The Feeding Ecology of the Invasive Chinese Mitten Crab, *Eriocheir sinensis*: Implications for California's Freshwater Communities

Leah Rogers Environmental Sciences, University of California, Berkeley

Abstract

The San Francisco Bay area is a highly invaded watershed, where 60% of the species present are non-native. The Chinese mitten crab, Eriocheir sinensis, is an invasive species of particular concern in California because of the ecological damage that it has caused in ecosystems throughout Europe. Despite this concern, little is known about the ecology of this freshwater, catadromous crab. To assess the impact that E. sinensis is having on California's freshwater communities, I characterized the feeding ecology of Chinese mitten crabs with a combination of foregut content analyses of crabs from south San Francisco Bay tributaries and feeding preference experiments. Foregut analyses show that E. sinensis feeds mostly on algae (28.7%) and detritus (49.3%), while occasionally feeding on aquatic invertebrates (8.4%). Feeding preference studies indicate that E. sinensis prefers resident benthic invertebrates (59.2% of food eaten), to green algae (21.7%), leaf detritus, (17.2%) and freshwater shrimp, Palaemonetes paludosus (6%). Preliminary benthic samples taken at the same sites show low benthic invertebrate abundance and diversity, which potentially explains discrepancies between gut contents and feeding preferences. The combined analyses indicate that E. sinensis has the potential to cause a shift in the food web structure due to its large population size and preference for aquatic invertebrates, in habitats where benthic invertebrates are rare and not diverse.

Introduction

Introduced species can a serious threat to the structure and function of natural communities and ecosystems. Introduced species cause these changes by outcompeting resident species, accelerating native species extinction rates, or by facilitating the establishment of other non-native species (Hill et al. 1993, Light et al. 1995, Adler et al. 1998). Habitat disturbances and increased development often facilitate the introduction and long-term establishment of non-native species (Moyle and Williams 1990), making habitats within or adjacent to urban areas prone to species introductions. The San Francisco Bay area represents one of the most highly invaded urban regions, where 60% of the aquatic species present are non-indigenous (Cohen and Carlton 1998). Many of the successful non-native aquatic species are invertebrates, and crustaceans such as the signal crayfish (*Pacifasticus leniusculus*), the red-swamp crayfish (*Procambarus clarkii*) the European green crab (*Carcinus maenus*) and the Chinese mitten crab (*Eriocheir sinensis*) are particularly common as invaders, (Cohen and Carlton, 1997, Cohen and Carlton 1998, Grosholz et al. 2000).

Despite the widespread invasion of crustaceans throughout Californian aquatic ecosystems, the community and ecosystem-level impacts of these invasions in freshwater have only recently been studied. In freshwater, crayfish have the potential to dominate the benthos both in population number and trophic influence, exerting strong direct and indirect effects on benthic communities (Light et al. 1995, Charlebois and Lamberti 1996, Nyström et al. 1999, Stelzer and Lamberti 1999). This dominance often occurs regardless of the presence of other ecologically similar crayfish (Hill et al. 1993).

The Chinese mitten crab is native to the Province of Fukien, China and the Korean Peninsula. It was first documented in the San Francisco Bay Area in 1992. According to Cohen and Carlton (1997), the Chinese mitten crab was either accidentally introduced to California via ship ballast water or it was intentionally introduced. The Chinese mitten crab is catadromous, migrating from freshwater habitats where it resides during its juvenile years to saltwater habitats to reproduce. The range of this species has spread to cover over several hundred square miles and population numbers are estimated to be in the millions throughout the freshwater and estuarine ecosystems of the San Francisco, San Pablo and Suisun Bays, the Sacramento Delta and the Central Valley since its introduction eight years ago (Vedhuizen and Stanish 1999).

The Chinese mitten crab has a history of successful invasion. It was introduced to Germany in 1912 and since then has become established in much of the rest of Europe and the Baltic States (Jadzdzewski and Konopacka, 1993). In many European countries, *E. sinensis* has adversely affected the ecology of aquatic habitats and the economy associated with these areas (Panning 1939, Hoestlandt 1948, Clark 1998). These adverse effects range from erosion and collapse of banks and levees (from crab burrows), to interference with commercial and sport fisheries (net damage, predation on and competition with harvested species) and alteration of community structure and function. In the San Francisco Bay area, hastened bank erosion in the South Bay since invasion is already evident (Halat 1997, Rudnick et al. 1999).

