THE ECOLOGY OF BIOLOGICAL INVASIONS: INTERACTIONS BETWEEN NATIVE AND INTRODUCED SALT MARSH GASTROPODS

by

JODY BERMAN

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

June 1989

An Abstract of the Thesis of

Jody Berman for the degree of Master of Science in the Department of Biology to be taken June 1989

Title: THE ECOLOGY OF BIOLOGICAL INVASIONS: INTERACTIONS BETWEEN NATIVE AND INTRODUCED SALT MARSH GASTROPODS

Approved: ______________________________
Dr. James T. Carlton

Three species of gastropods are commonly found in the salt marshes of Coos Bay, Oregon. Two of these species, *Assiminea californica* and *Littorina subrotundata*, are native, and the third, *Ovatella myosotis*, has been introduced from the Atlantic Ocean.

Experiments were conducted in order to determine whether the introduced snail has altered the distribution or abundance of the native species. Results demonstrated that the snails show vertical zonation in the marsh. *Ovatella* was most abundant in the high marsh, and *Assiminea* and *Littorina* were most common in the low marsh. Results of transplant and removal experiments indicated that physical factors played a critical role in maintaining observed patterns

of distribution. No evidence for competition for food or space was found amongst the three species.

The success of Ovatella in the salt marshes of Coos Bay, Oregon does not appear to come at the expense of the native gastropod species. Instead, Ovatella's success appears to stem from its ability to use spatial and trophic resources in the high intertidal unused by the native species.

VITA

NAME OF AUTHOR: Jody Berman

PLACE OF BIRTH: New York City, New York

DATE OF BIRTH: December 23, 1962

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of New Hampshire
University of Oregon
Marlboro College
Stanford University

DEGREES AWARDED:

Master of Science, 1989, University of Oregon
Bachelor of Science with high honors, 1985, Marlboro College

AREAS OF SPECIAL INTEREST:

Marine Ecology

PROFESSIONAL EXPERIENCE:

Teaching Assistant, Department of Zoology, University of New Hampshire, Durham, 1988 - 1989 academic year.

Experimental Biology Aide, Oregon Department of Fish and Wildlife, Charleston, fall 1987 through summer 1988.

Teaching Assistant, Department of Biology, University of Oregon, Eugene, 1986 - 1987 academic year and summer 1988.

AWARDS AND HONORS:

Sigma Xi Grants-in-Aid of Research, grants 1987 and 1988.

Lerner-Gray Fund for Marine Research, grant 1988

PUBLICATIONS:

Berman, J. (1988). Age and growth of hybrid bass in Tenmile Lakes, Oregon. Oregon Department of Fish and Wildlife, Southwest Region, Charleston, Oregon. 24 p.

ACKNOWLEDGEMENTS

I would like to express my sincerest gratitude to the following people: to Dr. James Carlton of the University of Oregon, for his help in designing and executing this research project; to the late Dr. Robert Terwilliger of the University of Oregon, Dr. Paul Reimers of the Oregon Department of Fish and Wildlife, and Dr. Larry Harris of the University of New Hampshire for their help in the editing of this mauscript. I also wish to thank Dr. Jonathan Geller for his help with editing, computers, statistics, and general moral support, Dr. Victoria Starczak for her help with statistics and her computer know-how and Ms. Carol Johnson of the South Slough National Estuarine Sanctuary for her artistry. Finally, I wish to thank Mr. Kelly Gestring for his never-ending field and lab assistance as well as other unmentionables.

