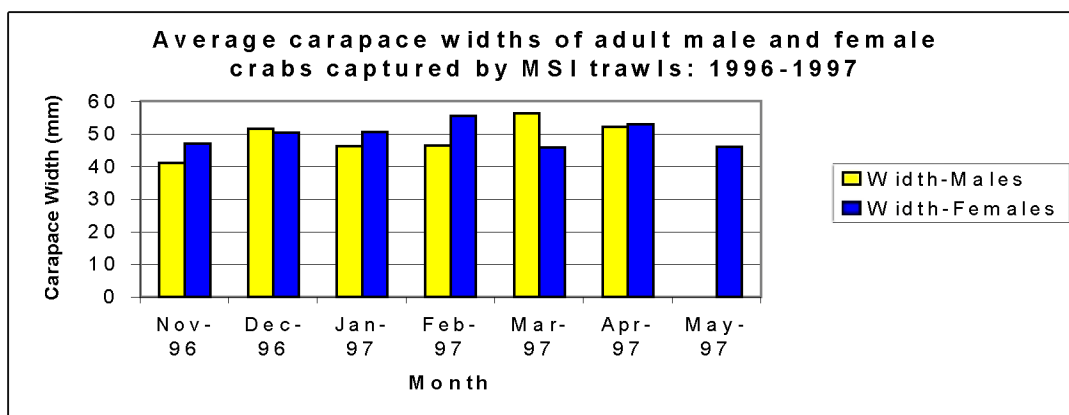


c)

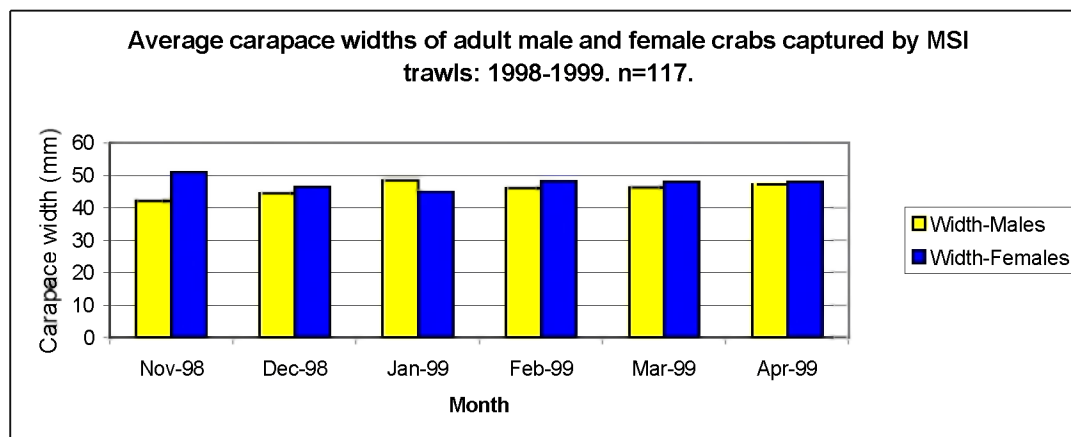
Figure 14. Sex ratios of adult Chinese mitten crabs caught by MSI trawls, South San Francisco Bay, CA, for the years 1996, 1996/1997 and 1998/1999.



a)