Previous studies and observations of the trophic impact of *E. sinensis* on freshwater communities from Europe and China have indicated that, like crayfish, mitten crabs are opportunistic omnivores (Thiel 1938, Panning 1939, Hoestlandt 1948, Dan 1984). Despite this knowledge, we have little data to characterize the feeding ecology and potential trophic impacts of a large mitten crab population in the urban San Francisco Bay area (Halat 1997, Rudnick et al. 1999). Mitten crab populations have increased dramatically over the last four years in the south San Francisco Bay area; in some streams, densities have increased from less than 5 burrows/m² to over 40 burrows/m², where each burrow is evidence of one crab inhabitant (Rudnick et al. 1999). Such a large mitten crab population size, is capable of causing major changes in local community structure and function, regardless of their feeding ecology. Future decisions made regarding the control of the mitten crab or protection of native communities will need to be aware of the feeding ecology of *E. sinensis* in California.

To address this need for knowledge, I assessed the natural diet of the mitten crab in three streams in Santa Clara County, California, through gut content analyses. The gut content analyses provide information on the current diet of the mitten crab in Santa Clara County. Based on a previous natural diet study of the Chinese mitten crab in the same habitat, I expected to find that *E. sinensis* feeds primarily on detritus and algae, very rarely feeding on invertebrate prey (Halat 1997, Rudnick et al. 1999). However, gut content analyses alone do not allow prediction of potential diets in other habitat areas.

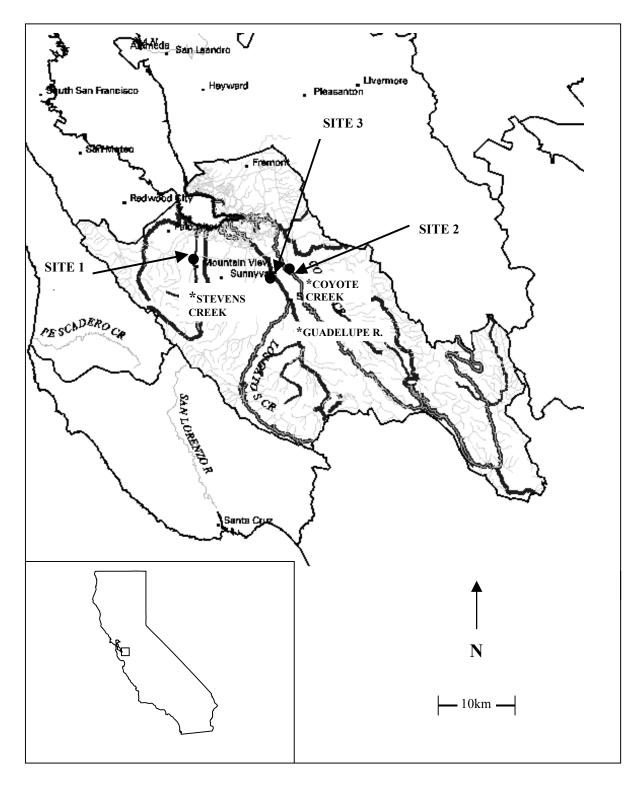


Figure 1. Map of the Coyote Creek watershed in Santa Clara County, California. The study sites are labeled where Site 1 is on Stevens Creek at Crittendon Road; Site 2 is on Coyote Creek at Charcot Road and Site 3 is on Guadelupe River at Montague Expressway. All three sites are approximately 5km upstream from the mouth of the river. This map is adapted from ICE MAPS, a resource of the UC Davis Information Center for the Environment.

Thus, several feeding preference experiments were also conducted to examine the potential range of diets of mitten crab populations in other California habitats (i.e., Sacramento Bay-Delta and southern California). This experiment assessed preferences for resident benthic invertebrates (such as oligochaete worms), leaf detritus, green algae and freshwater shrimp (*Palaemonetes paludosus*).

Study Sites

I chose three sites from three different creeks in Santa Clara County (Fig. 1). All of the sites are approximately 5 km from the mouth of stream. Each stream is labeled as follows: Stevens Creek at Crittendon Road, site 1; Coyote Creek at Charcot Road, site 2 and Guadelupe River at Montague Expressway, site 3. The sites differ in habitat type, flow and velocity of water, the hydroperiod, stream substrate and the riparian vegetation (Table 1).

site	September water temp (°C)	pН	salinity range (ppt)	tidally influenced	substrate type	burrows present	riparian vegetation
Stevens Creek (1)	21.5	8.4	<1-15	yes	soft sediment	yes	bulrush, cattail, shrubs, trees absent
Coyote Creek (2)	17.0	nd	0	no	stony	no	willow, cottonwood , tall grasses
Guadelupe River (3)	20.9	8	<1-5	yes	soft sediment	yes	bulrush, nettles (<i>Urtica</i>), cattail, few trees