This work was supported in part by a grant from the Lerner Gray Fund for Marine Research and two grants from Sigma Xi Grants-In-Aid of Research.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Introduced species are common members of many marine and estuarine communities (Elton, 1958; Hanna, 1966; Laycock, 1966; Carlton, 1975, 1979a, 1979b, 1987, 1989; Nichols & Thompson, 1985). Some of these introduced species are commercially important and were purposely added to existing communities. One such example is the importation of both Atlantic (*Crassostrea virginica*) and Japanese (*Crassostrea gigas*) oysters to the Pacific Coast of North America (Elton, 1958; Carlton, 1979a, 1979b, 1987). However, commercial ventures only account for relatively few case histories of introduced marine invertebrates. Most non-native marine and estuarine species arrived unintentionally: as associates of commercial species, as fouling organisms on ship's hulls or as ballast water organisms in the holds of shipping vessels (Allen, 1953; Druehl, 1973; Carlton, 1979a, 1979b, 1985, 1987).

Studies focusing on introduced species have provided conflicting results with respect to the impacts of invading species on the native community. For example, some studies have found that invaders have had a measurable, often devastating, impact on the native community (Elton, 1958; Lidicker & Anderson, 1962; Lidicker, 1966; Zaret & Paine, 1973; Lasenby et al., 1978; Morgan et al., 1978; Brenchley, 1982a, 1982b; Race, 1982; Bertness, 1984; Clark et al., 1984). However, other investigations have documented few changes in the native community as a result of species invasions (Birch, 1979; Roughgarden, 1986b; Simberloff, 1981). In direct contrast to other studies, some introduced species appear to have been successful in their new habitats because they utilized resources, such as food or space unused by the native species.

Three species of herbivorous gastropods co-occur throughout the salt marshes of the Coos Bay estuary in southern Oregon. These are the native prosobranch mesogastropods Assiminea californica (Tryon, 1865), Littorina subrotundata (Carpenter, 1865), and Ovatella myosotis (Draparnaud, 1805), a pulmonate which has been introduced from Europe.

This study examines whether the introduced snail Ovatella has altered the abundance or intertidal distribution of the native gastropod species, and whether the native and introduced species compete for trophic or spatial resources. These questions, taken together, should provide a foundation for examining whether there was an ecological impact of the introduction of Ovatella myosotis on the native gastropods Assiminea californica and Littorina subrotundata.

CHAPTER II

METHODS

Description of the Study Sites

This research was conducted from May, 1987 through May, 1988 in the Coos Bay estuary of southern Oregon (Figure 1). Studies were conducted in Charleston at the University of Oregon's Henry Metcalf Research Reserve, Metcalf Marsh (not within the reserve domains), and at the South Slough National Estuarine Research Reserve (Figures 1 - 3). At these sites human foot traffic was high, but other disturbances were minimal.

Metcalf Marsh (Figure 2) is a low, coarse sand marsh with a gently sloping shelf which rises from the tidal flat and contains relatively few tidal creeks and little fresh water input. In contrast, Metcalf Reserve is a typical salt marsh, with high levels of fresh-water input through the many tidal creeks. The South Slough marsh (Figure 3) was situated on a dike and was flat with no cliffs, pools or creeks. The study site is located between the Sloughside and Rhode's dikes at the bottom of the Estuary Study Trail, and was chosen for use as a replicate for the bayside

