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INTERSPECIFIC INTERACTIONS BETWEEN THE INTRODUCED ATLANTIC CRAB  
RHITHROPANOPEUS HARRISII AND THE NATIVE ESTUARINE CRAB  
HEMIGRAPSUS OREGONENSIS IN COOS BAY, OREGON

by

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A THESIS

Presented to the Department of Biology  
and the Graduate School of the University of Oregon  
in partial fulfillment of the requirements  
for the degree of  
Master of Science

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Approved: James T. Carlton  
James T. Carlton

## An Abstract of the Thesis of

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Title: INTERSPECIFIC INTERACTIONS BETWEEN THE INTRODUCED ATLANTIC  
CRAB RHITHROpanopeus harrisii AND THE NATIVE ESTUARINE CRAB  
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Rhithropanopeus harrisii is an introduced Atlantic crab in Coos Bay, Oregon. In Coos Bay, it occurs only in the uppermost estuary where salinities are seasonally low (<1 o/oo). Rhithropanopeus occurs at higher salinities in its native range, and tolerates higher salinities in the laboratory. A native crab, Hemigrapsus oregonensis, occurs in the estuary, but not as far up into the oligohaline and freshwater zones as Rhithropanopeus. In laboratory experiments, adult Hemigrapsus consume juvenile Rhithropanopeus. Hemigrapsus is significantly more aggressive than Rhithropanopeus. The absence of juvenile Rhithropanopeus at field sites where both species occur suggests that field interactions may be occurring. Taken together, these results and observations suggest that there may be a dynamic zone in the estuary where the distribution of

Rhithropanopeus is restricted by Hemigrapsus. Rhithropanopeus may find a refuge from Hemigrapsus in the oligohaline-freshwater zones of the estuary, such that Hemigrapsus may be exerting selective pressure on the Rhithropanopeus population favoring freshwater-adapted individuals.

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## TABLE OF CONTENTS

	Page
INTRODUCTION.....	1
Ecology of Biological Invasions.....	1
Atlantic Rhithropanopeus on the Pacific Coast.....	3
Estuarine Crabs in Coos Bay.....	6
Interactions Between <u>Hemigrapsus</u> and <u>Rhithropanopeus</u> .....	11
Alternative Hypotheses.....	12
Present Study.....	14
MATERIALS AND METHODS.....	16
Field Studies.....	16
General Survey.....	16
Transect Censuses.....	17
Field Transplants.....	19
Laboratory Studies.....	19
Predation.....	19
Competition for Shelter.....	22
Salinity Tolerance.....	24
RESULTS.....	25
Field Studies.....	25
General Survey.....	25
Transect Censuses.....	25
Field Transplants.....	32
Laboratory Studies.....	33
Predation.....	33
Competition for Shelter.....	36
Salinity Tolerance.....	38
DISCUSSION.....	39
BIBLIOGRAPHY.....	45

## LIST OF TABLES

Table	Page
1. Comparison of the Biology of <u>Rhithropanopeus harrisi</u> and <u>Hemigrapsus oregonensis</u> .....	7
2. Factors Potentially Limiting <u>Rhithropanopeus</u> to the Upper Estuarine Zones of Coos Bay.....	13
3. Experimental Design to Test for Predation among Crabs..	21
4. Incidence of Predation among <u>Hemigrapsus oregonensis</u> and <u>Rhithropanopeus harrisi</u> .....	33
5. Incidence of Predation between Adult <u>Hemigrapsus oregonensis</u> and Juvenile <u>Rhithropanopeus harrisi</u> According to the Presence or Absence of Food and Rocks in the Experimental Enclosure.....	35
6. Frequency of Aggressive Acts between <u>Hemigrapsus oregonensis</u> and <u>Rhithropanopeus harrisi</u> .....	37
7. Salinity Tolerance of <u>Rhithropanopeus</u> and <u>Hemigrapsus</u> ..	38

## LIST OF FIGURES

Figure	Page
1. <u>Rhithropanopeus harrisi</u> and <u>Hemigrapsus oregonensis</u> ...	4
2. Map of Coos River, Showing Location of Three Field Sampling Sites.....	18
3. Design of Cages Used to Test Survival of Transplanted Crabs.....	20
4. Design of Arenas Used to Test for Aggression and Competition for Shelter between Crabs.....	23
5. Distribution of <u>Hemigrapsus oregonensis</u> in Coos Bay....	26
6. Distribution of <u>Rhithropanopeus harrisi</u> in Coos Bay...	27
7. Mean Density and Standard Deviation of <u>Hemigrapsus</u> <u>oregonensis</u> from Feb.-June, 1988 at Site 1.....	29
8. Mean Densities and Standard Deviations of <u>Rhithropanopeus harrisi</u> at Three Sites in Coos River from Feb.-June, 1988.....	30
9. Size Distribution of <u>Rhithropanopeus</u> Found at Three Sites in Coos River.....	31
10. Predation of Large Male <u>Hemigrapsus oregonensis</u> on <u>Rhithropanopeus harrisi</u> .....	34

## INTRODUCTION

### Ecology of Biological Invasions

The ecology of introduced species (biological invasions) is a relatively new field. Only recently in evolutionary time have exotic species been introduced by humans, whether accidentally or intentionally, into environments in which they had never before been found (Elton, 1958). The responses of species introduced into new habitats have varied: some have quickly died out, others have persisted in the new environment, while still others have flourished in their new habitat at the expense of native species. By studying the differential success of invading organisms and the differential receptiveness of particular communities to invasions, it may be possible to predict the relative success of an invasion as well as to predict the effect of that invasion on the assemblage of native species.

In the marine environment, the introduction of non-native species often goes unnoticed, either because of the small size of the organisms themselves, or because knowledge of local species for most marine environments is incomplete (Carlton, 1979). Thus, when a new species is discovered in a particular region, biologists often incorrectly assume that its discovery, but not its presence, is a

new phenomenon. However, the estuary has proved to be an ecosystem in which biological invasions can be monitored and studied with relative ease. The estuary also appears to be an ecosystem which is particularly susceptible to invasion.

Reasons for the success of introduced species in estuaries can be hypothesized and focus on disturbance and modes of transport. Estuaries are often artificially disturbed, as humans have historically used these inlets as harbors for commercial activities. These disturbances, in the form of dredging, filling, damming, pilings, jetties, etc., are thought to displace some native species, which are not able to tolerate the new disturbed habitat, and at the same time provide a colonizable microhabitat for other more "weedy" species (Harper, 1965). Many authors have thus suggested a connection between disturbance and invasion (Elton, 1958; Harper, 1965). The mode of dispersal for marine biological invasions is generally connected to human activities which occur in or near estuaries. Some of these dispersal modes include the transport of organisms in the ballast water of ships, inadvertent movement along with commercial transplants (oysters, clams, fish, etc.), and as "fouling" on the hulls of ships. These dispersal routes often both originate and terminate in an estuarine environment.

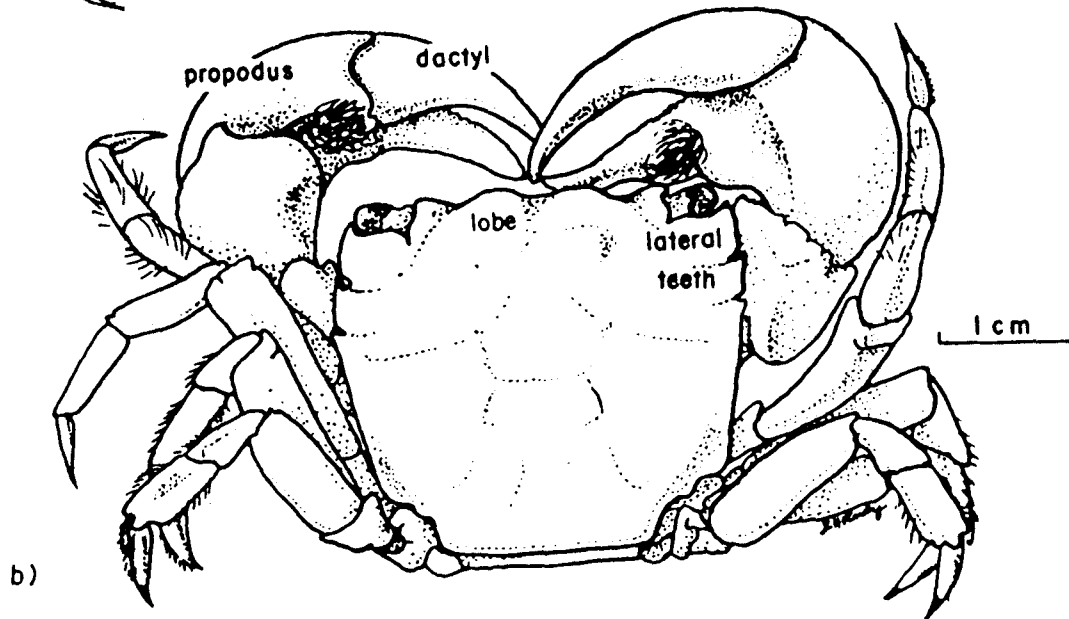
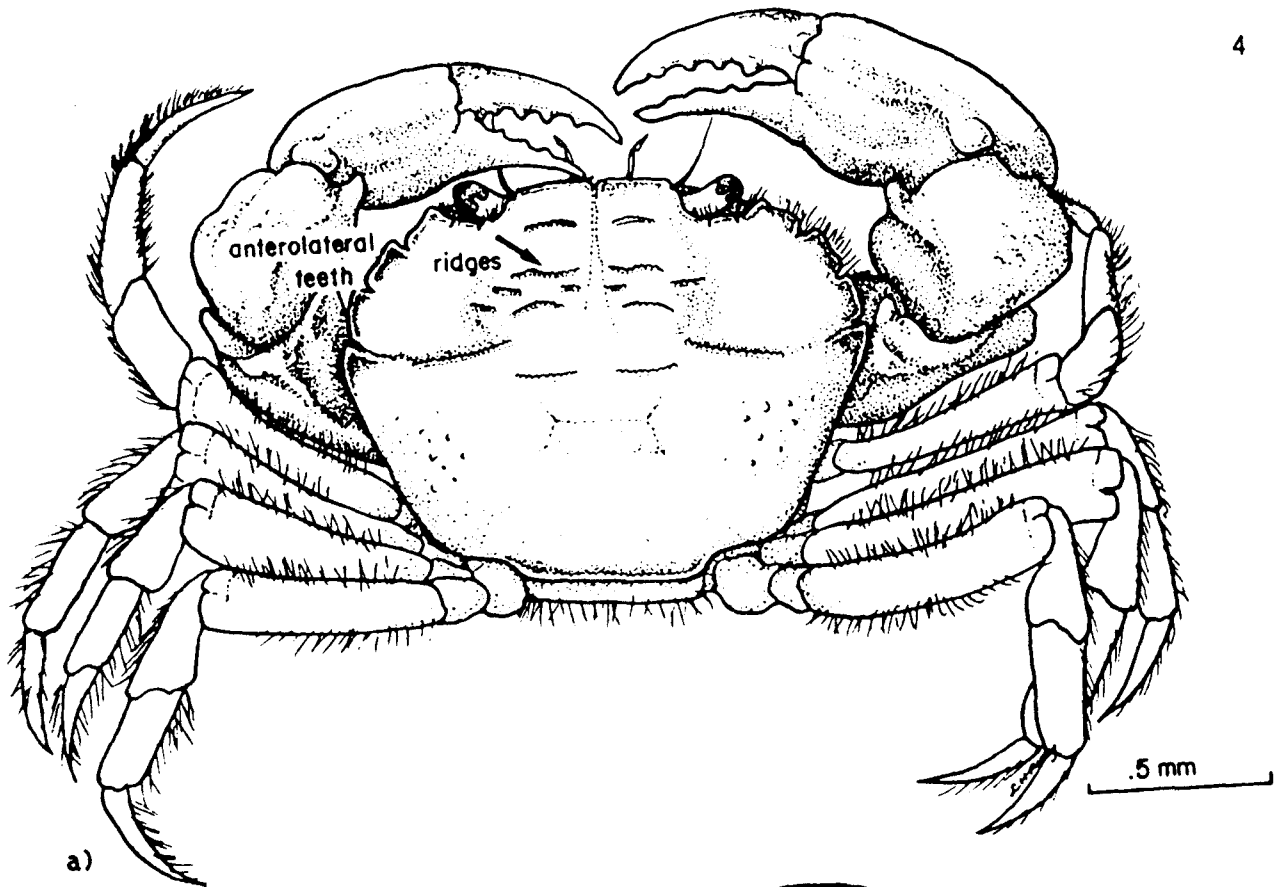
Estuaries, in addition to accomodating exotic species, are well known as highly productive environments in which many organisms reproduce exclusively. Estuaries are utilized by many commercially important fish and shellfish at some point in their life cycle. Many researchers have noted that introduced species may take

resources away from native species (Zaret and Paine, 1973; Brenchley and Carlton, 1983), and may alter food chains in a way that will prove detrimental not only to resident estuarine organisms, but also to those migratory organisms which use the estuary as a feeding or breeding ground. Conversely, many non-native species of annelids, crustaceans, and mollusks may contribute to the trophic web of an estuary, potentially enhancing native predator populations (Baker, 1988).