Table 1. Characteristics from three sites in Santa Clara County used to collect crabs for gut content analysis. All sites are approximately 5 km upstream from the mouth of the stream. All data were collected September 1999, at the time of crab collection. nd = no data

Stevens Creek (site 1) and Guadelupe River (site 3) are characterized by mud-covered or clay banks and soft-sediment streambeds. These two streams have turbid water, with a daytime temperature of approximately 19-21°C in September (measured in the shade). Coyote Creek (site 2) has a stony streambed and clear, shallow water, with an average shaded temperature of 16-18°C in September. Sites 1 and 3 are tidally influenced, with a depth change of 2-3 meters from low to high tide, though site 1 has a larger salinity range than site 3 (Table 1). Site 2 is upstream of any tidal influence. Sites 1 and 3 are characterized by

cattail (*Typha*) and bulrush (*Scirpus*) vegetation, with few or no riparian trees present, while site 2 is characterized by numerous cottonwood (*Populus*) and willow (*Salix*) trees in addition to bulrush and tall grasses.

Methods

Gut Content Analysis Crabs were collected from late August through late October from each of the three sites with a trowel (to excavate burrows) or with small aquarium fish nets. A total of 103 crabs were collected, 46 from site 1, 24 from site 2 and 33 from site 3. Immediately after catching the specimens, crabs were placed in an ice-chest and upon return, transferred to a freezer for storage. All crabs were frozen for at least 48 hours before dissection.

Prior to dissection, each crab thawed in water for approximately 30 minutes. Each crab's weight, sex, carapace width and length were recorded. I removed the foregut for dissection, and assigned a visual estimate of gut-fullness based on an index of 1-4, with 1 equal to 0 to 25% gut fullness and 4 equal to 75 to 100% gut fullness (Wilhelm, in press). Gut contents were placed on a 24-grid Petri dish, and each grid was analyzed separately using a dissection microscope. Gut contents were separated into four main categories: algae, leaf detritus, animal and inorganic material using a visual assessment. Each food type in a grid was assigned a number 1-10 based on the percentage of the total area of the grid that the food type covered (Amundsen et al. 1996). All animal matter was identified to the lowest taxonomic level possible.

Three preliminary benthic samples (using a Surber sampler) were taken at site 2 to determine the abundance and diversity of aquatic invertebrates available to compare with the gut content data.

Within and between each site, one-way ANOVA was used to determine if each food type was consumed equally. A Tukey HSD Test was used to reveal the significant differences between each food type consumed.

Feeding Preference Experiments I collected 18 crabs from the same sites used to collect gut content analysis specimens. Each experiment consisted of six 5-gallon aquaria (with one crab and four food types) and two controls (four food types without crabs). Each feeding experiment lasted 24 hours and was replicated three times with the same crab.

The crabs were starved for three days prior to the experiment to clear the guts of remaining food (Kim and DeWreede 1996). After the gut clearance period, each crab was presented with four food choices of equal wet weight: resident benthic invertebrates from Santa Clara Co. streams (dragonfly larvae [Odonata] and oligochaete worms [*Tubifex* spp.], green algae (*Cladophora* spp.), stream conditioned leaf detritus, and freshwater ghost shrimp (*Palaemonetes paludosus*). With the exception of the ghost shrimp and oligochaete worms, all of the food choices presented to the crabs were collected from the sites from which the crabs were collected.

The controls were matched to the experimental tanks, but without a crab. After 24 hours, the food was removed from the control and experimental aquaria and weighed. To calculate the loss of each food type during the experiment, the wet weight of food left over was substracted from the wet weight of the food added to the aquaria for both experimental and control tanks. To calculate the amount of food eaten by each crab, the mean percent loss of food of the control tanks was subtracted from the actual loss of food from the experimental tanks. I assumed that there was no autogenic change in the organisms present during the study period of 24 hours.

Ghost shrimp, *Palaemonetes* spp., are not native to south San Francisco Bay area streams. However, there is a native and endangered ghost shrimp, the California freshwater shrimp (*Syncaris pacifica*), that inhabits streams in Sonoma, Napa and Marin counties. *Palaemonetes paludosus* is similar in morphology to *Syncaris pacifica*. Therefore, I included *Palamonetes paludosus* in the feeding experiment to obtain a coarse estimate of the mitten crab's preference for and ability to capture the similar *Syncaris pacifica*.