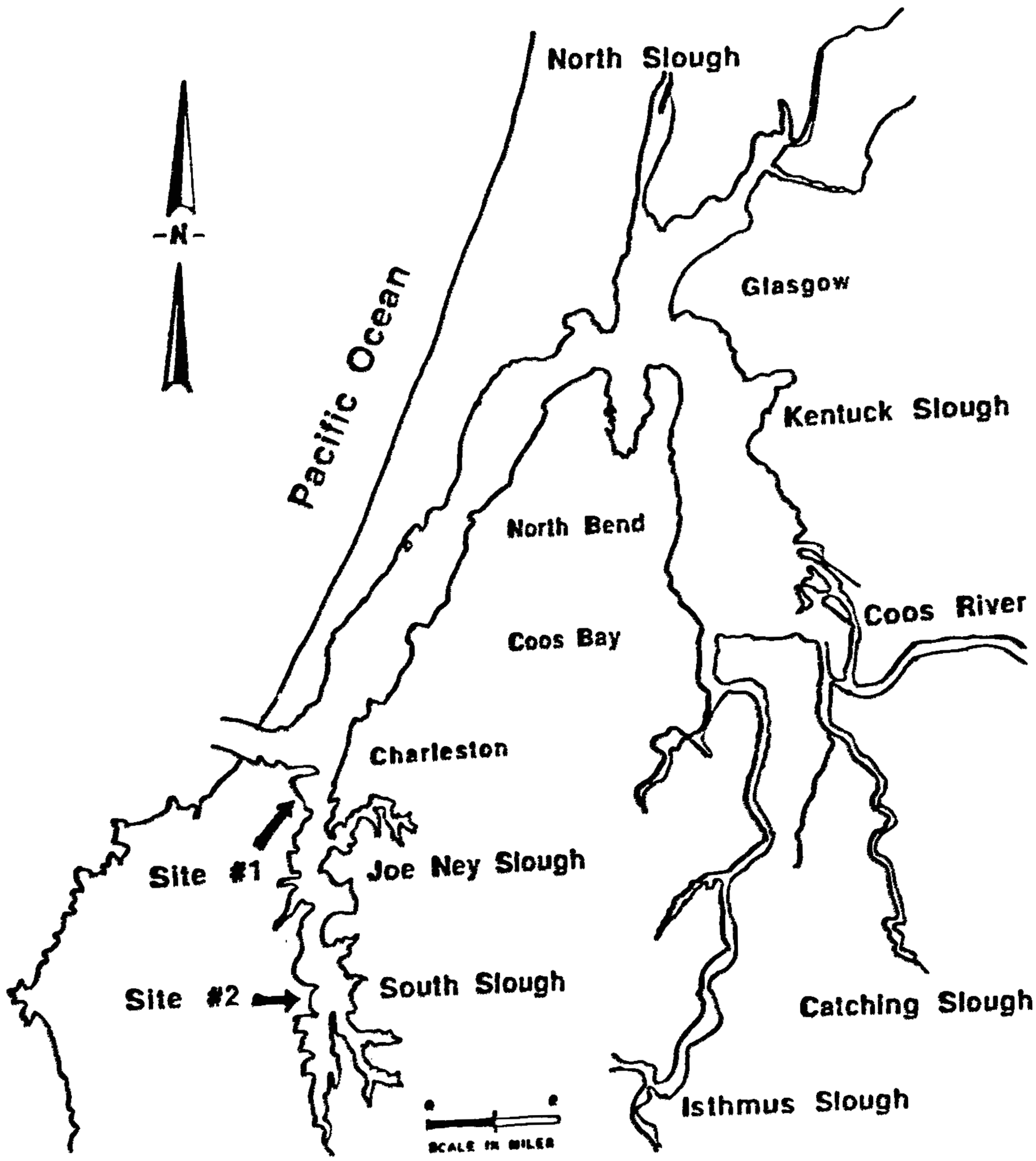

FIGURE 1. Map of Coos Bay, Oregon including the location of the Metcalf Marsh (Site #1) and South Slough (Site #2) study sites.