In order to better understand biological invasions, it would be useful to be able to predict the effects of exotic species on native communities. What is the ability of a given organism to colonize a particular community, and what effect will that species have on the native species assemblage once established in the community? One approach to these questions, and an approach which can increase predictive ability, is the study of past introductions of exotic species, and the effects of these introductions on native species assemblages.

#### Atlantic Rhithropanopeus on the Pacific Coast

One such historical introduction on the Pacific Coast of North America was discovered in the late 1930s, when the the Atlantic mud crab Rhithropanopeus harrisi (Gould, 1841) was found in San Francisco Bay. Rhithropanopeus (Fig 1a) is a small (21.3 mm maximum width on Atlantic Coast, 22 mm maximum width in Coos Bay) xanthid crab which is very common in the upper parts of Atlantic estuaries (Ryan, 1956). Rhithropanopeus was probably transported from the



Figures 1a-b. Rhithropanopeus harrisi and Hemigrapsus oregonensis. a) Rhithropanopeus harrisi. b) Hemigrapsus oregonensis. (From Rudy and Rudy, 1983).

Atlantic coast as juveniles or adults in commercial shipments of oysters or as larvae in the ballast tanks of ships. Rhithropanopeus was first found in Coos Bay, Oregon in 1952 by Hedgpeth, although Carlton (1979) believes that this late discovery may be an artifact due to the timing of exploration. It is unknown how Rhithropanopeus arrived in the bays and estuaries of Oregon, but the same mechanisms, namely oyster transport and ballast water, may be responsible. Rhithropanopeus is now found in at least four estuaries on the Oregon coast: Coos Bay (Hedgpeth, 1952), Netarts Bay (Stout, 1976, as reported in Carlton, 1979), Yaquina Bay (Pisciotta, 1978), and the Umpqua River (Miller, as reported in Carlton, 1979). Its existence in the Umpqua River is particularly puzzling, since this river does not have any major shipping or oystering and dispersal of the species is generally thought to depend on these activities. Larval export out of Coos Bay and subsequent transport into the Umpqua River mouth, 35 km north of Coos Bay, is a possible explanation (Carlton, pers. comm.).

In its native environment on the Atlantic Coast, Rhithropanopeus is a common inhabitant of tidal flats and oyster beds in a salinity range of 2.8 to 18.6 o/oo. It occasionally occurs in fresh water as well (Ryan, 1956). It is always found associated with some kind of shelter - oyster bars, living and decaying vegetation, old cans, rocks and other debris (Williams, 1984). Its known range is from the southwestern Gulf of St. Lawrence, Canada, to Veracruz, Mexico (Williams, 1965). It has also been introduced to Europe and to the Panama Canal (Naylor, 1960; Turoboyski, 1973; Marchand, 1979; Williams, 1984). The crab was found in the old

Dutch Zuider Zee, a brackish inland sea, but gradually diminished after the sea was closed in 1936 (Buitendijk and Holthius, 1949). In 1939 it was reported in large numbers from southern Russia, in the estuaries of the Dnestr and Bug Rivers, and has also been found in the Black and Caspian Seas, in northwestern European rivers such as the Loire, and in brackish waters of Romania and Bulgaria (Williams, 1984). While Rhithropanopeus is believed to have been transported from the Atlantic to the Pacific coasts of North America via commercial oyster culture or in ballast water, the mechanism of its transport in the nineteenth century in Europe is not clear. Given its propensity for living in crevices, it may have crossed the Atlantic on well-fouled ships.

#### Estuarine Crabs in Coos Bay

In addition to the relatively new presence of Rhithropanopeus, several native crab species occur in the upper Coos Bay estuary. The most common is Hemigrapsus oregonensis (Dana, 1851) (Fig 1b), an abundant crab of bays, estuaries, and harbors, as well as outer shores, from Alaska to Baja California. Two other species, Cancer magister (Dana, 1852) and Cancer productus (Randall, 1839) invade the upper estuary in the summer, when freshwater flow is at a minimum, but only Hemigrapsus and Rhithropanopeus are year-round residents of the upper estuarine zone. Basic aspects of the distribution, biology, and ecology of Rhithropanopeus and Hemigrapsus are summarized in Table 1.

TABLE 1. Comparison of the Biology of Rhithropanopeus harrisi and Hemigrapsus oregonensis. Rhithropanopeus traits are based on studies of Atlantic coast populations.

Trait	<u>Rhithropanopeus</u>	<u>Hemigrapsus</u>
Latitudinal Range	20-45° N Lat (1)	25-60° N Lat (2)
Temperature Range	9-30 degrees C (3)	5-28 degrees C (2)
Horizontal Range (in estuary)	upper/middle (3)	middle/lower (4)
Vertical Range (in intertidal zone)	low (3)	low to high (4)
Habitat Preference	in mud under rocks or among debris (3)	under or among rocks (4)
Feeding Preference	omnivorous (5)	herbivorous/ omnivorous (4)
Mean / Maximum Size	9 / 21 mm (1)	15 / 35 mm (2)
Timing of Reproduction	May - Sept. (3) (1x / yr)	Feb. - Sept. (8) (2x / yr)
Adult Salinity Range	0-18.6 o/oo (3)	3-35 o/oo (4)
Adult Salinity Tolerance	0-40 o/oo (6)	3-40 o/oo (4)
Larval Salinity Range	3-28 o/oo (7)	Not Known
Larval Salinity Tolerance	5-35 o/oo (6) (optimal=20 o/oo)	Not Known

(1) Williams, 1984; (2) Rudy and Rudy, 1983; (3) Ryan, 1956; (4) personal observation; (5) Odum and Heald, 1972; (6) Christiansen and Costlow, 1975; (7) Cronin, 1982; (8) Knudson, 1964.

The larval stages of Rhithropanopeus have been studied extensively. Hood (1962) noted that there are four zoeal and one megalopa stage before settlement. Christiansen and Costlow (1975) found that the optimal conditions for larval development were 20 o/oo at 20-25 degrees Celsius. Megalopae as well as some zoeae reared in full strength seawater or pure freshwater showed abnormalities in growth. Cronin (1982) and Cronin and Forward (1983) found that the larvae of Rhithropanopeus are retained in the upper parts of estuaries, where development proceeds most effectively. The mechanism for estuarine retention is a vertical migration pattern; larvae tend to migrate to the region of no net flow on outgoing tides and thus maintain themselves in the upper estuary.

The megalopae settle out as small (2-4 mm) benthic crabs. Males in Chesapeake Bay were found to reach sexual maturity at 4.5 mm carapace width, and females at 4.4-5.5 mm. The adults continue to grow and molt to a maximum size of 21.3 mm carapace width in males and 16 mm in females (Ryan, 1956). Adult Rhithropanopeus are excellent osmoregulators, and can tolerate salinities of 0-40 o/oo (Christiansen and Costlow, 1975). Additionally, the species tolerates a wide range of temperatures: from 9-30 degrees Celsius (Christiansen and Costlow, 1975). Juvenile and adult Rhithropanopeus are omnivorous. Detritus and some small crustaceans comprised part of the diet of a population in a mangrove swamp in Florida (Odum and Heald, 1972).

Since its introduction, some aspects of the biology of Rhithropanopeus have been examined on the Pacific Coast. Jones (1940) documented the introduction, and compared osmoregulation of Rhithropanopeus with osmoregulation of some native crabs, including Hemigrapsus. He found that as salinity approaches zero, Rhithropanopeus maintains its ability to osmoregulate, but Hemigrapsus dies because it is unable to osmoregulate (Jones, 1941). Smith (1967) also studied the osmoregulatory mechanism of Rhithropanopeus, and found that Rhithropanopeus osmoconforms at moderate salinities, and osmoregulates at extreme salinities. Pisciotto (1978) documented the distribution, biology, and ecology of Rhithropanopeus in Coos Bay. He found Rhithropanopeus to be abundant in the upper estuary, but never found Hemigrapsus at sites where Rhithropanopeus was found. In some cursory experiments, he found that Rhithropanopeus was more tolerant of low salinities than Hemigrapsus. Also, he documented two cases of predation on small (7 mm) Rhithropanopeus by a larger (19 mm) Hemigrapsus. He found bits of algae, sand grains, and in one case, part of a crab carapace in the branchial baskets of several Rhithropanopeus collected from the field. In the lab, he noted that Rhithropanopeus was most active at night (Pisciotto, 1977). Carlton (1979) summarized much of the known information on the introduction and ecology of Rhithropanopeus on the Pacific coast. Rudy and Rudy (1983) summarized the biology and ecology of Rhithropanopeus in Coos Bay.

Hemigrapsus oregonensis is a common native estuarine crab from Alaska to Baja California. The carapace width of males reaches a maximum of 35 mm, while females grow nearly as large (Rudy and Rudy,

1983). It is a true estuarine crab in that it prefers somewhat brackish waters to full seawater. In San Francisco Bay, it was found in waters ranging from 17.5 to 31.6 o/oo (Schmitt, 1921). Dehnel (1967) reports that Hemigrapsus can tolerate salinities down to 5 o/oo. In Coos Bay, it has been found living in 3.0-4.0 o/oo, and living next to (but not in) freshwater (pers. obs.). It prefers quiet waters, rocky habitats within estuaries, muddy bottoms of estuaries, eelgrass and Enteromorpha. This crab often burrows in the mud or sand under rocks, feeding most commonly at night (Batie, 1983). It is thought to be primarily a herbivore, scraping algae off the rocks (Rudy and Rudy, 1983), though it can be omnivorous in some situations. Hemigrapsus is the dominant small intertidal crab of Pacific estuaries. It is a good osmoregulator, and thus can live further up many estuaries than some of the Cancroid crabs.

Thus, Rhithropanopeus and Hemigrapsus are similar in their size, habitat, feeding, temperature and salinity preference. However, they differ strikingly in minimum salinity tolerance (of adults) and also differ slightly in the timing of their reproduction (Table 1).