A linear regression was performed to analyze the relationship between carapace size and feeding preferences. A one-way ANOVA was performed to show whether each food was consumed in equal amounts. This was followed by Tukey's HSD test to discern specific differences between food types. All analyses were done using SYSTAT (version 8). Despite the new methods described by Roa (1992) and Lockwood (1998) regarding the analysis of feeding preference experiments, I used a one-way ANOVA because of the level of specificity I was seeking with such clear results was much lower than that implicit in the new analytical methods.

Results

Gut Content Analysis Of the specimens collected for gut content analysis, 22.3% of them had empty guts. Most of these empty gut crabs had recently molted, or were preparing to molt (52.2%), and 91.3% of all empty gut crabs were from site 1. The male to female ratio differed between sites, varying from 3:1 at site 2 to 1:1 at site 3 (Table 2). The size of the crabs varied substantially between the sites (Table 2); crabs from site 2 were larger than crabs from site 3, which were larger than crabs from site 1. The variance of the different sizes between sites did not account for the variance in the diets between sites. Thus, the effect of size on the diet consumed by crabs was not significant, as determined by an analysis of covariance (p>0.2). Therefore, I excluded the effect of size from further analyses, focusing on the effect of site location on diet.

Overall, the gut content analyses revealed that crabs consume mostly algae (31.5%, 17%, 37.6%, for sites 1, 2 and 3, respectively) and detritus (46%, 66.8%, 35%), while consuming a relatively small amount of animal matter (5.5%, 0.9%, 2%; Fig. 2).

Site	mean carapace width (mm)	M : F ratio	% empty gut	% recent molts	% crabs that ate animal matter	Total % animal matter in gut	Animal taxa present in gut
Stevens Creek (1) n = 46	19.8 ± 0.9	2.7 : 1	45.6	47.6	36.0	15.9 ± 3.7	Oligochaeta
Coyote Creek (2) n = 24	48.7 ± 1.9	3 : 1	0	0	29.2	$\textbf{3.1}\pm\textbf{0.1}$	Trichoptera (Hydroptilidae, other), Crustacea (Decapoda)
Guadelupe River (3) n = 33	34.9 ± 0.8	1:1	0.06	100	41.9	$\textbf{4.9} \pm \textbf{0.9}$	Crustacean (Decapoda): Procambarus clarkii, Eriocheir sinensis Diptera, Trichoptera
Total South Bay n = 103	31.6 ± 1.3	2 : 1	22.3	52.2	36.3	7.9 ± 1.6	

Table 2. Characterization of crabs collected for gut content analysis. The percent of recent molts is calculated as a percentage of total empty gut crabs. No recently molted crabs had food in their gut. The percent of crabs that ingested animal matter is calculated only for crabs with > 25% gut fullness. The total percentage of animal matter in the gut is averaged from crabs with animal matter present in the gut. Crabs that did not eat animal matter are not included.

Between sites, there were significant differences between the percentage of the gut fullness accounted for by algae (p=0.004), detritus (p<0.0001), animal (p=0.016), but no differences between sites were found for the amount of inorganic material consumed (p=0.27). Crabs from site 1 consumed more animal matter than site 2 crabs, site 2 crabs ate more algae and detritus than site 3 crabs and site 2 crabs ate more detritus than site 1 crabs (Fig. 2).

Within each site, all of the ANOVA tests were significant (p<0.0001). At site 1, (Stevens Creek), algae and detritus did not significantly differ in amount of gut contents; detritus was not different from inorganic matter, which was not different from animal matter. At site 2, (Coyote Creek), algae were greater than detritus, animal and inorganic matter. Detritus was not different from inorganic matter, but animal matter was less than all other food types. At site 3, (Guadelupe River), algae and detritus were not significantly different, but both were greater than animal and inorganic matter (Fig. 2).

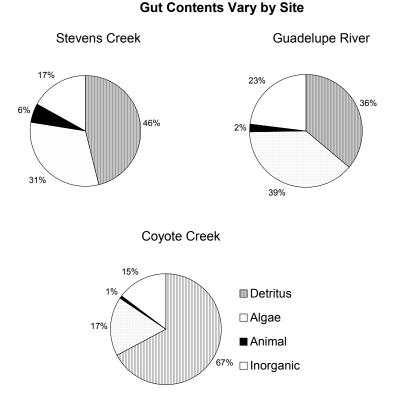


Figure 2. Gut content analysis results at each site, presented as average percentage of all guts. Crabs with less than 25% of the gut full were left out of this analysis.