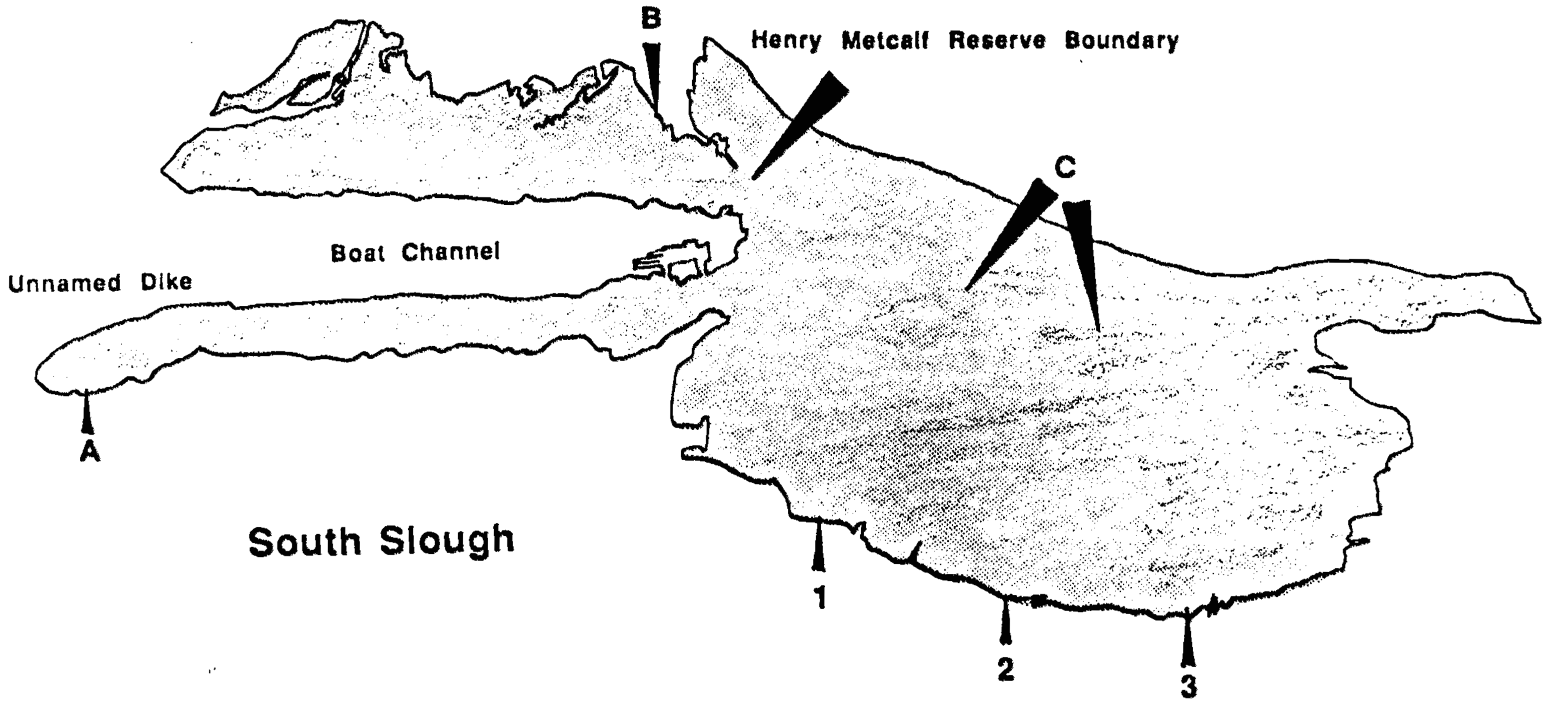

FIGURE 2. Map of Metcalf Marsh site, showing the location of transect lines (1, 2, & 3), the cage sites for the high (B) and low (A) reciprocal transplant experiments and the two density manipulation sites (C).