The physical conditions in Coos Bay are generally within the physiological tolerances of both of these two species. Salinity within the bay is highly variable by season. From the mid-summer to late fall, most of the bay is quite saline, up to 35 o/oo throughout the lower and middle bay. In winter and spring, however, there is a salinity gradient from the upper to lower bay, ranging from 0 o/oo in the Coos River to 35 o/oo at the mouth of the bay. The increase in salinity from the river to the mouth of the bay is generally

linear. Temperature in the bay also fluctuates seasonally, but the overall range is from about 12 to 25 degrees Celsius. Temperatures are much more variable in the upper bay than in the lower bay (Rudy and Rudy, 1983). Rocky intertidal areas, with muddy or sandy substrates are abundant throughout the bay (Pisciotta, 1978 and pers. observation). There are some regions of the Coos River and upper bay which are heavily silted, and have no exposed rocks.

#### Interactions Between Rhithropanopeus and Hemigrapsus

Following the discovery of Rhithropanopeus on the Pacific coast, several authors speculated that Rhithropanopeus and Hemigrapsus may interact competitively (Jones, 1940; Pisciotta, 1978; Carlton, 1979). Additional evidence for this is that Rhithropanopeus is found in salinities as high as 18.6 o/oo on the Atlantic coast, whereas in Coos Bay and San Francisco Bay Rhithropanopeus does not extend into those salinities where Hemigrapsus occurs (Jones, 1940; Pisciotta, 1978). Conversely, Rhithropanopeus has normally been found on the Atlantic coast in salinities down to 2.8 o/oo and occasionally in fresh water, whereas in Coos Bay for much of the year it is commonly found in salinities of 0.1 o/oo or less, suggesting that interactions with Hemigrapsus may have selectively "pushed" Rhithropanopeus into less saline habitats.

Jones (1940) noted that following a relatively dry year Hemigrapsus was able to move up into San Pablo Bay and increase its population, which "doubtless caused a decrease in the number of"

Rhithropanopeus, though no quantitative studies were done. He also noted that "Hemigrapsus oregonensis is far more active and aggressive than Rhithropanopeus, so that competition for food and shelter between the two could only result in the dominance of Hemigrapsus," but again, no studies were performed. Pisciotto (1978) concluded that "comparisons between Rhithropanopeus and Hemigrapsus oregonensis revealed nearly identical food preferences, activity patterns, and habitat preferences, so that the two are most surely competitors." However, he also did not perform any experiments to test this competition hypothesis.

#### Alternative Hypotheses

Other factors may be responsible for leading to the observed distributional patterns of Rhithropanopeus in the upper estuary (Table 2). One possibility is that Rhithropanopeus simply "prefers" the low salinity and seasonally high temperature regime of its current range. The salinity of the lower bay is high in summer and as mentioned before, Rhithropanopeus larvae are known to suffer abnormalities in growth at high salinity. Also, the moderate temperatures of the lower bay may be too cool for Rhithropanopeus larvae, as they develop optimally at 20-25 degrees Celsius. Another possibility is exclusion from the lower bay by a marine parasite. In fact, the parasitic isopod Portunon conformis occurs in some California populations of Hemigrapsus oregonensis (in 21.2 % of crabs in one sample from San Francisco Bay) (Morris et al., 1980). Fourth, competition or predation may occur between Rhithropanopeus

TABLE 2. Factors Potentially Limiting Rhithropanopeus to the Upper Estuarine Zones of Coos Bay.

Factor	Remarks
Salinity Tolerance	Larvae develop abnormally in full seawater but optimal development is at moderate salinities. Adults tolerate wide range, and are found in 18.6 o/oo on Atlantic Coast.
Temperature Tolerance	Adults tolerate coldest temperatures throughout Coos Bay; larvae develop best at warm temperatures (20-25 degrees Celsius). Unknown if cold temperatures could hinder development in Coos Bay.
Larval Transport/ Horizontal Regulation	Larvae actively maintain position in upper estuary; unknown if larvae transported down bay can survive (see text for discussion of occurrence in Umpqua River), and note abnormal development in full seawater.
Food Resources	Considered omnivorous; not believed to require food unique to upper estuary.
Interactions with native <u>Hemigrapsus</u>	May compete with, be preyed upon, or disturbed by <u>Hemigrapsus</u> , thus limiting down-bay distribution.
Interactions with other native species	Other predators that may be abundant in the lower estuary may limit down-bay occurrence by feeding on adult crabs (fish and birds) or larvae (annelids and other crustaceans). Other infaunal or epifaunal competitors may exist.
Parasites, disease	Isopod parasite of <u>Hemigrapsus</u> may also infect <u>Rhithropanopeus</u> and limit distribution. Other parasites may exist.
Substrate Availability	Eurytopic with regard to habitat, but most abundant in mud under rocks; habitat found throughout Coos Bay. However, may prefer finer grained mud of upper bay.

and other native species aside from crabs. Fifth, Rhithropanopeus may prefer or require a specific prey item not found in the lower bay. Sixth, the larvae of Rhithropanopeus may be selectively retained in the upper estuarine zones, as they are known to do so in their native habitat (Cronin, 1982; Cronin and Forward, 1983). Finally, Rhithropanopeus may require a specific substrate type only found in the upper bay, as the sediment there is generally finer grained than the sediment of the lower bay.

#### The Present Study

Most previous studies have assumed or inferred that competitive or predatory interactions between Rhithropanopeus and Hemigrapsus may restrict Rhithropanopeus to the upper estuary. No previous studies have attempted to address experimentally these hypothesized interactions. This study focuses on the possible interactions between the two species and the effect that such interactions might have on the observed distribution pattern. Specifically, the following questions are addressed: 1) What is the distribution and abundance of Rhithropanopeus in Coos Bay, and do the patterns of distribution indicate that competition or predation with Hemigrapsus may be occurring? 2) Can adult Rhithropanopeus survive the physiological conditions of the lower bay where Hemigrapsus is found? 3) Will Hemigrapsus prey on Rhithropanopeus adults or juveniles in the laboratory, and if so, under what conditions is predation most likely to occur? 4) Will Rhithropanopeus and Hemigrapsus interact aggressively in the laboratory for shelter?

5) What is the minimum salinity tolerance in the laboratory of both Rhithropanopeus and Hemigrapsus?

## MATERIALS AND METHODS

### Field Studies

#### General Survey

In order to determine the local habitat and distribution of Rhithropanopeus and Hemigrapsus, a field survey of upper Coos Bay and adjacent sloughs was performed between October, 1987 and March, 1988. Searches were made in all of the major sloughs (Kentuck, North, Larson, Coalbank, Isthmus, Pony, South, Joe Ney, Catching, Haynes Inlet and Coos River). At each new site, a minimum 1 hour search was performed. Rocks were overturned along the low tide line, and the presence of different species of crabs was recorded. From this survey, the current range of both Hemigrapsus and Rhithropanopeus was established, and the region in which the two ranges overlap was established. Data were compared to previous surveys of Rhithropanopeus in Coos Bay done by Pisciotto (1978) and others.

## Transect Censuses

In order to quantify the seasonal abundance of Rhithropanopeus and Hemigrapsus, permanent transects were established at three different sites where Rhithropanopeus is found in the Coos River (Fig. 2). At each site, three separate transect lines spaced at least 20 meters apart were marked with stakes. Along the transect line, seven plots were laid out. The first plot was at the MLLW (Mean Low Low Water) line, with the rest of the plots at one-meter intervals along a line perpendicular to the water, and covering the entire intertidal zone. Due to the steep slope of the intertidal profile, there was approximately a 0.3 meter rise between plots along each transect line. Each transect plot was censused for crabs on February 27, March 14, April 18, May 4, May 17, and June 2 of 1988. On each sampling date at each site, salinity, temperature, and tidal height were recorded.

Within each plot, I overturned all rocks which were located inside the perimeter of a 1/16 meter square which was laid over the plot. All crabs found by overturning rocks within the square were tallied, recording the size, sex, and species of individuals. Size of individuals was measured by placing a small metric ruler next to the specimen, and estimating the carapace width. Sex of individuals was determined by examining the telson; a narrow telson indicates a male crab while a wider telson indicates a female. Rhithropanopeus, with a round, brown carapace can be easily distinguished from Hemigrapsus with its square, green carapace. Rhithropanopeus is often partially buried in the mud, whereas Hemigrapsus generally is more active than its introduced counterpart.

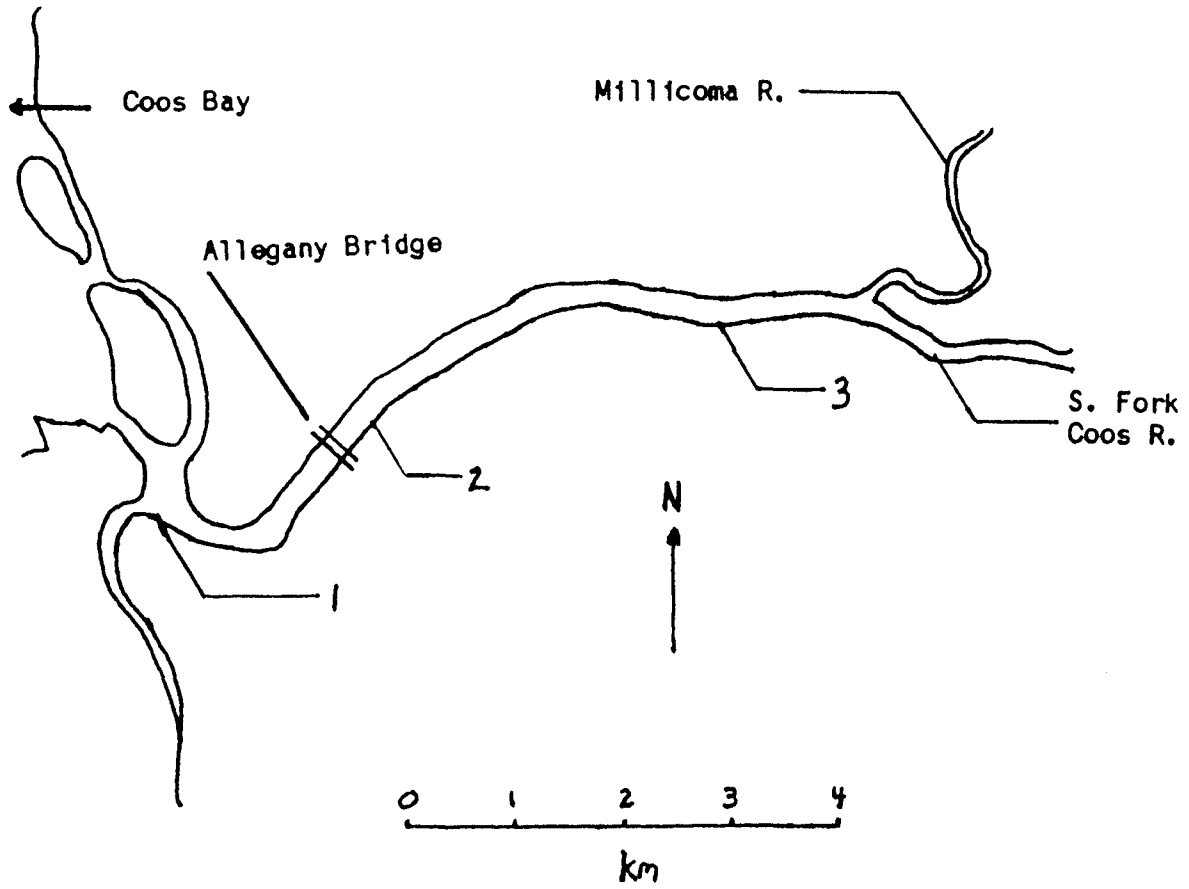


Figure 2. Map of Coos River, showing location of three field sampling sites.