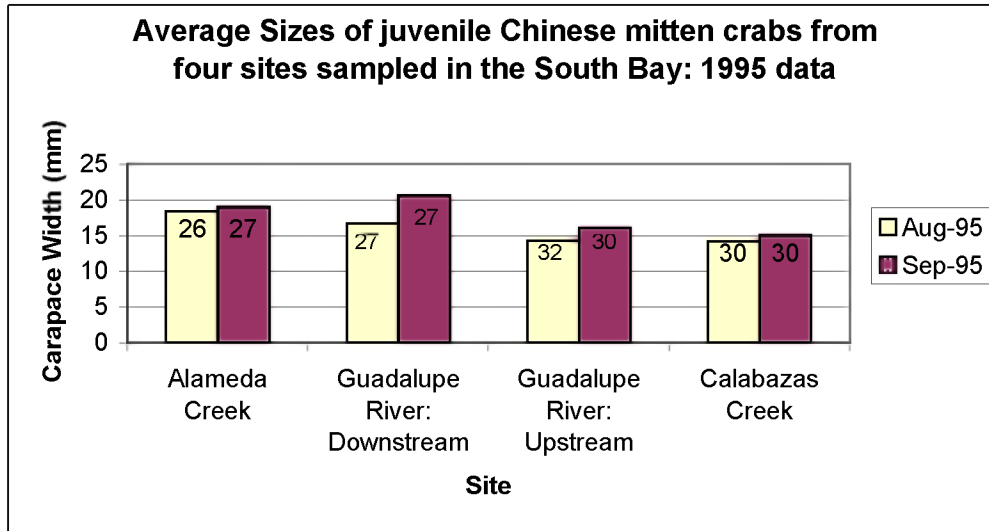


b)

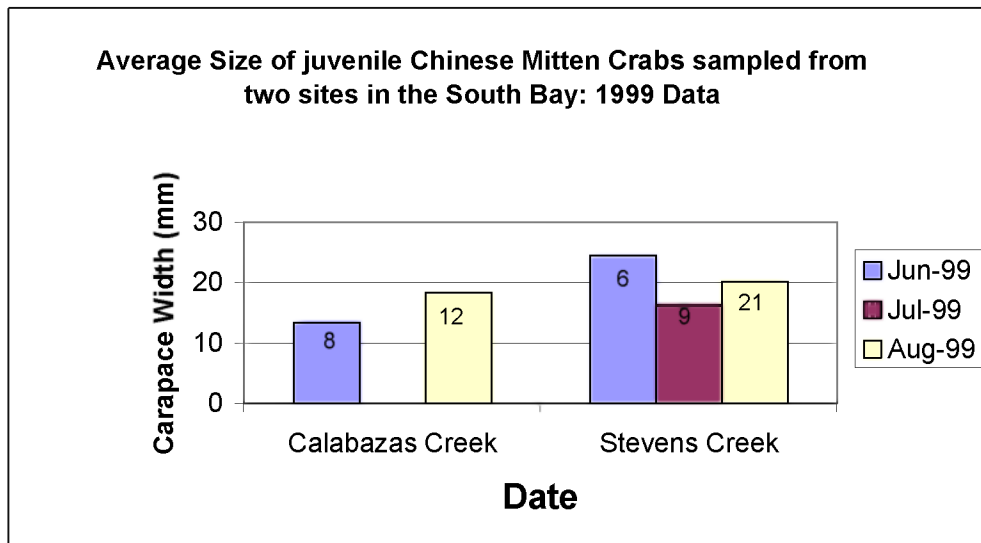


c)

Figure 15. Average sizes of adult male and female mitten crabs, as measured by carapace width, captured by MSI trawls, South San Francisco Bay, CA: 1996, 1996/1997, 1998/1999. Male sizes are indicated by light colored bars: female sizes are indicated by dark colored bars. No data is given for males in May of 1997 because no males were collected during this month.



a)



b)

Figure 16. Average size of Chinese mitten crabs, as measured by carapace width, sampled from tidally influenced tributaries to the South Bay, CA. In 1995, four sites were used in August and September; in 1999, two sites were used: Calabazas Creek was sampled in June and August, and Stevens Creek was sampled in June, July and August. Numbers within the bars refer to sample size for each average.