On average, 36.3% of crabs had consumed animal matter, although it only constituted 7.9% of their total gut contents (Table 2). Further analysis of the animal matter present in the guts, indicated that the crabs had consumed oligochaete worms, Trichoptera larvae (Hydroptilidae spp.), crustaceans (crayfish [*Procambarus clarkii*] and mitten crabs [*Eriocheir sinensis*]), Diptera larvae and Plecoptera larvae.

The benthic samples taken from site 2 show that there is low taxonomic diversity (7 orders of benthic invertebrates present/m²) and low abundance $(39 \pm 20 \text{ individuals/m^2})$. The taxa present, from the composite of all samples, summed by Order: Diptera (52 individuals), Pelecypoda (49), Oligochaeta (12), Coleoptera (1), Polychaeta (1), Acari (1), Gastropoda (1). **Feeding Preference Experiments** The crabs used during the experiment ranged in size from 16mm to 51mm carapace width, and the male to female sex ratio was 1.75:1, which is approximately the average sex ratio across all the collection sites. During the course of the feeding experiments, one crab died (female, 61mm) after the first trial, and these data were not included in the resulting analysis.

Feeding Preferences Vary by Size

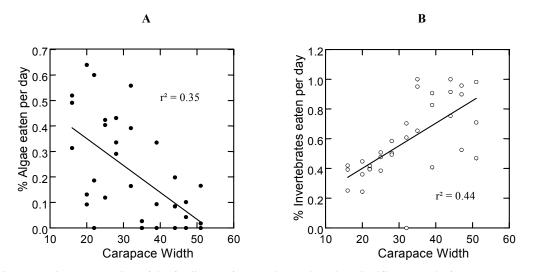
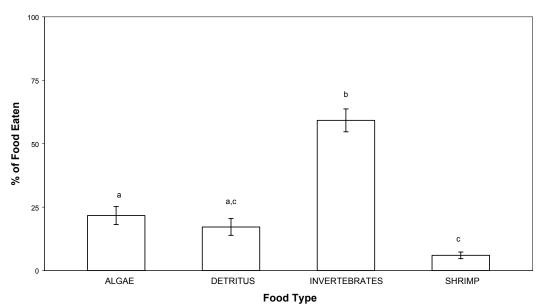


Figure 3. Linear regression of the feeding preference data. There is a significant trend of decreasing algae (A) and increasing resident invertebrate (B) consumption with increasing size, as measured by carapace width (p<0.001). Closed circles = algae, open circles = invertebrates.

Overall, *E. sinensis* exhibited a significant preference for resident invertebrates over algae, detritus and freshwater shrimp. This preference increases with increasing size of the consumer ($r^2=0.44$, p<0.001; Fig. 3). Resident invertebrates fed to the crabs were oligochaete worms (*Tubifex* spp.) and odonate (dragonfly) larvae, both sedentary and easily digestible aquatic invertebrates. There was also a significant trend of decreasing algae consumption with increasing size ($r^2=0.35$, p=0.0003). There was no significant trend of consumer size and percent consumption of detritus or freshwater shrimp. The crabs consumed, on average, 59.2% resident invertebrates, 21.7% green algae, 17.2% leaf detritus, and 6% freshwater shrimp, *Palaemonetes paludosus* (Fig. 4). There were significant differences in the amount of each food type consumed (p<0.0001). Algae and detritus consumption were not significantly different (p>0.2), while crabs consumed significantly more insects than any other food type (p<0.05), and significantly less shrimp than any other food type (p<0.05, Fig. 4).



Feeding Preferences of the Chinese Mitten Crab

Figure 4. This graph shows the mean percent of each food type eaten during all feeding trials. *E. sinensis* prefers resident invertebrates (shown as "invertebrates") significantly more than any other food type. Preferences which are significantly different from each other are represented by different letters as determined by Tukey's test for HSD (p<0.05).

Medium size rocks (4-6cm diameter) were provided as shelter in the aquaria for both consumer and prey. *E. sinensis*, when not feeding, hid behind the shelter. Although no observations were made during the evening, the crabs were observed eating sporadically at

all hours of the day. Odonate larvae and freshwater shrimp utilized the shelter, but only the freshwater shrimp was able to swim fast enough to escape capture by *E. sinensis*. However, as shown by the data, mitten crabs were successful in preying on shrimp. *Tubifex* spp. immediately formed clusters and generally sought out shelter underneath the detritus or algae present in the aquarium. *E. sinensis* did not use much effort to find and feed on *Tubifex*. In many instances, *E. sinensis* began feeding on *Tubifex* seconds after they were placed in the aquarium.