## Field Transplants

In order to determine if the ranges of the two species are mutually exclusive, reciprocal transplants of Rhithropanopeus and Hemigrapsus were made into the other species' range. The crabs were transported July 8, 1989; cages were checked for mortality and salinity was recorded after 1, 8 and 14 days. Transported individuals were kept in cinder block cages designed to exclude other crabs (Figure 3). This experiment tested the null hypothesis that Rhithropanopeus is not excluded from the lower bay by physiological limitations. Cages were deployed at two sites: one 100 meters south of the Coos Bay city dock, within the natural range of Hemigrapsus, and one in Coos River, 3 kilometers upstream from the Allegany bridge, within the natural range of Rhithropanopeus. At each site, three replicates of two treatments were established. The treatments were four Rhithropanopeus caged alone, and four Hemigrapsus caged alone. Small rocks with attached macroalgae were placed inside the cages, providing some food and shelter for the crabs.

## Laboratory Studies

### Predation

In order to determine if predation occurs between Hemigrapsus and Rhithropanopeus, pairs of crabs were confined together in small (10 x 10 cm) plastic containers with holes in the sides for water

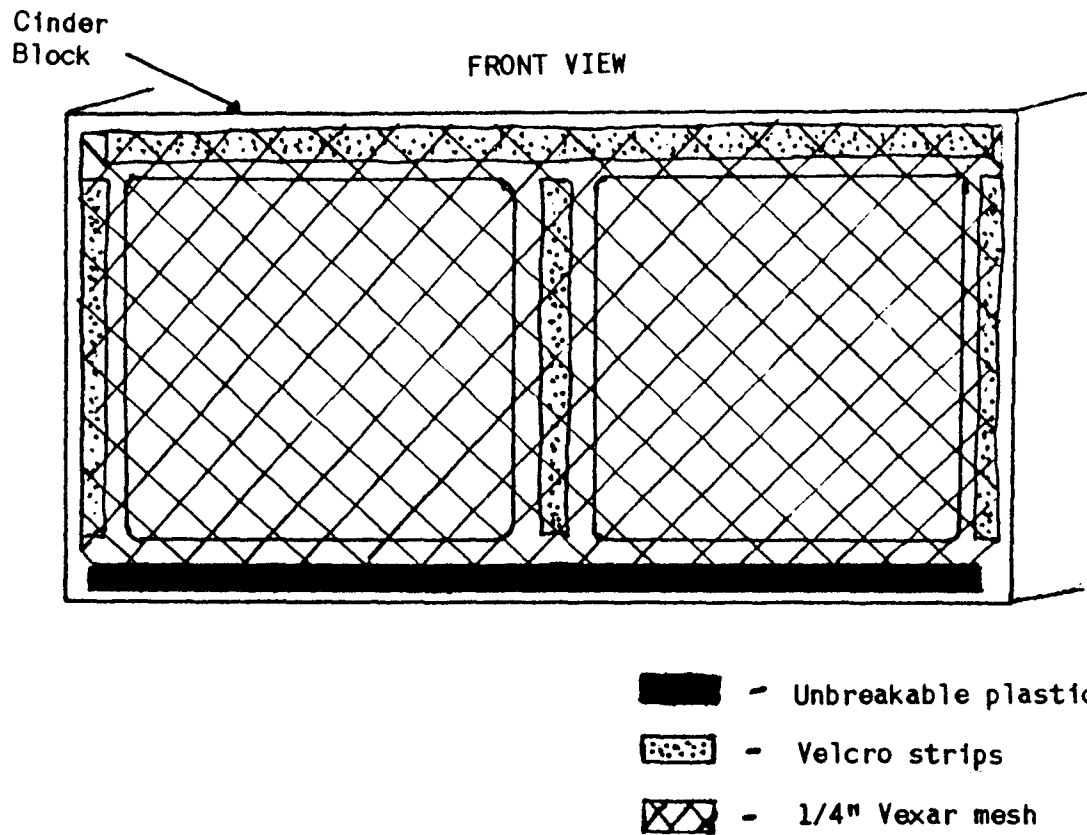


Figure 3. Design of cages used to test survival of transplanted crabs. Cinder blocks are 39 x 19 x 19 mm.

circulation. Specimens for these laboratory tests were collected 100 meters up river from the Allegheny Bridge in Coos River. Predation was tested among adults, between adults and juveniles, and among juveniles of both species (Table 3). Both interspecific predation and intraspecific predation were tested. The containers were kept submerged in running seawater. Containers were checked at 24-hour intervals, and victims of predation were replaced with a live individual of the same species and size.

TABLE 3. Experimental Design to Test for Predation among Crabs. Each treatment consisted of five replicates of two crabs (one from each indicated stage) enclosed in a plastic container (see text). Boxes were checked at 24-hour intervals; if predation had occurred, then prey was replaced.

	<u>Hemigrapsus</u>		<u>Rhithropanopeus</u>	
	ADULT	JUVENILE	ADULT	JUVENILE
<u>Hemigrapsus</u> ADULT	X	-----	-----	-----
<u>Hemigrapsus</u> JUVENILE	X	X	-----	-----
<u>Rhithropanopeus</u> ADULT	X	X	X	-----
<u>Rhithropanopeus</u> JUVENILE	X+	X	X	X

+ -- subsequent variables of food, rocks, and prey size also tested

Several additional experiments were performed to determine the conditions under which predation was most likely to occur. For adult Hemigrapsus and juvenile Rhithropanopeus, a series of experiments tested predation in the presence and absence of an

alternate food source, crushed mussels (Mytilus sp.), and in the presence and absence of rocks (5-6 small rocks and one large rock). In another series of experiments, adult Hemigrapsus were confined with individual Rhithropanopeus of different sizes to test for a possible maximum prey size that can be handled by Hemigrapsus. In these experiments, the crabs were placed in containers as above with rocks, but they were not provided with an alternate food source.

A video camera was used to record the mechanism by which Hemigrapsus is able to kill and consume individual Rhithropanopeus. Plastic containers as above were used to hold the specimens, except that a glass plate was used to cover the enclosure to allow for observation. The camera was placed approximately 1 meter from the container, which was sloped at about a 30-degree angle towards the camera to allow viewing from directly above. An auxiliary light (100 watts) was placed next to the camera, shining directly onto the container. Boxes were left for 2 hours with the camera recording at normal speed; if after 2 hours no predation had occurred, the tape was rewound and the process repeated. Four different adult male Hemigrapsus (>20 mm carapace width) were used as predators.

#### Competition for Shelter

In order to determine if Rhithropanopeus and Hemigrapsus compete for shelter, I constructed artificial enclosures in which shelter was limited (Fig. 4). Artificial shelters were constructed from 1.25 cm plywood and cinder blocks. Each piece of plywood was

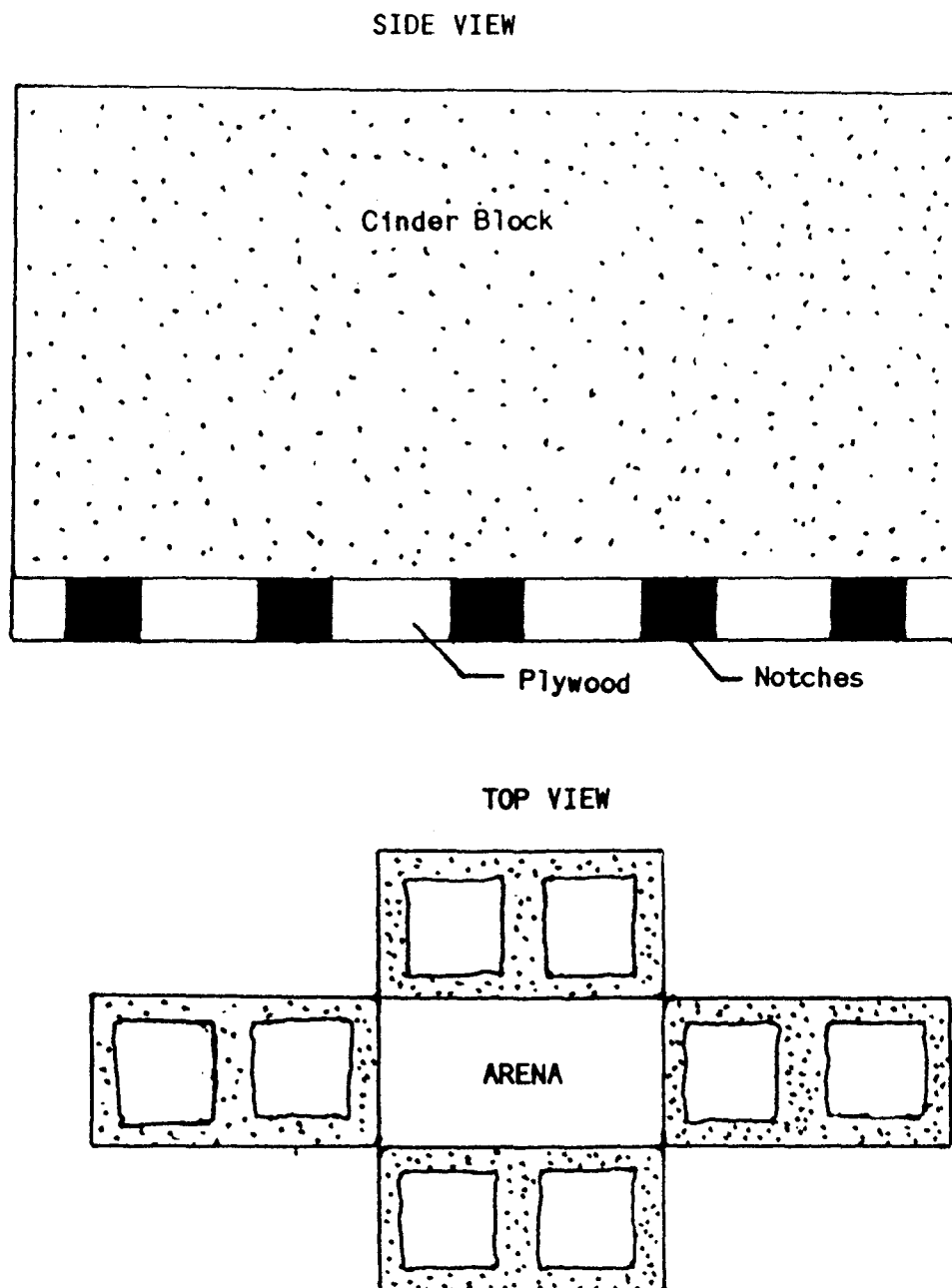


Figure 4. Design of arenas used to test for aggression and competition for shelter between crabs. Cinder blocks are 39 x 19 x 19 mm.

cut so that it exactly covered one face of the cinder block. Then, notches of 3 cm depth and 4.5 cm width were cut into the plywood. The cinder blocks were placed on top of the plywood, and the entire structure submerged in a water table with 15 cm depth of running seawater. This created an enclosed arena with a limited number of submerged crevices, which the crabs readily used as shelter. For each trial, 12 males and 12 females of each species of crab, Rhithropanopeus and Hemigrapsus, were added to an artificial shelter enclosure with only 12 crevices, so that shelter space was in demand. During the course of the experiment, aggressive encounters between individuals were observed and tallied, and ultimately the crabs in and out of the shelter were recorded.

#### Salinity Tolerance

To determine if Rhithropanopeus is more capable of tolerating low salinities than Hemigrapsus, basic osmoregulatory capacities of the two species were studied in the lab. Four individuals of each species were placed in containers of varying salinities: 30 o/oo, 10 o/oo, 6 o/oo, 4 o/oo, 2 o/oo, and fresh water. Salinities were achieved by mixing full strength seawater (30 o/oo) with different amounts of fresh spring water. This was a stress salinity test in that no attempt was made to acclimate the crabs to lower salinities; they were directly immersed in the test concentrations. Mortality was recorded after 24 hours and again after 48 hours.