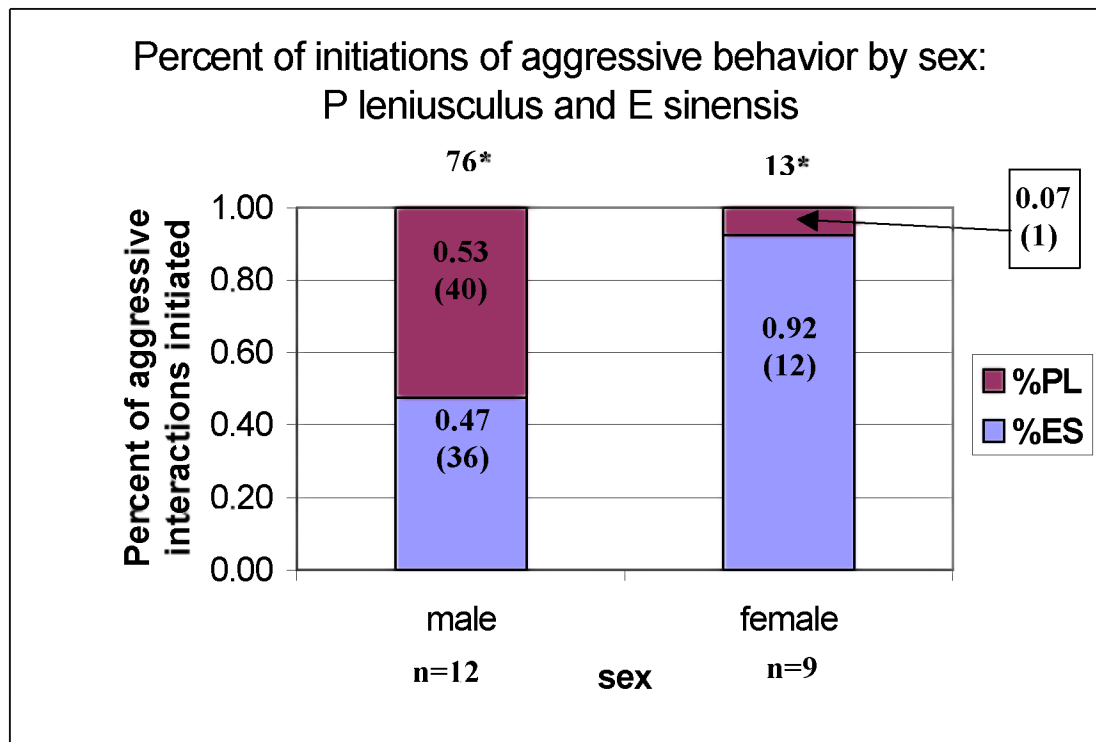


Figure 17. Aggressive behaviors initiated by Chinese mitten crabs, *Eriocheir sinensis*, (ES) and signal crayfishes, *Pacifastacus leniusculus*, (PL) in behavioral experiments. Aggressive behavior is defined by when the animal exhibits the following categories of behavior: *push*, *threat*, *strike*, *fight*. Columns are labeled with percentages of aggressive behavior initiated and number of aggressive behaviors initiated in parentheses below the percentage. Total number of experiments conducted is listed below each column (n) with number of total interactions in all experiments listed at the top of each column. The values for total interactions (76 and 13) are starred to indicate a significant difference between the number aggressive behaviors initiated by females of both species and the number initiated by males ($p < 0.05$).