Discussion

There is a large discrepancy between the results of the gut content analysis (GCA) and the feeding preference experiments. The GCA results show that the major components of the mitten crab diet are algae and detritus, however, the feeding experiments show that mitten crabs prefer invertebrates to all other food types. This discrepancy can be partially attributed to three main factors that are specific to this study. First, it is difficult to distinguish softbodied invertebrates from detritus in gut content analysis, especially when there has been a considerable time lapse since ingestion. In addition, there are low invertebrate abundance and diversity, with the exception of chironomid larvae, pelecyopod clams, oligochaete and annelid worms. The last factor contributing to little animal matter in the mitten crab diet may be that crabs are not able to catch invertebrate prey in the wild. This scenario is unlikely, as studies conducted in Germany show that invertebrates can account for up to 33% of the diet of the mitten crab (Thiel 1938, Hoestlandt 1948). It is more likely that mitten crabs are confined to eating slow moving, conspicuous invertebrates, or dead animal matter. Nyström et al. (1999) showed that crayfish primarily prey on sedentary, conspicuous invertebrates such as soft-shelled snails and some insect larvae. Since both mitten crabs and crayfish are benthic, omnivorous crustaceans, I assume that mitten crabs have similar prey preferences. This assumption is corroborated by a preliminary feeding preference trial, where mitten crabs were unable to eat live Coleoptera (water beetles) and Ephemeroptera larvae (mayflies), both fast moving insects. However, I have shown that mitten crabs prefer to eat invertebrates to their current diet of algae and detritus, and will likely prey more heavily on sedentary invertebrates when they are present in higher abundance.

Recent studies have shown that high densities of crayfish $(5-22/m^2)$ can reduce the abundance of benthic macroinvertebrates in artificial streams and exclosure/enclosure experiments (Lodge et al. 1994, Charlebois and Lamberti 1996, Parkyn et al. 1997). This is especially true for Gastropoda and Trichoptera, orders that appear to be particularly vulnerable to crayfish predation, probably due to their relatively sedentary existence. *E. sinensis* has been reported to reach densities up to 15-30 crabs/m² in south Bay streams (Rudnick et al. 1999). Such high densities of mitten crabs could similarly reduce abundance of resident benthic communities, particularly in areas where the prey taxa present sedentary and conspicuous, and therefore easily caught.

Despite the apparent similarities between the diets and probable prey preferences of *Procambarus clarkii* and *E. sinensis*, *E. sinensis* has been shown to be dominant to *P. clarkii*, (Rudnick et al. 1999). Rudnick et al. showed that most of the competitive interactions between the two species involved access to shelter, rather than food, and no apparent negative effect on *P. clarkii* populations was found. This information shows that the likelihood of *E. sinensis* completely replacing *P. clarkii* is small, and that most competition between the two species will be focused on shelter, and will allow both species to cohabit the same areas in south Bay streams.

A study conducted in 1996 from similar south San Francisco Bay streams showed that only 2% of all crabs analyzed had invertebrate parts in the gut, while I found that over 35% of the crabs had consumed animal matter (Rudnick et al. 1999, Halat 1997). However, these differences could be attributed to different methods (none were noted in Rudnick et al. 1999 or Halat 1997) or to differences in available food items.

There were no differences in the types of food consumed between smaller and larger crabs, based on the gut content analysis data. This contradicts a previous study done in the crab's native range (Dan et al. 1984) suggesting that crabs switch from herbivory/detritivory to carnivory as they mature. This finding supports the statement that the mitten crab is an opportunistic consumer, eating what is available, regardless of size (Thiel 1938, Hoestlandt 1948, Rudnick et al. 1999). However, I did find that smaller crabs ate fewer resident invertebrates as a total percentage of food consumed in the feeding experiments than did larger crabs. This finding is most likely due to an increased ability to catch and handle prey in a confined place with increasing size, considering the fact that crabs in their natural habitat

did not exhibit any change in diet with size. Larger mitten crabs were also more likely to feed immediately after the food items were placed in the aquarium, whereas smaller crabs tended to hide for at least 30 minutes prior to feeding. This extra time allowed all prey species to find refuge (near rocks or detritus), prior to the onset of feeding. The time difference between larger and smaller crab predation likely resulted in more successful predation on behalf of larger crabs.