## RESULTS

### Field Studies

#### General Survey

Hemigrapsus was found to be abundant throughout the upper and lower bay, and well into most of the adjoining sloughs (see Fig. 5). Rhithropanopeus was only found in the Coos River, which empties into Coos Bay (Fig. 6). There was a small amount of overlap in the two ranges at one site near the mouth of the Coos River. Here, however, the upper limit of Hemigrapsus coincides approximately with the lower limit of Rhithropanopeus. Pisciotto (1978) made a similar survey of Coos Bay, and found a population of Rhithropanopeus in Haynes Inlet as well as in Coos River. J. Megahan (pers. comm.) has reported Rhithropanopeus from Isthmus Slough and Joe Ney Slough. However, I failed to find any Rhithropanopeus in Haynes Inlet, Isthmus Slough, or Joe Ney Slough.

#### Transect Censuses

Over the six sampling dates, Rhithropanopeus individuals were present at each of the three sites, but Hemigrapsus individuals were only found at site 1 (closest to the higher salinity waters of Coos

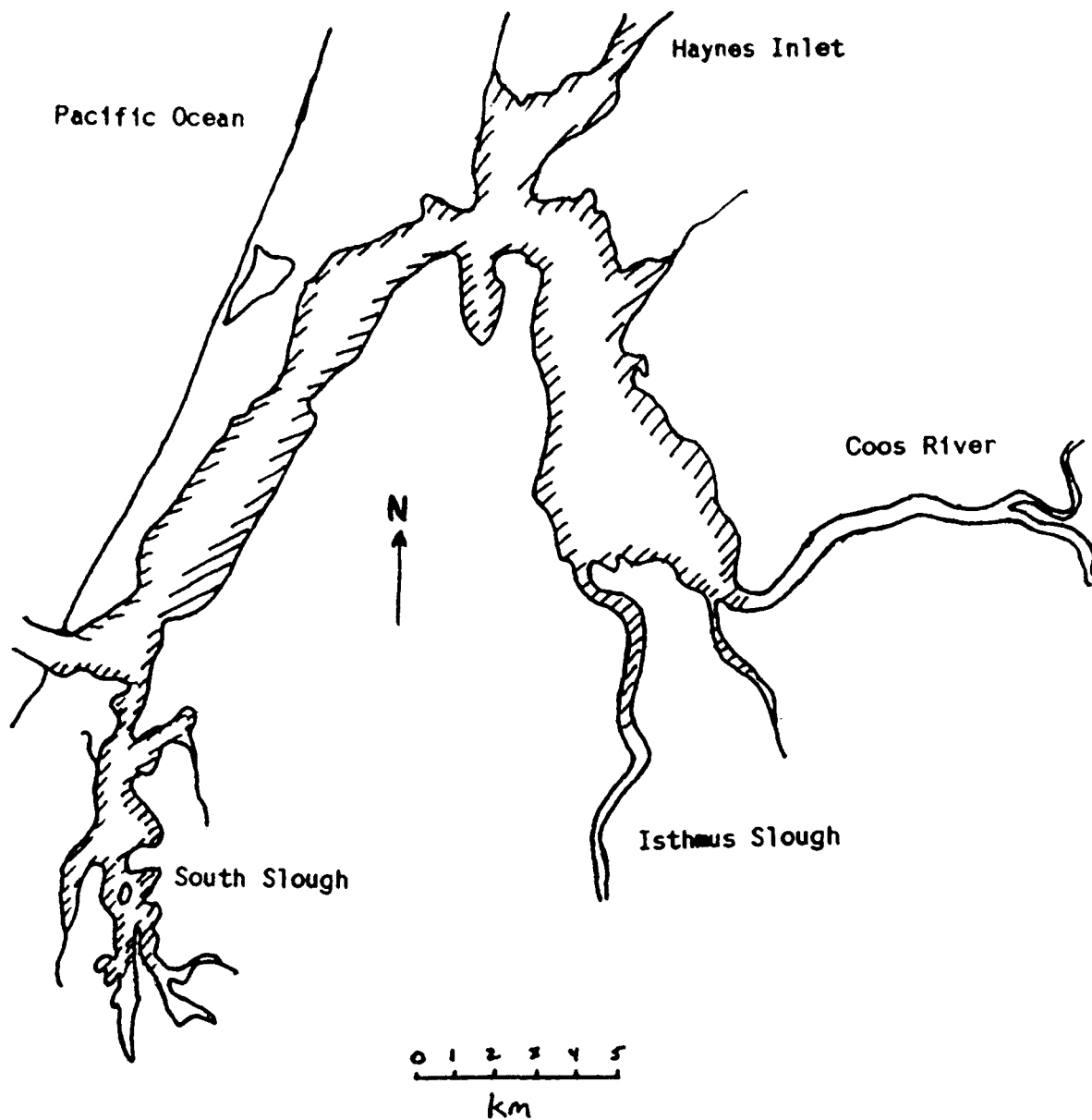


Figure 5. Distribution of *Hemigrapsus oregonensis* in Coos Bay.

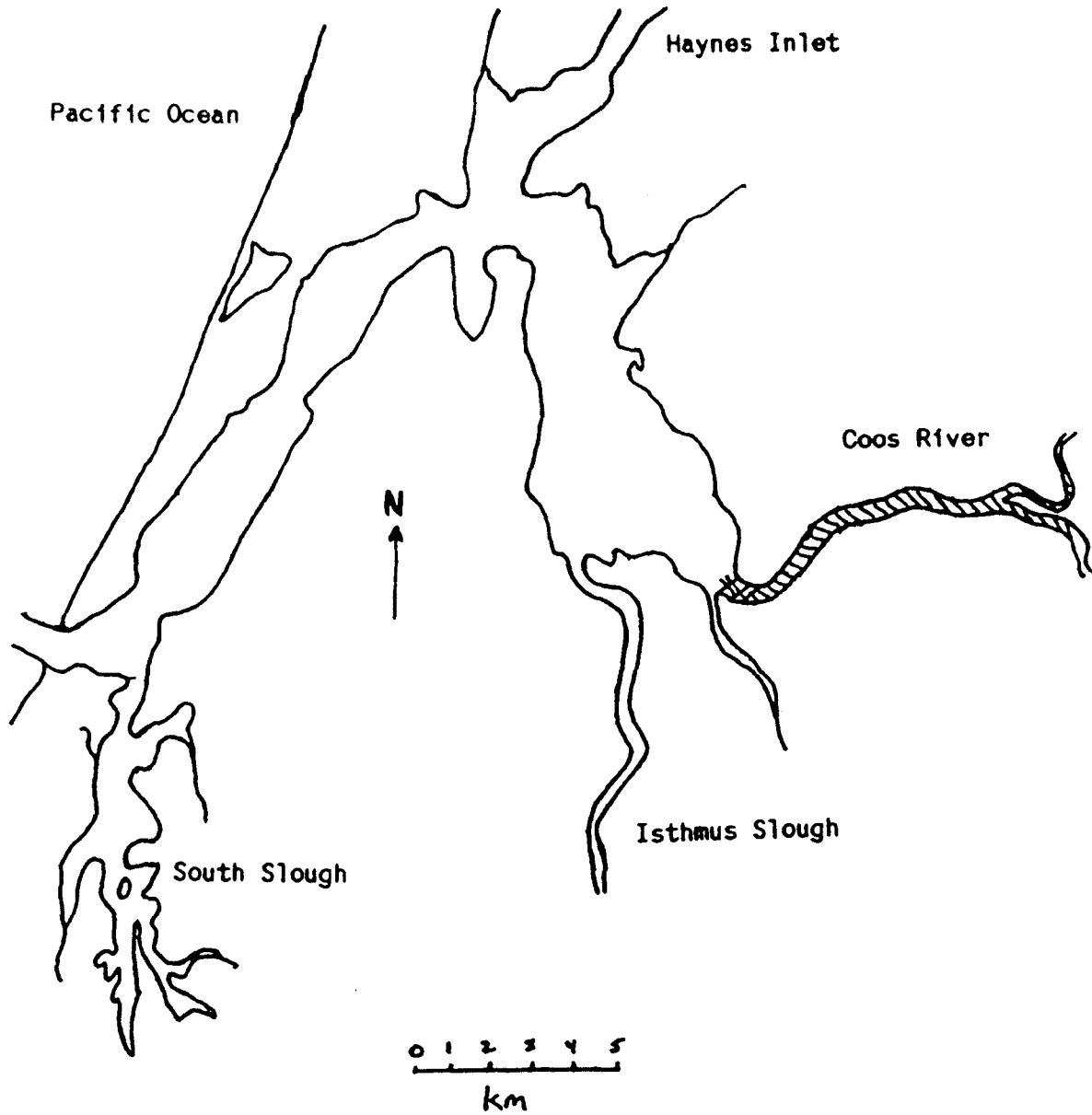


Figure 6. Distribution of Rhithropanopeus harrisi in Coos Bay. Note cross-hatched section where distribution of R. harrisi overlaps with distribution of H. oregonensis.

Bay). At this first site, densities of both Hemigrapsus (Fig. 7) and Rhithropanopeus (Fig. 8a) were relatively low. Additionally, as shown in Figures 8b and 8c, the mean density of Rhithropanopeus increased dramatically in the sites further from the region of the bay inhabited by Hemigrapsus. Densities were highly variable between plots, as suitable habitat for both species was patchy. However, crabs were almost entirely found in plots 0-3 meters from MLLW (only one crab was ever found farther than 3 meters from MLLW). The mean densities per plot over the six months at each of the three sites, computed by taking the mean of the means (grand mean) for each site, were  $0.083 \pm .06$  for Site 1,  $0.648 \pm .36$  for site 2, and  $2.498 \pm .82$  for Site 3 ( $\pm$  one standard deviation). A one-way analysis of variance by site showed that there was a significant difference among the sites ( $F=24.53$ ;  $P<.001$ ). Subsequent planned comparisons by sites showed that Site 1 density did not differ significantly from Site 2 ( $F=2.87$ ;  $P>.05$ ), but Site 2 density was significantly lower than Site 3 ( $F=26.93$ ;  $P<.001$ ) and Site 1 was significantly lower than Site 3 ( $F=45.89$ ;  $P<.001$ ). There did not appear to be any pattern in the distribution of males and females either within or between sites. Also, there did not appear to be any seasonal changes in crab populations at any of the sites.