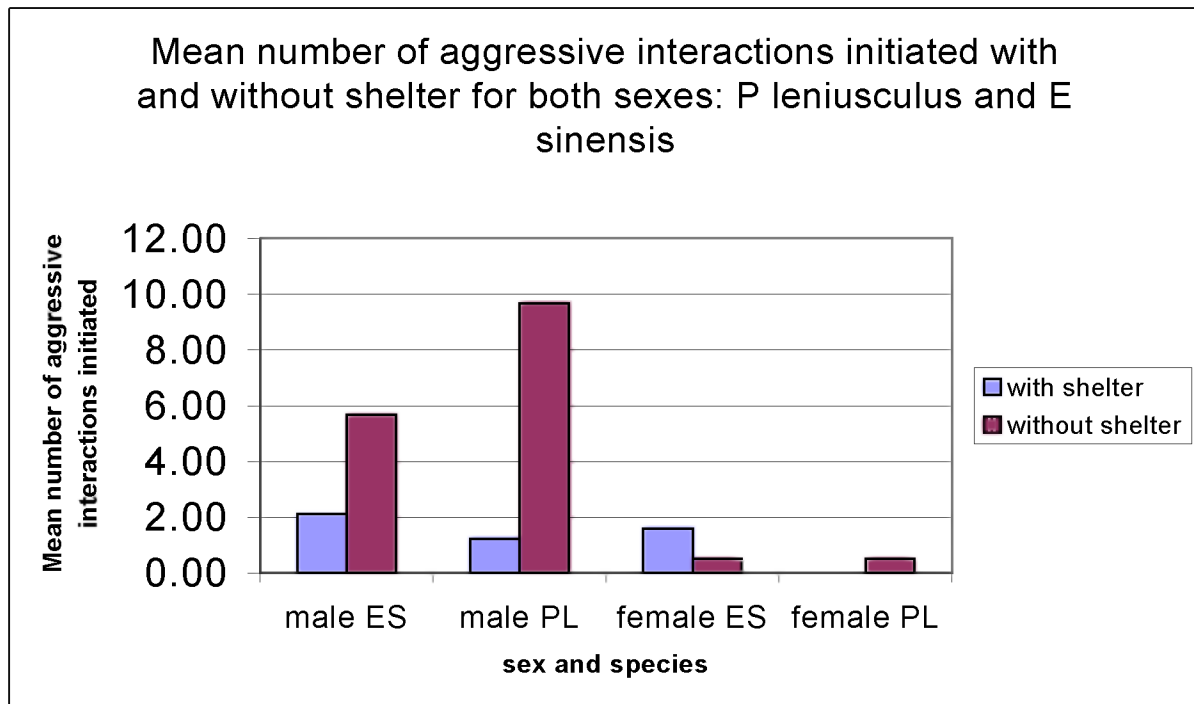


Fig 18. Aggressive interactions of males and females of each species, comparing interactions where a shelter was provided to interactions where no shelter was provided. Aggressive behavior is defined by when the animal exhibits the following categories of behavior: *push*, *threat*, *strike*, *fight*. There is a significant difference in the number of aggressive interactions by male Chinese mitten crabs between experimental runs with shelter provided and experiments with no shelter provided ($p < .05$). For male-male interactions, number of interactions with shelter = 9, number of interactions without shelter=3. For female-female interactions, number of interactions with shelter = 7, number of interactions with shelter=2.

Mitten Crab Distribution in the State Water Project (March 1999)



Figure 19. Distribution of the Chinese mitten crab throughout the State Water Project of California. Compiled March 1999 and furnished by the California Department of Water Resources.