Mitten crabs of all sizes are capable of eating the freshwater shrimp (Palaemonetes paludosus), a similar species to the endangered California freshwater shrimp (Syncaris pacifica), which inhabits tributaries of the San Pablo Bay. This shows that the mitten crab is a potential predator of this endangered shrimp, where their habitat ranges overlap. The mitten crab is present in at least one stream where S. pacifica has been reported in the past (Sonoma Creek, Sonoma County, CA; USFWS 1997). Currently, it has been reported in Tomales Bay tributaries (Marin County) and some San Pablo Bay tributaries (Sonoma County). S. pacifica feeds mostly on detritus and resides underneath overhanging banks stabilized by riparian vegetation. The mitten crab poses more than one threat to the survival of the dwindling population of California freshwater shrimp, whose population is estimated to be less than 2000 individuals (USFWS 1997). The burrowing activity of E. sinensis could reduce the amount of suitable habitat for S. pacifica. In addition, mitten crabs use overhanging vegetation as shelter upstream. The feeding preference experiments indicate that E. sinensis is capable of capturing and preying on P. paludosus, indicating that E. sinensis is capable of preying on S. pacifica. Although there are likely to be behavioral differences between the shrimp species, it is notable that the mitten crab was able to prey on shrimp at all, given that other fast moving prev escaped predation (Ephemeroptera larvae and Coleoptera; L.A. Rogers, unpublished data).

Overall, the mitten crab has a serious potential to affect the freshwater benthic communities they inhabit, due to their population size. Presently, they are consuming leaf litter detritus and algae in south San Francisco Bay tributaries, both important food sources for many aquatic insects and resident crayfish. This may cause negative indirect effects for grazing and shredding aquatic insects; effects that could be channeled up the food chain to negatively impact populations of predatory insects and fish. In addition, they are also capable of directly preying on insects and other invertebrates, which could lower these

invertebrate population numbers even further. These effects are not to be confined to the south San Francisco Bay region alone. The results from the feeding preference studies show that mitten crab populations will feed on a wide variety of foods, though they prefer animal matter. These results can be inferred to predict the diet of the mitten crab in other streams and rivers in California. Given the presence of sedentary, conspicuous and relatively softbodied invertebrates, the mitten crab will presumably have a diet richer in animal matter than south Bay crabs. E. sinensis is consuming 30-100% of their diet as invertebrates (mostly native clam species, Pisidae) in tributaries of San Pablo Bay, (L.A. Rogers, unpublished data). Thus, the findings that E. sinensis is primarily feeding on algae and detritus in the south Bay are not transferrable to other habitats. Although E. sinensis is an opportunistic feeder, though they have been shown to have the highest growing rate on a diet composed of 60% animal matter (Mu et al. 1998). Thus, like crayfish, when given a habitat rich in preferred prey items, they will presumably change their diet commensurately. Finally, given the large mitten crab population, it is hard to ignore the fact that they are or will have an impact on the local freshwater communities. More experimental studies, simulating realistic environments are necessary to determine the full range of the feeding behavior and ecology of E. sinensis to make specific predictions of the effects E. sinensis will have on California's stream communities

Acknowledgements

I am grateful to D.A. Rudnick and T.L. Dudley for their helping collect specimens, for stimulating discussions and advice on this project. I thank J.F. Bêche for his help in collecting specimens and Prof. Vince Resh for advice and use of his laboratory space and equipment. I would also like to thank Scott Siegfried from the Bureau of Land Management for collecting crabs in Tracy. This research was funded by a Biology Fellows Program grant from the Howard Hughes Medical Institute and a CALFED Bay-Delta awarded to Vince Resh and Deborah Rudnick.

References

Adler, P.B. et al. 1998. Understory succession following a dieback of Myrica faya in Hawai'i Volcanoes National Park. Pacific Science 52: 69-78.