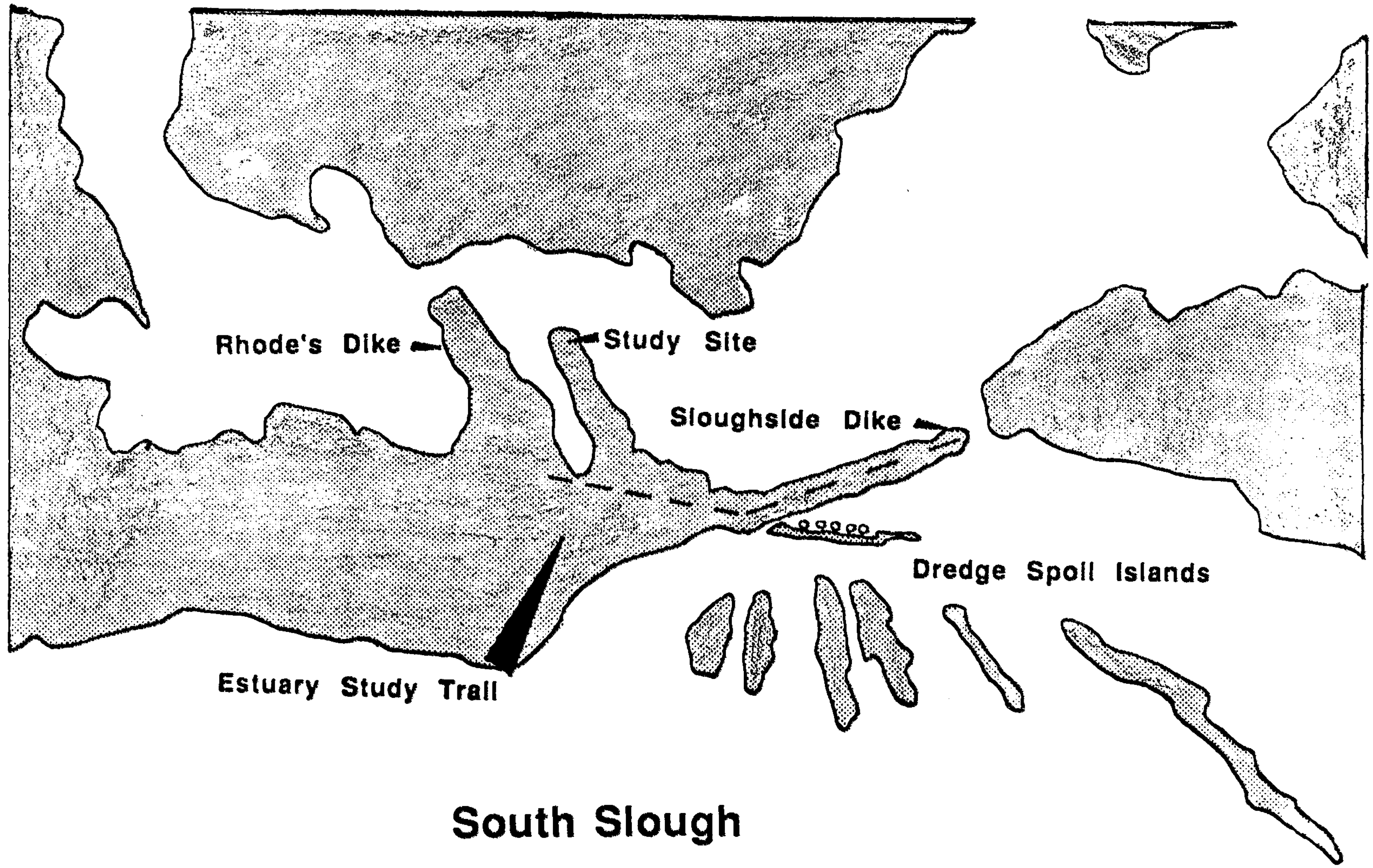

FIGURE 3. Map of South Slough site, showing the location of the study site in which the experimental cages were placed.

section of Metcalf Marsh based on its similar population levels of the three snail species, similar vegetation, tidal level and level of human foot traffic.

The vegetation at both Metcalf and the South Slough marshes is dominated by the halophytes Salicornia virginica and Distichlis spicata. However, the vegetation at Metcalf is amongst the most diverse found in Coos Bay marshes (Hoffnagle et al., 1976). Other noteworthy plant species found at this site include Cuscuta salina (the orange salt marsh dodder commonly found parasitizing Salicornia) and Cordylanthus maritimus (saltmarsh birds beak) a federally-listed endangered species known only from two sites in the state of Oregon.