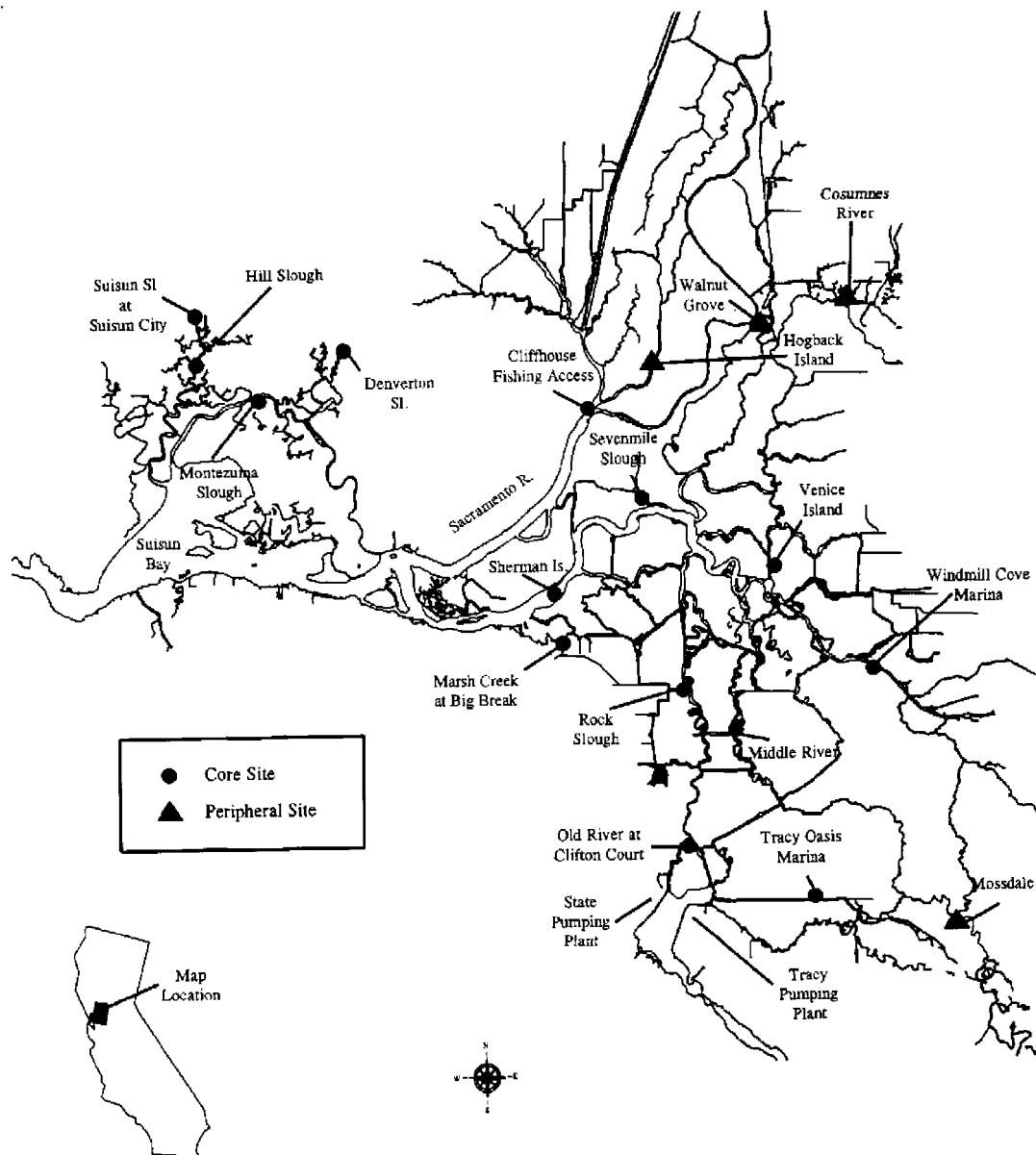
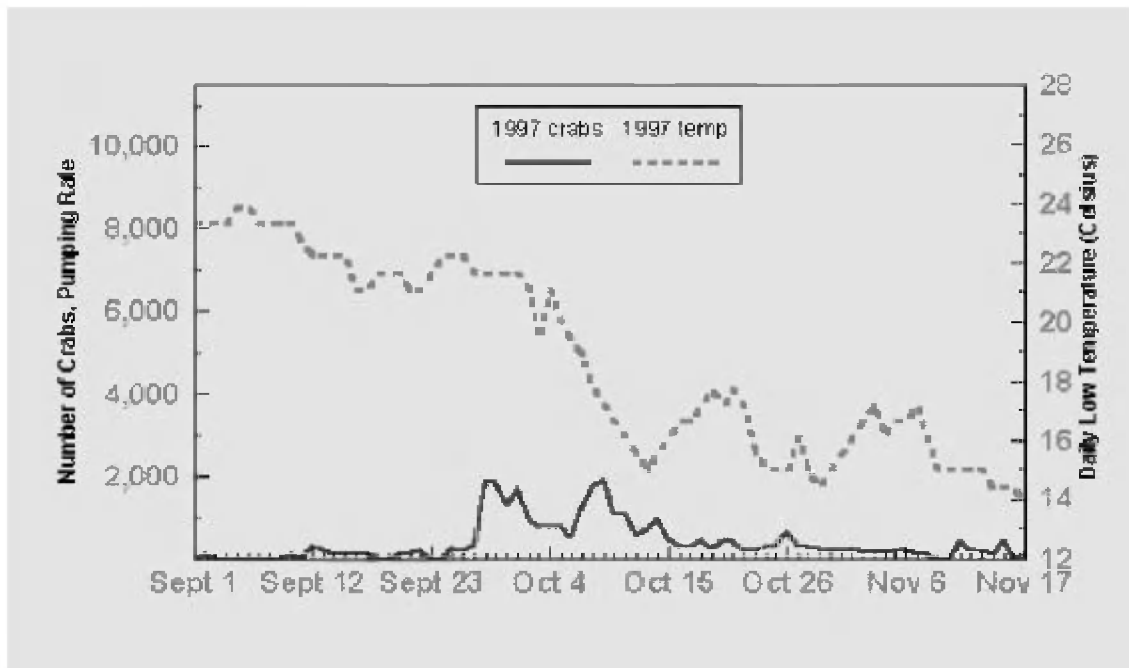