Juvenile Rhithropanopeus were notably absent from Site 1 as shown in Figure 9. During the course of two years' observations, no immature Rhithropanopeus individuals were ever found at the site where the two species of crabs co-occur. Yet in plankton tows near these sites, zoeal Rhithropanopeus were captured in the fall of 1988 (C. Hewitt, pers. comm.). Juveniles were found at Site 2, but they

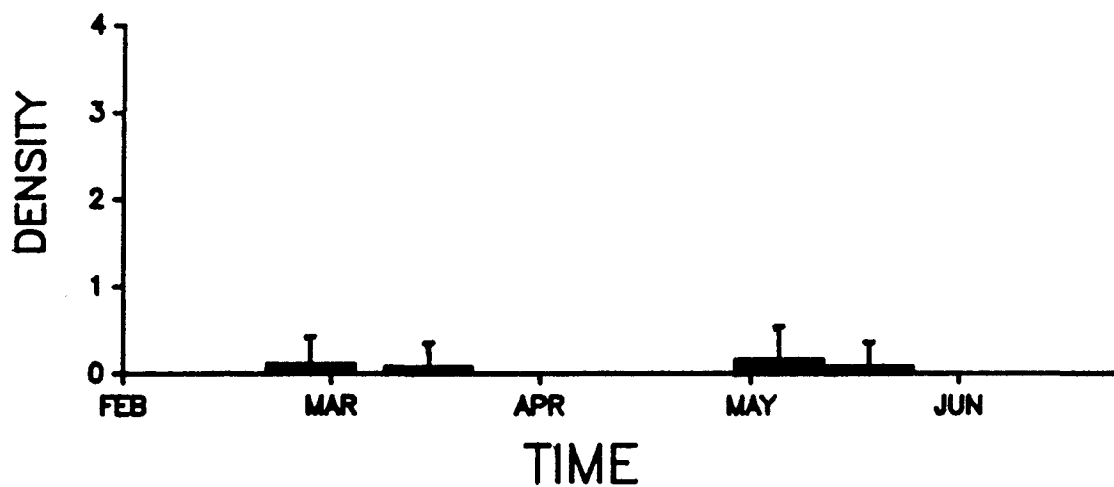
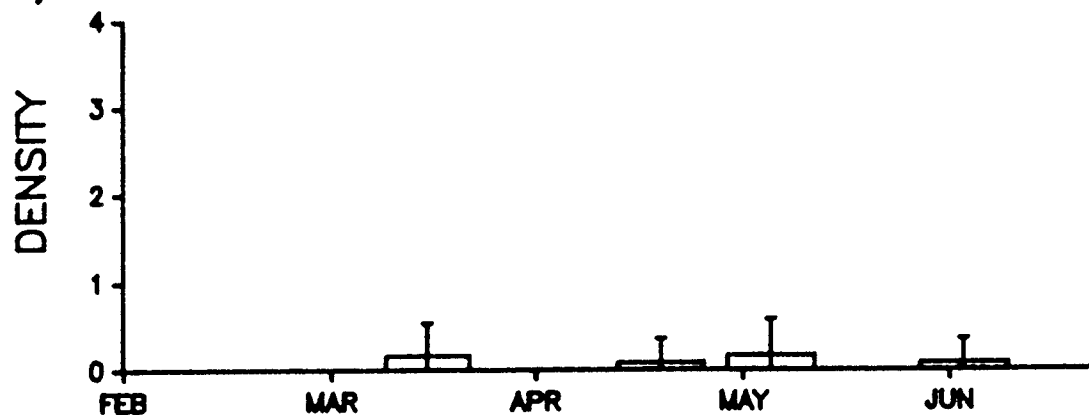
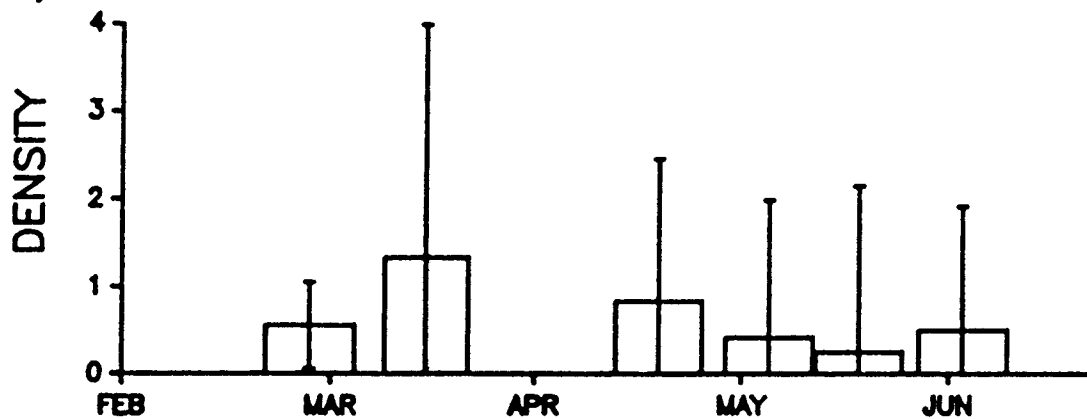


Figure 7. Mean density and standard deviation of *Hemigrapsus oregonensis* from Feb.-June, 1988 at Site 1. Figures represent the average number of crabs found per plot for all plots from 0-3 meters from MLLW.

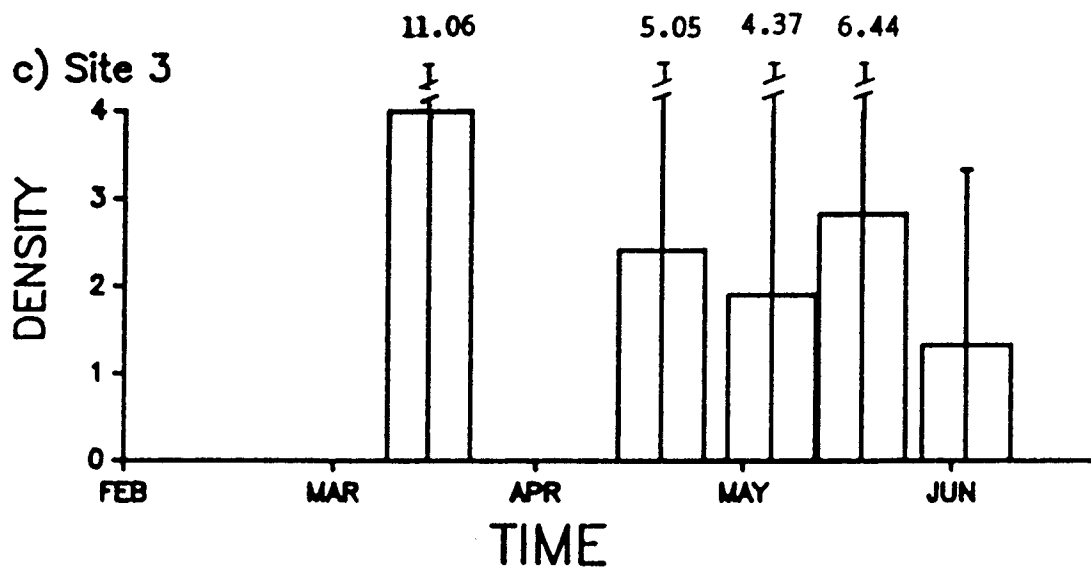
a) Site 1



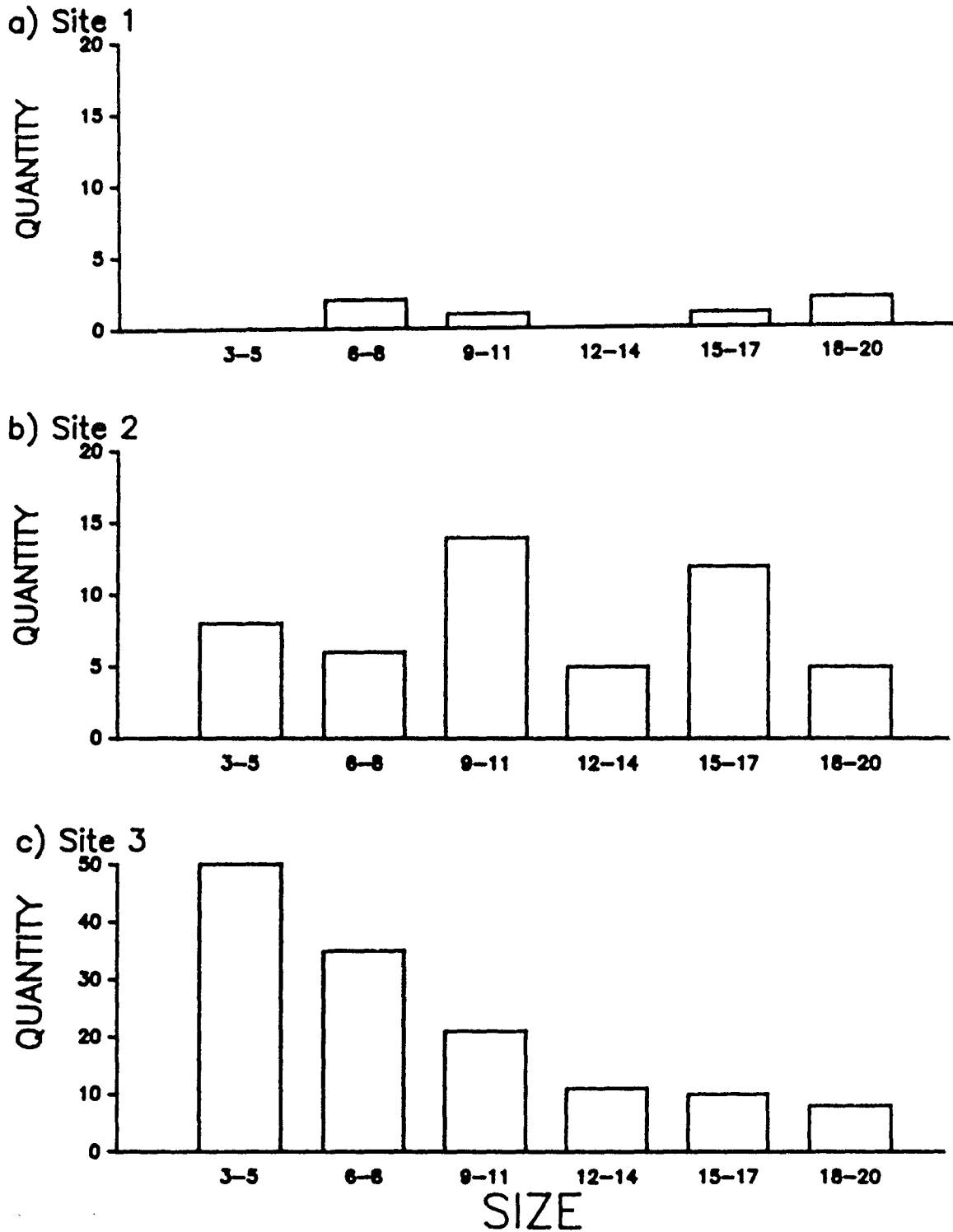
b) Site 2



c) Site 3



Figures 8a-c. Mean densities and standard deviations of *Rhithropanopeus harrisii* at three sites in Coos River from Feb.-June, 1988. Figures represent the average number of crabs found per plot for all plots from 0-3 meters from MLLW.



Figures 9a-c. Size distribution of *Rhithropanopeus* found at three sites in Coos River. Sizes are measured in mm carapace width. Data include all crabs found in transect plots from Feb.-June, 1988.

were most abundant at Site 3, well beyond the region in which Hemigrapsus has been found (Fig. 9).

Salinity measurements, taken at low tide during sampling trips, were very low, ranging from 0.0-0.1 o/oo for all three sites from February through June, 1988. When measured during high tides, the salinity rose slightly at Site 1, reaching 5.3 o/oo on March 13 and 8.2 o/oo on April 16. However, at Sites 2 and 3, the salinity remained at 0.0-0.1 during these high tides. (Low tide salinities near Site 2 in July, 1989 were 2-4 o/oo). Salinity at Site 1 on Oct. 25, 1987 was 25.5 o/oo, indicating a wide seasonal salinity range at this site. Temperature over the five-month period was 14-17 degrees Celsius.

#### Field Transplants

Mortality in all cages was low initially, with all crabs in all cages surviving after one day and most surviving after eight days. However, after the end of 14 days, there had been substantial mortality among the caged Hemigrapsus. Mortality was most severe in the cages within their natural range. An average of 3 of the 4 caged individuals in the 3 replicated cages had died after 14 days. Mortality for Hemigrapsus was less severe at the site within the range of Rhithropanopeus, with an average of 2 of 4 individuals dying in those three replicates. In all replicates at both sites, no Rhithropanopeus died. For the 14 day period, low tide salinity measurements were 2-4 o/oo at the upper site and 18-25 o/oo at the lower site.