Description of the Study Species

Assiminea californica

The genus Assiminea has a worldwide distribution, although it reaches highest abundance and diversity in tropical regions of southeast Asia (Abbott, 1958; Little & Andrews, 1977; Fortun et al., 1981). This genus is commonly found in brackish waters of coastal salt marshes, protected bays and estuaries

(Burch, 1946a; Abbott, 1958; Carlton & Roth, 1975). Assimineid snails are encountered with equal frequency submerged in brackish water, salt water or on moist substrate (Abbott, 1958; Little & Andrews, 1977; Brown, 1971, 1980).

On the Pacific coast of North America the estuarine Assiminea californica (= A. translucens (Carpenter, 1864)) has a distribution which extends from Vancouver, British Columbia to Cabo San Lucas, Baja, California (MacDonald, 1969a, 1969b; Rudy & Rudy, 1983). A. californica is a minute snail, growing to about 4 mm in height in Coos Bay. It has a glossy chestnut shell grading in color from the nearly black spire to the body whorl which is often almost transparent. The shell is globose, stoutly conical, thin, and smooth. The operculum is very thin and almost colorless.

Assiminea californica is dioecious with no observable sexual dimorphism (Fowler, 1976, 1977a). In the salt marshes of central California copulating pairs can be observed at all times of the year (Fowler, 1977a). The egg capsules are single, spherical and approximately one half millimeter in diameter. Assiminea females push the egg capsules into the mud (Fowler, 1977a; Fretter & Graham, 1978; Fortun et al., 1981). The egg capsules are covered with a sticky film of mucus to which mud and detritus particles adhere. This makes the eggs visually undetectable within a few days (Fowler, 1976, 1977a, 1977b).

The veliger stage develops completely within the egg capsule, the young snail emerging through a split in the capsule wall and crawling away from the empty case (Fowler, 1977a). No field studies have been conducted on the developmental time of *Assiminea californica*. However, Fortun, et al. (1981) found that the European *A. grayana* had a developmental time of three to seven weeks and Fowler (1977a) found that under laboratory conditions, *A. californica* eggs hatch in three weeks and that hatching was delayed if the relative humidity was too low.

Throughout the world several *Assiminea* species coexist with other gastropod species, the most common of these being pulmonates in the family Melampidae (Abbott, 1958; Brown 1971, 1980). In Europe, *Assiminea grayana* is associated with *Ovatella myosotis* (Smith, 1951; Fortun et al., 1981). In Africa, Madagascar and Mauritius, *Assiminea* species are found associated with *Melampus* species (Brown, 1971, 1980). On the East coast of North America, *Assiminea modesta* is found associated with the native *Melampus bidentatus* and the introduced *Ovatella myosotis* (Baranowski, 1971). On the north Pacific coast of North America, *Assiminea* californica is usually found in the same habitat as the native Littorina subrotundata and the introduced Ovatella myosotis (MacDonald, 1969a, 1969b; Carlton & Roth, 1975; Fowler, 1977a).

Littorina subrotundata

The genus Littorina has a worldwide distribution, and in general has been well studied. Littorina subrotundata, however is an exception. To date few reports have been published containing any information on this species (Burch, 1945, 1946b; Talmadge, 1962; Duggan, 1963; Keen, 1970). It was formerly known as Algamorda newcombiana (Hemphill, 1877) (Taylor 1981).

Littorina subrotundata is a small (to 6 mm in height in Coos Bay), light brown, and rounded. There are four whorls. A chink between the columella and the inner lip is a diagnostic feature.

Egg masses of 15-40 eggs per mass are laid in June and July in moist locations where they will be submerged during most high tides. The early egg masses are light in color and tough in texture and become darker and softer as they age. The larvae emerge from these egg masses and crawl away as fully formed juvenile snails (pers. obs.). Hatchlings occur in mid

July with increasing abundance through late July and early August.