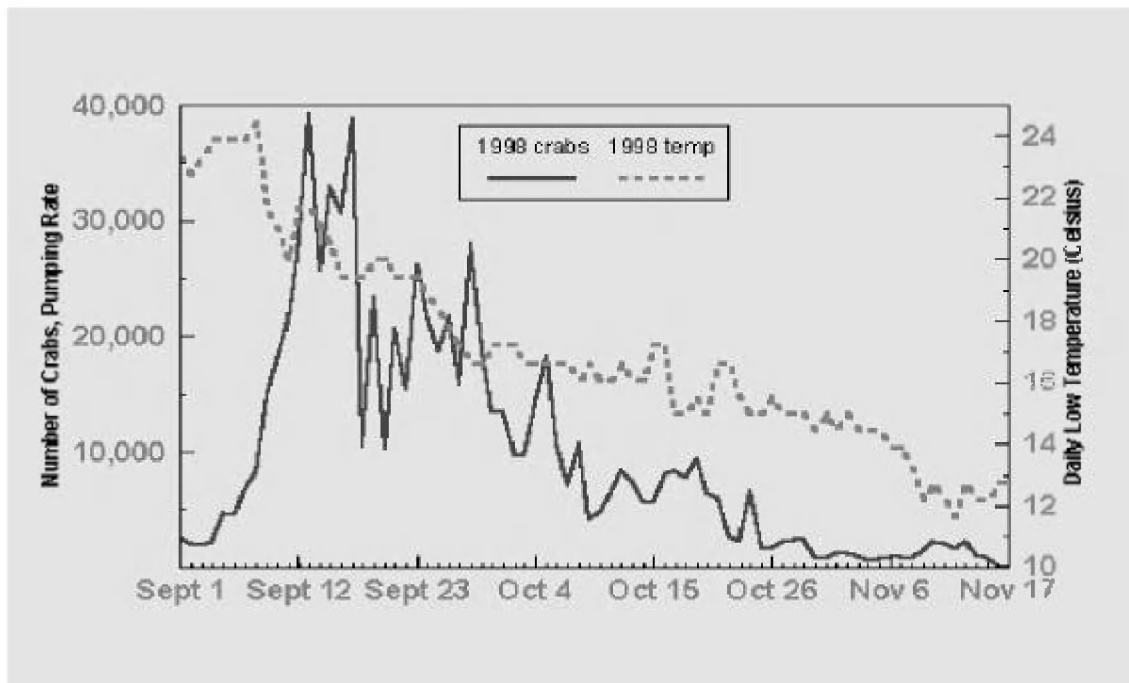