Laboratory Studies

Predation

Large Hemigrapsus proved to be consistent and effective predators on juvenile and small adult Rhithropanopeus. In a five day experiment, large Hemigrapsus consumed an average of 1.6 juvenile Rhithropanopeus each. In contrast to this, under the same conditions, Hemigrapsus did not consume any conspecific juveniles. Hemigrapsus was a much more effective predator on small Rhithropanopeus than on large Rhithropanopeus (Fig 10). Adult Rhithropanopeus did not prey significantly on either its own young or the young of Hemigrapsus. Also, no predation occurred between adults of the same species or between adults of different species (Table 4).

TABLE 4. Incidence of Predation among Hemigrapsus oregonensis and Rhithropanopeus harrisi. Numbers are mean crabs eaten over a five-day period,  $\pm$  standard deviation.

	<u>Hemigrapsus</u>		<u>Rhithropanopeus</u>	
	ADULT	JUVENILE	ADULT	JUVENILE
<u>Hemigrapsus</u> ADULT	0	-----	-----	-----
<u>Hemigrapsus</u> JUVENILE	0	0	-----	-----
<u>Rhithropanopeus</u> ADULT	0	0	0	-----
<u>Rhithropanopeus</u> JUVENILE	1.2 $\pm$ 1.6	0	0.2 $\pm$ 0.4	0

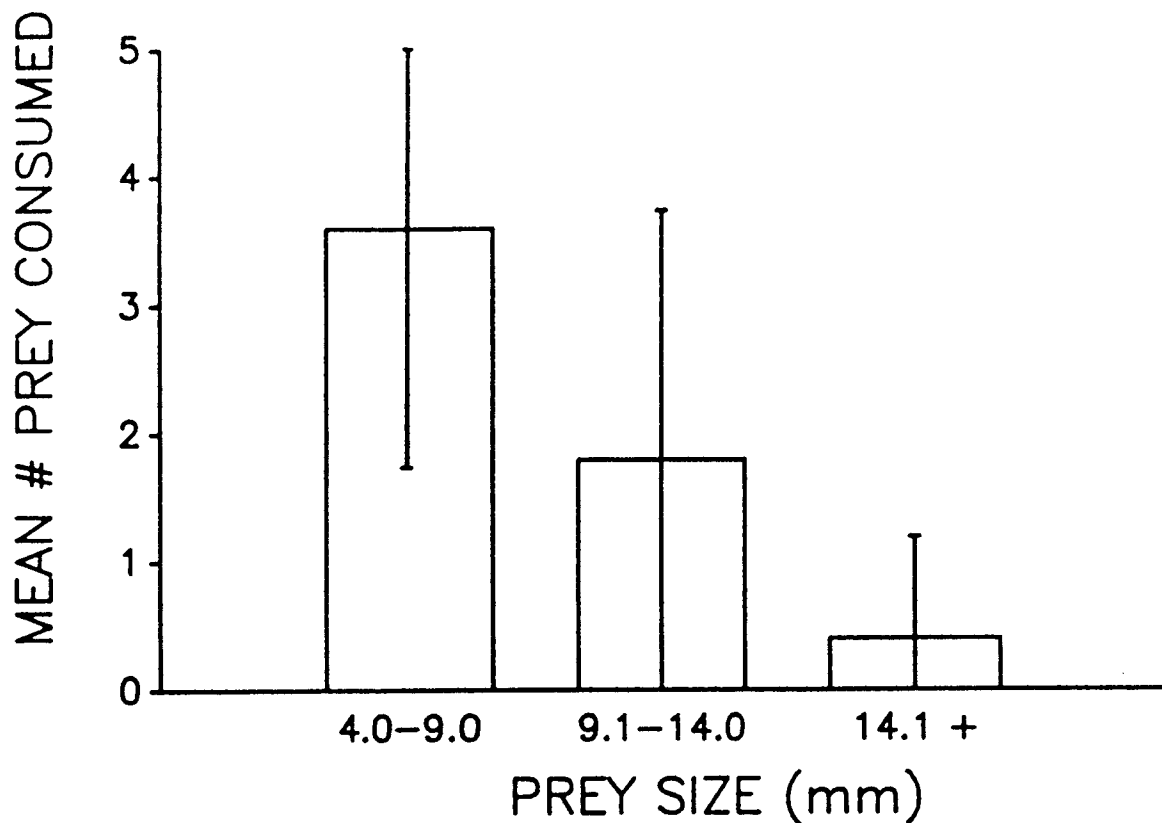


Figure 10. Predation of large (20+ mm carapace width) male Hemigrapsus oregonensis on Rhithropanopeus harrisi. Experiment ran for 5 days; fresh prey items were supplied each day provided that the old prey item had been consumed. Thus, a maximum of 5 prey could have been consumed by each predator. (N=5 for each prey size; error bars are standard deviation).

The added variables of rocks and alternate food sources had different effects on the rate of predation. In the presence of an alternate food source of crushed mussels, the rate of predation on Rhithropanopeus by Hemigrapsus decreased, although not significantly. However, the presence of small rocks had the opposite effect on predation; adult Hemigrapsus were significantly more likely to prey on Rhithropanopeus when small rocks were provided (Table 5).

TABLE 5. Incidence of Predation between Adult Hemigrapsus oregonensis and Juvenile Rhithropanopeus harrisi According to the Presence or Absence of Food and Rocks in the Experimental Enclosure. Numbers are mean Rhithropanopeus eaten by one Hemigrapsus in a five-day trial  $\pm$  standard deviation.

	FOOD	NO FOOD
ROCKS	1.4 $\pm$ 0.48	3.1 $\pm$ 1.85
NO ROCKS	0	1.2 $\pm$ 1.6

Results of two-way ANOVA:

significance of food... F=3.945; P>.05 (ns)

significance of rocks.. F=5.730; P<.05

df within subgroups = 16

During the course of videotaping predatory encounters, it was noted that large Hemigrapsus often push the rocks around with their walking dactyls, and in some cases this had the effect of "pinning" the potential prey Rhithropanopeus into a corner from which there was less chance of an escape. It did not appear that Hemigrapsus intentionally moved the rocks to pin the prey, since this behavior

was also consistently observed in non-predatory situations.

Most instances of predation appeared to indicate a consistent method used by Hemigrapsus in attacking smaller Rhithropanopeus. In videotaped encounters, large (20+ mm carapace width) male Hemigrapsus circled the enclosure, with smaller Rhithropanopeus moving away in response to the approach of the larger crab. When Hemigrapsus was able to corner the smaller crab, it maneuvered the prey into one of the two large chelae and grasped the still live crab in a dorsal to ventral position. The other chela was then used to tear off the dorsal half of the carapace, killing the crab and exposing the body meat. Occasionally, Hemigrapsus would tear off chelae or several walking legs prior to actually killing the crab. In non-videotaped laboratory predation experiments, carcasses of Rhithropanopeus missing the dorsal half of their carapace were frequently found, suggesting the same mechanism of predation. In many cases, Hemigrapsus did not consume the walking legs or chelae.

#### Competition for Shelter

When placed in artificial arenas with limited shelter, Hemigrapsus was more aggressive than Rhithropanopeus. In two separate thirty-minute observation periods, I observed four distinct aggressive encounters: 1) pushing of another crab with chelae; 2) pinching of rear legs; 3) threat display; and 4) shaking and pinching of another crab. In these encounters, Hemigrapsus was the aggressor almost four times as often as Rhithropanopeus (Table 6).

TABLE 6. Frequency of Aggressive Acts between Hemigrapsus oregonensis and Rhithropanopeus harrisi During a Thirty-minute Observation Period. 24 Rhithropanopeus and 24 Hemigrapsus were placed in the experimental enclosure.

AGAINST:	AGGRESSOR	
	<u>Hemigrapsus</u>	<u>Rhithropanopeus</u>
<u>Hemigrapsus</u>	45	9
<u>Rhithropanopeus</u>	9	6

Aggressive acts were most commonly observed when two crabs were outside the entrance to a crevice, or when one crab tried to enter an occupied crevice. Generally, the occupant of the crevice was the aggressor. Only once did I observe an eviction (of a Hemigrapsus by another Hemigrapsus). After a period of 24 hours, 11 Rhithropanopeus and 6 Hemigrapsus were found in the 12 crevices (some crevices had double occupancy -- if so always 2 Rhithropanopeus). The difference in shelter occupancy between species was not significant. I attribute this to the differential use of shelter by the two species. Individual Hemigrapsus were more active and mobile in the enclosure (they climbed out of the water much more frequently than Rhithropanopeus), so that at any given time they were less likely to use the shelter provided. In contrast, Rhithropanopeus generally stayed in the water as might be expected for a lower intertidal species, and rarely left the crevices and cracks that it obtained.

## Salinity Tolerance

Rhithropanopeus was able to withstand lower salinities than Hemigrapsus. All Hemigrapsus placed in fresh water died within 24 hours, but two of four Rhithropanopeus were alive after 48 hours (Table 7).

TABLE 7. Salinity Tolerance of Rhithropanopeus and Hemigrapsus. Numbers indicate survivors out of 4 crabs after 24 hours/48 hours.

Species	Salinity (o/oo)						
	30	10	8	6	4	2	0
<u>Rhithropanopeus</u>	4/4	4/4	4/4	4/4	4/4	4/3	4/2
<u>Hemigrapsus</u>	4/4	4/4	4/4	4/4	4/3	3/1	0/0

Pisciotta (1977) found that Rhithropanopeus could tolerate fresh water conditions for even longer periods; of six crabs placed in 0 o/oo salinity, two survived for six weeks. These results are also supported by the work of Smith (1967), who found that Rhithropanopeus was able to alter its permeability to water for extended periods of time, thus explaining their survival in near fresh water.

## DISCUSSION

When a species is introduced to a new environment, the characteristics of that new environment are rarely, if ever, identical to the conditions in which the species has previously existed. Therefore, the species must adjust its role in the new environment to best utilize the resources with which it is now presented.

The introduction of Rhithropanopeus to estuaries on the Pacific coast seems to have resulted in such an adjustment in resource utilization. Rhithropanopeus has successfully invaded and established itself in Coos Bay and other Pacific coast estuaries in regions where native crabs have been unable to do so. While Rhithropanopeus is naturally found in upper estuarine zones, a larger portion of the population appears to be living further up in the estuarine zone on the Pacific coast than in its native range.

The overlap in distribution of Rhithropanopeus and Hemigrapsus in Coos Bay is relatively small. These co-occurrences may be seasonally and spatially transient. Pisciotto (1978) found several hundred meters of unoccupied territory in Coos River between the ranges of Hemigrapsus and Rhithropanopeus. Additionally he found the upper limit of Hemigrapsus to extend 1 km farther up river than was found in this study. The lower boundary of Rhithropanopeus in

1978 was also 1 km farther up river. I found that although there was a limited region of overlap, each species is more abundant in the other areas of its local range. Also, juvenile Rhithropanopeus are not found at the site of overlap.