Littorina subrotundata occurs in salt marshes and estuaries of the Pacific coast of North America from Heah Bay, Washington to Humbolt Bay, California (Taylor, 1981). As far as it is known, throughout its range Littorina subrotundata co-occurs with both Assiminea and Ovatella (MacDonald, 1969a, 1969b; J. T. Carlton, pers. comm., 1988).

Ovatella myosotis

Ovatella is a member of the family Melampidae whose greatest numbers and diversity are found in the salt marshes and estuarine mudflats of the world (Paulson, 1957). Melampids are typically high littoral snails, capable of living without water for extended periods of time (Seeleman, 1968).

Ovatella myosotis (= Phytia setifer (Cooper, 1872)) is a small (to 8 mm) pulmonate gastropod. Exterior shell colors vary from light brown to violet to opaque white; the interior is porcelainous (Carlton & Roth, 1975). The shell is olive shaped, with a pointed spire and an one half of the shell length (Ellis, 1926; Rudy & Rudy, 1983). There are three folds "teeth" in the columella. Small rigid hairs are present on the edges of the sutures present in the juveniles, but not in the adults (Ellis, 1926; Meyer, 1955).

Ovatella is most commonly found in salt marshes under rotting boards and debris (Meyer, 1955; Hanna, 1966; MacDonald, 1969a; Jorgensen, 1971; Carlton, 1979a). *Ovatella* may also be found on isolated stones or mounds in salt marshes; the stones may be covered by water only 4 hours out of 12 (pers. obs.). During extremely long dry periods *Ovatella* remains in thick bunches of grass or seeks out crevices while other gastropods may be totally absent (Fowler, 1977a).

The biology of *Ovatella* has been investigated in Europe, but ignored in North America (Carlton, 1979a). *Ovatella* is hermaphroditic and mating occurs primarily in the spring and summer (Meyer, 1955; Seeleman, 1968). Clutches of 15 to 80 eggs per mass are laid in the summer (Meyer, 1955; Seeleman, 1968; Fowler, 1977a). The eggs are pushed into the sediment or attached to the bases of emergent vegetation where they are covered by mud and rendered visually undetectable within a short period of time. The veliger stage occurs completely within the egg capsules and the snails emerge as fully formed juveniles (Meyer, 1955; Seeleman, 1968; Fowler 1977a).

These snails have been shown to be

predominantly annuals in parts of their natural range (Jorgensen 1971), while other studies have found that they regularly live to two years of age with individuals of four years of age, fairly common (Meyer, 1955). To date no work on age and growth has been conducted on North American populations of Ovatella myosotis.

The natural range of O. myosotis is the salt marshes and estuarine mudflats of Western and Northern Europe (Hanna, 1966; Jorgensen, 1971; Carlton, 1979a, 1979b). In the early 1800's O. myosotis appeared in New England, probably as a result of the early shipping industry (Gould, 1870; Carlton, 1979a). O. myosotis was first found on the Pacific Coast of North America in San Francisco Bay in 1871 (Cooper, 1886; Carlton, 1979a). While the first recorded observation of Ovatella in Coos Bay is in 1965, it probably arrived in the early 1900's, as Coos Bay has been active in shipping since the 1800's (Carlton, 1979a).

The most probable mechanism for the introduction of Ovatella to the Pacific coast of North America is as a secondary introduction from the seaports of our Atlantic coast. In fact, it is likely that Ovatella arrived with shipments of Atlantic oysters which were at their peak for the 50 years following the California Gold Rush. Mechanisms such as fouling or wet ballast would likely have brought Ovatella to San Francisco prior to 1871 (Carlton, 1979a).

On the Pacific Coast of North America O. myosotis ranges from Boundary Bay, British Columbia to Baja California. In northern California Ovatella most frequently occurs with Assiminea californica. In San Francisco Bay it is often much more abundant than Assiminea (Fowler, 1977a). In Oregon and parts of Washington Ovatella occurs with Littorina subrotundata as well as Assiminea (Duggan, 1963; Carlton, 1979a). In still more northern locations (Birch Bay, Washington) Ovatella occurs with Assiminea and the Japanese Cecina (Carlton, 1979a). In southern California Ovatella occurs with Melampus olivaceus and Cerithidea californica (Carlton, 1979; Rudy & Rudy, 1983).