Figure 20. Monitoring sites for the Sacramento-San Joaquin Delta Chinese mitten crab survey.

Refer to Table 3 for individual site names. Map is from Holmes and Osmondson (1999).



a)



b)

Figure 21. Comparison between estimated number of Chinese mitten crabs collected daily at the Tracy Fish Collection Facility, Tracy, CA, and daily low water temperature. Figure 21a presents 1997 data; figure 21b presents 1998 data. Figures provided by Scott Siegfried, TFCF.

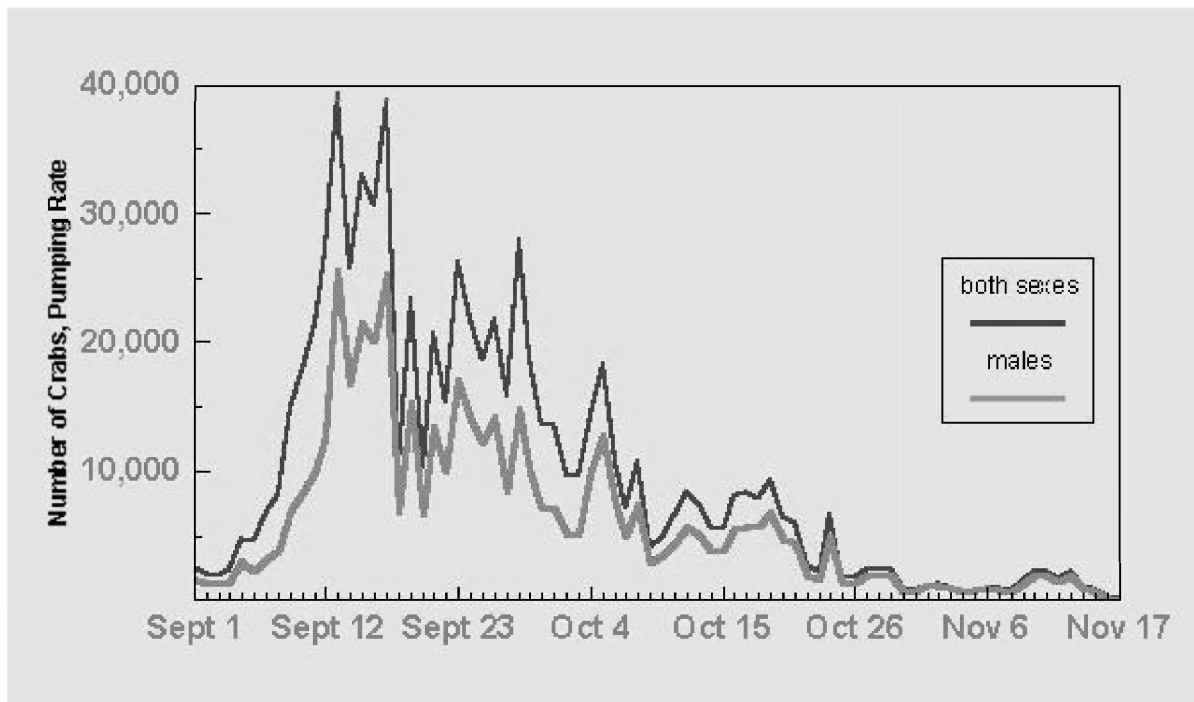


Figure 22. Sex ratio of Chinese mitten crabs collected daily at the Tracy Fish Collection Facility expanded from 10-minute fish counts, September 1 – November 18, 1998. Based on sex ratio data of TFCF mitten crabs verified by Kathy Hieb, Bay-Delta Division, California Department of Fish and Game. Graph furnished by Scott Siegfried, US Bureau of Reclamation, TFCF.

Table 1. Summary Statistics for MSI trawls for adult Chinese mitten crabs: 1994-1999.

Year	Total # Crabs	Catch Per Unit Effort	Average Carapace Width	Sex Ratio(Male/Female)
1994/1995	66	0.12	unknown	85%
1995/1996	81	0.16	46	40%
1996/1997	75	0.11	49	42%
1998/1999	117	unknown	47	65%
Total number, all years:	339		Total Average Sex Ratio, all years:	44%

Table 2. Summary statistics for Chinese mitten crab (*Eriocheir sinensis*) - signal crayfish (*Pacifasticus leniusculus*) behavioral experiments.

	<i>Eriocheir sinensis</i>	<i>Pacifasticus leniusculus</i>	<i>Eriocheir sinensis</i>	<i>Pacifasticus leniusculus</i>
	Male	male	female	female
total number of interactions	36	40	12	1
average number interactions	3.0	3.3	1.3	0.1
standard error	0.8	1.6	0.6	0.1
mean number of aggressive initiations for experiments without shelter	5.7	9.7	0.5	0.5
standard error	1.5	4.9	0.5	0.5
Mean number of aggressive inititiations for experiments with shelter	1.9	1.1	1.8	0.0
standard error	0.7	0.6	0.7	0.0

Table 3. Juvenile mitten crab densities (crabs/m²) in 1997 and 1998 at monitoring sites throughout the Delta (see Figure 20 for site map). From Holmes & Osmondson 1999.