- Amundsen, P.A., Gabler, H.M., and Staldvik, F.J. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data -modification of the Costello (1990) method. Journal of Fish Biology 48: 607-614.
- Charlebois, P.M. and G.A. Lamberti. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. Journal of the North American Benthological Society 15: 551-563.
- Clark, P.F., et al. 1998. The alien Chinese mitten crab, *Eriocheir sinensis*, in the Thames catchment. Journal of the Marine Biological Association of the United Kingdom 78: 1215-1221.
- Cohen, A.N. and J.T. Carlton. 1998. Accelerating invasion in a highly invaded estuary. Science 279: 555-557.
- Cohen, A.N. and J.T. Carlton. 1997. Transoceanic transport mechanisms: introduction of the Chinese mitten crab, *Eriocheir sinensis*, to California. Pacific Science 51: 1-11.
- Dan, Q.K., et al. 1984. The ecological study of the catadromous crab *Eriocheir sinensis* going upstream. Tung wu hsueh tsa chih (Chinese Journal of Ecology) 6: 19-22.
- Grosholz, E.D. et al. 2000 (in press). The impacts of a nonindigenous marine predator in a California bay. Ecology 81.
- Halat, K.M. 1996. The distribution and abundance of the Chinese mitten crab (*Eriocheir sinensis*) in southern San Francisco Bay, 1995-1996. M.Sc. Thesis, University of California, Berkeley.
- Hill, A.M. et al. 1993. Invasion of an occupied niche by the crayfish *Orconectes rusticus*: potential importance of growth and mortality. Oecologia 94: 303-306.
- Hill, M.P. and O'keefe, J.H. 1992. Some aspects of the ecology of the freshwater crab *Potamonautes perlatus* (Milne Edwards) in the upper reaches of the Buffalo River Eastern Cape Province, South Africa. South African Journal of Aquatic Sciences 18(1-2): 42-50.
- Hoestlandt, H. 1948. Recherches sur la biologie de l'*Eriocheir sinensis* H. Milne Edwards (Crustace brachyoure). Annales de l'Institut Oceanographique 24(1): 1-116.
- Jadzdzweski, K. and A. Konopacka. 1993. Survey and distribution of crustacea malacostraca in Poland. Crustaceana 65(2): 177-191.
- Kim, J.H. and R.E. DeWreede. 1996. Distribution and feeding preferences of a high intertidal littorinid. Botanica Marina 39: 561-569.

- Light, T., et al. 1995. Decline of the Shasta crayfish (*Pacifasticus fortis* Faxon) of Northeastern California. Conservation Biology 9: 1567-1577.
- Lockwood III, J.R. 1998. On the statistical analysis of multiple-choice feeding preference experiments. Oecologia 116: 475-481.
- Lodge et al. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology 75: 1265-1281.
- Moyle, P.B. and J.E. Williams. 1990. Biodiversity loss in the temperate zone: decline of the native fish fauna of California. Conservation Biology 4: 275-284.
- Mu, Y.Y. et al. 1998. Effects of protein level in isocaloric diets on growth performance of the juvenile Chinese hairy crab, *Eriocheir sinensis*. Aquaculture 165:139-148.
- Nyström, P., et al. 1999. Influence of an exotic and a native crayfish species on a littoral benthic community. Oikos 85: 545-553.
- Panning, A. 1939. The Chinese mitten crab. Report of the Board of Regents of the Smithsonian Institution 3508: 361-375.
- Parkyn, S.M. et al. 1997. Effects of crayfish (*Paranephrops planifrons*: Parastacidae) on instream processes and benthic faunas: a density manipulation experiment. New Zealand Journal of Marine and Freshwater Research 31: 685-692.
- Peterson, C.H. and R.E. Renaud. 1989. Analysis of feeding preference experiments. Oecologia 80: 82-86.
- Roa, R. 1992. Design and analysis of multiple-choice feeding preference experiments. Oecologia 89: 509-515.
- Rudnick, D.A., et al. 1999. Economic and ecological impacts of the Chinese mitten crab (*Eriocheir sinensis*) in San Francisco Bay. Technical Completion Report, University of California Water Resources Center UCAL-WRC-W-881. Berkeley, CA. 106pp.
- Stelzer, R.S. and G.A. Lamberti. 1999. Independent and interactive effects of crayfish and darters on a stream benthic community. J. North American Benthological Society 18: 524-532.
- Thiel, H. 1938. Die allgemeinen Ern\u00e4hrungsgrundlagen der chinesischen Wolhandkrabbe (*Eriocheir sinensis* Milne-Edwards) in Deutschland, insbesondere im Einwanderungsgebiet im weiteren Sinne. Mitt. Aus dem Hamburg. Zool. Mus. & Inst. in Hamburg 47: 50-64.
- U.S. Fish and Wildlife Service. 1997 Draft California Freshwater Shrimp (*Syncaris pacifica* Holmes) Recovery Plan. U.S. Fish and Wildlife Service, Portland, OR. 87+pp.

- Veldhuizen, T.C. and S. Stanish. 1999. Overview of the life history, distribution, abundance and impacts of the Chinese mitten crab, *Eriocheir sinensis*. California Department of Water Resources, Environmental Studies Office, Interagency Program, Sacramento, CA. 22+pp.
- Wilhelm, F. M., et al. (in press). The seasonal food habits of bull trout from a small alpine lake in the Canadian Rocky Mountains. Transactions of the American Fisheries Society.