The minimum salinity tolerance of Rhithropanopeus is less than that of Hemigrapsus, results consistent with those of Jones (1941), Smith (1967) and Pisciotto (1978). Both in the field and in the laboratory Rhithropanopeus was found to tolerate fresh water. In the lab, they may tolerate these conditions for up to six weeks (Pisciotto, 1978). In the field, they apparently tolerate fresh water for at least that long. In the current study, high tide salinity readings of 0.0-0.1 o/oo were recorded between February and May of 1988 in the upper Coos River where Rhithropanopeus is found. Hemigrapsus, on the other hand, is less able to tolerate very low salinities (Dehnel, 1967). However, Hemigrapsus is able to increase its survivorship in fresh water by behavioral regulation. In the laboratory, if given the opportunity, Hemigrapsus will climb out of low-salinity water and stay out for up to 6 hours (Hellman, 1989). This observation may explain Hemigrapsus' year-round residence at Site 1, where low tide salinities commonly reach 0 o/oo in the winter, but high tide salinities are slightly higher (5-8 o/oo). Perhaps here they actively move out of the fresh water at low tide.

Other studies have shown that introduced species have greater physiological tolerances than their native counterparts. Kinzie (1968) found that in Hawaii the introduced stomatopod Gonodactylus falcatus was more tolerant of low salinities than the native stomatopod Pseudosquilla ciliata. This differential salinity

tolerance was considered to be one possible reason for the success of the invasion. In the Mojave River of Southern California, the introduced Mojave tui chub Gila bicolor mohavensis was found to be better adapted to high temperatures and low oxygen tension than the native arroyo chub Gila orcutti (Castleberry and Cech, 1986).

The survival of caged Rhithropanopeus in the lower bay is further evidence that they are physiologically capable of tolerating lower bay conditions. The survival of some Hemigrapsus at the Coos River site outside of their natural distribution (but not outside of their natural salinity range) is more puzzling. While I have found Hemigrapsus living at Site 1 in 3-4 o/oo, the same salinity that occurred at this experimental transplant site during low tides over the two week period, I have never found Hemigrapsus living this far up river. It may be that Hemigrapsus' preference for higher salinities behaviorally suppresses migration into the Coos River where they could physiologically exist in mid-summer. Conversely, the freshwater inundation throughout most of the year at this site may leave only a small temporal window open for upper-river colonization. Other factors may be responsible as well.

As this experiment was conducted only in July, different results of the same reciprocal transplants might be expected over a season-wide study. For example, in winter, the salinity would be much lower in the Coos River and Hemigrapsus would not be expected to tolerate a two-week transplant into fresh or near-fresh water.

In the laboratory, Hemigrapsus is an aggressive predator on juvenile Rhithropanopeus. Predation occurred most frequently when rocks were present with no food. Since Hemigrapsus often pulls off

several chelae or walking legs prior to killing the crab, it may be possible to use the absence of one or more appendages as an indication of predation or attempted predation either in the field or in the laboratory. I did not observe Rhithropanopeus missing appendages in the field, but Rhithropanopeus was only found with Hemigrapsus at one field site. Rhithropanopeus was rarely observed to prey on conspecific juveniles, and no predation between adults was observed.

The conditions of the laboratory predation experiments are not assumed to represent natural conditions. However, both density and environmental heterogeneity in the lab were representative of these parameters in the field. Since both species require a specific microhabitat beneath rocks, the realized field density of crabs is higher if unsuitable habitat (such as open mudflat areas) is not included. For this reason, I feel that the density of crabs in the predation boxes was representative of realized field densities of crabs. Also, the presence of rocks in the predation boxes provided a more heterogeneous environment that is more typical of field habitats.

Hemigrapsus was found to be more aggressive in the lab than Rhithropanopeus. In a study of stomatopods in Hawaii, Kinzie (1968) found that the introduced Gonodactylus falcatus was much more aggressive than the native Pseudosquilla ciliata. The introduced stomatopod would drive the native stomatopod out of artificial "burrows" and would kill the native stomatopod if left in the same tank for a period of time (Kinzie, 1984). However, in this study,

Hemigrapsus was not observed to evict or kill adult Rhithropanopeus when competing for shelter.

The present limited distribution of Rhithropanopeus in Coos Bay may partially be explained by predatory and aggressive interactions with Hemigrapsus. The zone of overlap, albeit narrow, appears to be a dynamic boundary where transient and seasonal interactions between these two crabs limit the downward dispersion of Rhithropanopeus. The predation of Rhithropanopeus juveniles by Hemigrapsus in the laboratory, coupled with the absence of juvenile Rhithropanopeus at Site 1 (the region of overlap) suggests that Hemigrapsus may be partially limiting the distribution of Rhithropanopeus by preying on any juvenile Rhithropanopeus which settle in the range of Hemigrapsus.

In addition, Hemigrapsus could sufficiently "disturb" Rhithropanopeus of all life stages by aggressive interactions and prevent the latter's colonization of the lower bay. Two assumptions are inherent in this hypothesis: one, that the aggressive interactions observed in the lab are typical of field encounters and two, that Rhithropanopeus is sufficiently disturbed by the aggressive nature of Hemigrapsus that it cannot live in regions occupied by Hemigrapsus. These assumptions remain to be examined in the field.

Along with Jones (1941) and Pisciotto (1978), I speculate that these predatory and aggressive interactions may be mechanisms restricting Rhithropanopeus to the upper estuary. Jones (1941) speculated that seasonally low fresh water flow could lead to periodic invasion by Hemigrapsus into the range of Rhithropanopeus.

This idea is supported by the present results and the results of Pisciotto (1978); currently, Hemigrapsus does not live as far up the Coos River as it did in 1978, and Rhithropanopeus now lives farther down river than it did in 1978. Additionally, it is possible that Rhithropanopeus has developed certain different biological, physiological and ecological characteristics to permit its survival in the upper regions of Pacific estuaries. Ryan (1956) reported that Rhithropanopeus occasionally enters but is not commonly found in fresh water on the Atlantic coast. However on the Pacific coast, Rhithropanopeus is commonly found in fresh or near fresh water (Jones, 1941; Smith, 1967; Pisciotto, 1978; personal observation). It may be that selection pressure exerted by Hemigrapsus on the Rhithropanopeus population favors only those crabs which are particularly well-adapted osmoregulators. Thus the possibility exists that the West coast populations of Rhithropanopeus are becoming more tolerant of low salinities than are the East coast populations. It would be interesting to determine if Rhithropanopeus adults and larvae are undergoing such physiological selection.

## BIBLIOGRAPHY

- Baker, P. 1988. Predation on an introduced snail by native crabs. M.S. Thesis, University of Oregon.
- Batie, R.E. 1983. Rhythmic locomotor activity in the intertidal shore crab, Hemigrapsus oregonensis (Brachyura, Grapsidae) from the Oregon coast. *Northwest Science* 57: 49-57.
- Brenchley, G.A., and J.T. Carlton, 1983. Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. *Biological Bulletin* 165: 543-558.
- Buitendijk, A.M., and L.B. Holthius. 1949. Note on the Zuiderzee crab, Rithropanopeus harrisi (Gould) subspecies tridentatus (Maitland). *Zoologische Mededelingen Deel XXX: No. 7: 95-106.*
- Carlton, J.T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. University of California at Davis, PhD thesis, Davis, CA.
- Castleberry, D.T., and J.J. Cech, Jr. 1986. Physiological responses of a native and an introduced desert fish to environmental stressors. *Ecology* 67(4): 912-918.
- Christiansen, M.E., and J.D. Costlow, Jr. 1975. The effect of salinity and cyclic temperature on the larval development of the mud crab Rhithropanopeus harrisi (Brachyura: Xanthidae) reared in the laboratory. *Marine Biology* 32: 215-221.
- Cronin, T.W. 1982. Estuarine retention of larvae of the crab Rhithropanopeus harrisi. *Estuarine, Coastal, and Shelf Science* 15: 207-220.
- Cronin, T.W., and R.B. Forward, Jr. 1983. Vertical migration rhythms of newly hatched larvae of the estuarine crab, Rhithropanopeus harrisi. *Biological Bulletin* 165: 139-153.
- Dehnel, P.A. 1967. Osmotic and ionic regulation in estuarine crabs. Pages 541-547 in George H. Lauff, editor. *Estuaries*. The Horn-Shafer Company, Baltimore, Maryland.

- Elton, C.S. 1958. The ecology of invasions by animals and plants. Methuen and Co., London, England.
- Forward, R.B. Jr. et al. 1984. Control of diel vertical migration: Photoresponses of a larval crustacean. *Limnology and Oceanography* 29(1): 146-154.
- Harper, J.L. 1965. Establishment, aggression, and colonization in weedy species. Pages 261-268 in H.G. Brown and G.L. Stebbins, editors. *The Genetics of Colonizing Species*. Academic Press, New York, New York.
- Hellman, C.N. 1989. Osmoregulatory pattern of the euryhaline shore crab, Hemigrapsus oregonensis. Unpublished M.S. Thesis, University of California, Berkeley.
- Hood, M.R., 1962. Studies on the larval development of Rhithropanopeus harrisi (Gould) of the family Xanthidae (Brachyura). *Gulf Research Reports* 1(3): 122-130.
- Jones, L.L. 1940. An introduction of an Atlantic crab into San Francisco Bay. *Proceedings of the Sixth Pacific Science Congress* 3: 485-486.
- Jones, L.L. 1941. Osmotic regulation in several crabs of the Pacific coast of North America. *Journal of Cellular and Comparative Physiology* 18: 79-92.
- Kinzie, R.A. III 1968. The ecology of the replacement of Pseudosquilla ciliata (Fabricius) by Gonodactylus falcatus (Forsk.) (Crustacea; Stomatopoda) recently introduced into the Hawaiian Islands. *Pacific Science* 22: 464-475.
- Kinzie, R.A. III 1984. Aloha also means goodbye: a cryptogenic stomatopod in Hawaii. *Pacific Science* 38: 298-311.
- Knudson, J.W. 1964. Observations on the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. *Pacific Science* 18: 3-33.
- Marchand, J. 1979. Observations sur des populations naturelles de Rhithropanopeus harrisi tridentatus dans l'estuaire de la Loire: fréquence des mues et taux de croissance des femelles adultes. *Cahiers de Biologie Marine* 20: 461-469.
- Morris, R.H. et al. 1980. *Intertidal invertebrates of California*. Stanford University Press, Stanford, California.
- Naylor, E. 1960. A North American xanthoid crab new to Britain. *Nature* 187: 256-257.

- Odum J.T., and E.M. Heald, 1972. Trophic analyses of a mangrove swamp community. Transactions of the American Fisheries Society, 92 (2): 170-173.
- Pisciotta, R.J. 1977. The distribution of Rhithropanopeus harrisi in Coos Bay. Unpublished paper on file, Oregon Institute of Marine Biology, Charleston, Oregon.
- Pisciotta, R.J. 1978. The biology of an introduction: Rhithropanopeus harrisi. M.S. Thesis, University of Oregon, Eugene, Oregon.
- Rudy, P.P. Jr., and L.H. Rudy. 1983. Oregon estuarine invertebrates. U.S. Fish and Wildlife Service, Portland, Oregon.
- Ryan, E.P. 1956. Observations on the life histories and the distribution of the Xanthidae (mud crabs) of Chesapeake Bay. American Midland Naturalist 56: 138-162.
- Schmitt, W.L. 1921. The marine decapod crustacea of California. University of California Publications in Zoology 23: 1-470.
- Smith, R.I. 1967. Osmotic regulation and adaptive reduction of water-permeability in a brackish-water crab, Rhithropanopeus harrisi (Brachyura, Xanthidae). Biological Bulletin, 133: 643-658.
- Turoboyski, K. 1973. Biology and ecology of the crab Rhithropanopeus harrisi ssp. tridentatus. Marine Biology 23: 303-313.
- Williams, A.B. 1965. Marine decapod crustaceans of the Carolinas. Smithsonian Institution Press, Washington, DC.
- Williams, A.B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC.
- Zaret T.M., and R.T. Paine 1973. Species introduction in a tropical lake. Science 182: 449-455.