Site Location	Mean density 1997	Mean Density 1998
Suisun Marsh:		
Suisun Slough	1.5	3.0
Hill Slough	1.3	0.3
Montezuma Slough	0.4	0.1
Denver Slough	1.7	0.2
Sacramento-San Joaquin Delta		
Cliffhouse	0.3	0.1
Sevenmile Slough	0.0	0.0
Windmill Cove	0.0	0.0
Middle River/Jones Tract	0.4	0.0
Old River/Clifton Court	0.0	0.0
Big Break/Marsh Creek	n.s.	0.0
Rock Slough	0.0	0.0
Tracy Oasis	0.2	0.0
Sherman Island	0.2	0.7
Venice Island	0.0	0.2
Hogback	0.0	0.0
Walnut Grove	0.0	0.0
Middle River	0.0	n.s.
Mossdale Crossing	n.s.	0.0
Cosumnes River	n.s.	0.0
n.s.= not sampled		

Mitten Crabs and Crayfish (confidential survey, for research purposes only)

We are trying to summarize the effects of the introduced Chinese mitten crab on the crayfish fishery in the Sacramento River and San Joaquin River Delta. Please help us by answering the following questions based on your observations. Return this survey to us in one of the pre-addressed, stamped envelopes when it is convenient for you.

--When did mitten crabs first appear in your crayfish traps (month/year)?

--How have the numbers of mitten crabs trapped changed over the past few years?

--Approximately how many crabs per 100 traps do you find now?

--Do you also find mitten crabs crawling on the outside of your traps when you haul them up? If so, how many would be attached per 100 traps?

--Have you observed any interactions between crayfish and crabs in your traps, such as aggressive behavior by the crabs towards the crayfish (or vice-versa)?

--Do you feel that mitten crabs are affecting your crayfish fishing in any way?

--Using the map on the other side please circle the approximate area where you fish.

--Other comments would be appreciated:

For questions, please contact:

Professor Vince Resh

ESPM/IB

201 Wellman Hall

University of California

Berkeley, CA

510-642-3327

Appendix 1. Survey sent to crayfish fishermen regarding effects of the Chinese mitten crab on crayfishing efforts. Map referred to in questionnaire is a map of the river systems of West and South Sacramento, CA, the general area where questionnaire recipients conduct their fishing.

Hypothesized General Attributes of Invasive Species (from Ricciardi and Rasmussen 1998)	Examples of ecology of the Chinese mitten crab which match these attributes
1. Abundant and widely distributed in original range	Original habitat extends from west coast of North Korea south along nearly the entire coast of China to Hong Kong and inland along rivers as far as 1250km
2. Wide environmental tolerance	Extremely euryhaline throughout juvenile, adult and some stages of larval life; wide range of temperature tolerance throughout life; found in San Francisco Bay in a wide variety of stream habitats including concrete-lined levees, low-order streams, intermittent streams and channelized levees
3. High genetic variability	Phenotypic plasticity suggests genetic variability; work of Li et al. (1993) found broad genetic diversity
4. Short generation time	Larvae to sexually mature adult ranges as early as approximately 8 months up to 5 years
5. Rapid growth	First year juveniles grow an average of 4mm per molt, majority grow to sexual maturity (>34mm; see below) within 1-2 years
6. Early sexual maturity	Gravid females found at as small as 35mm, sexual maturity can be reached within 1 year
7. High reproductive capacity	Gravid females release 250,000 to 1 million eggs (rate of survival to larval stage in nature unknown)
8. Broad diet	Opportunistic detritivores/scavengers, extremely wide dietary range
9. Gregariousness	Form closely-packed, even interconnected burrows as juveniles; observed migrating together in the thousands and feeding in groups of 10 to 20 (personal observations).
10. Possessing natural mechanisms of rapid dispersal	Crabs reported to migrate upstream at a rate of 1-5km/day (Panning 1938)
11. Commensal with human activity	Main hypotheses are that crab either arrived in ballast water of transport vessels, or was introduced for human consumption and accidentally or intentionally released

Appendix 2. Comparison between the ecology of the Chinese mitten crab and generalized attributes of successful invasive species. The 11 general attributes of invasive species given in this table were outlined by Ricciardi and Rasmussen (1998) and were compiled from the work of several other authors (including Groves and Burdon 1986; Lodge 1993) who have written about identifying species prone to invade new environments. The Chinese mitten crab can be considered a ‘model invader’ when viewed in terms of these attributes, as its ecology matches every category described above.