Field Studies: Observations

Population Estimates

Three permanent transect lines spaced 15 meters apart were established at Metcalf Marsh in May, 1987 (Figure 2). The lines ran from just below the lower limit of the marsh vegetation to the zone above the high tide line. Permanent 20 by 20 cm sampling stations (quadrats) were established at six meter intervals along each line (n = 28).

All snails were counted in each quadrat at two week intervals. Empty shells, non-experimental snail species and snails smaller than 1 mm were not included in the count, but were recorded as being present. Snails not obviously alive were returned to the lab for observation. Noted were obvious microhabitat differences (that is, whether the snails were on the substrate or on the vegetation), and association patterns.

As a check on the accuracy of this counting method for estimating population abundances, an area away from the transect lines was counted in the field. Then the entire quadrat (piece of sod) was excavated and brought back to the lab and completely dissected to obtain a count of live snails present. This was repeated twice a month for the first three sampling months.

Vegetation Sampling

Vegetation sampling was conducted once per season at both the Metcalf (August 4, 1987, November 11, 1987, February 13, 1988, May 19, 1988) and South Slough (August 16, 1987, November 18, 1987, February

15, 1988, May 14, 1988) sites. At Metcalf Marsh sampling was done at three-meter intervals along the transect lines, while at the South Slough site the sampling was conducted in rows between the cages. The sampling was conducted using two sizes of "pin frames", a one meter frame for the areas outside the cages or quadrats and a 20 cm frame for measurements taken within each quadrat or cage. Each pin frame had 10 evenly spaced spikes. At each station five replicate estimates of percent cover were made. Estimates were made by placing the pin frame on the ground and then recording the identity of the first plant species touched by the pin on the frame. The relative proportion of these pins covered by various species, therefore, represented estimates of percent cover.

Field Diets

Data were obtained on the field diets of *Assiminea* and *Ovatella* to determine any dietary differences. Forty individuals of each species were collected on October 1, 1987 (20 from areas of allopatry and 20 from areas of sympatry). These were brought to the lab where each shell was individually washed with 95% acetone and rinsed with distilled water to minimize organic material introduced into the laboratory. The animals were then kept for 24 hours in a cool, dark environment in individual plastic containers with a few ml of 0.3 micrometer filtered seawater. The containers were cleaned at 12 hour intervals, and fecal pellets were removed. Pellets were examined immediately using a compound microscope. All items were identified to the lowest taxonomic level possible and scored as to their relative level of abundance (rare, common, or abundant).

At the time of the snail collections for the diet studies, 3 field samples were taken from the substrate and from the stems of halophytic vegetation in both the high and low marsh areas. This was done such that comparisons could be made between the food available in the high and low zones as well as between the food items available and the gut contents of the three snail species.

Field Studies: Experiments

Growth Rates

An experiment was conducted at the South Slough marsh (Figure 3) to determine if the mean growth rate of a species when caged only with conspecifics differed from the mean growth rate when individuals were caged with an equal number of non-conspecific individuals. A series of pairwise competition experiments were established using caged individuals in both single (control) and mixed (experimental) species associations. Trials which included all three species caged together were not conducted.

Individuals used in the study were collected from areas of sympatry at Metcalf Marsh. There were minimal size variations among the specimens of each species used in the experiments in order to avoid any size related differences in growth rates.

Snails were marked in the laboratory by placing a thin line of nail polish on the outer lip such that any new growth could be measured past the mark. These data were then used to estimate growth rates of the snails (Behrens, 1971).

Cages were constructed of untreated 1 by 2 cm strips of wood formed into 15 cm cubes and covered with nylon window screening of approximately 1.5 mm mesh (Figure 4). The legs of the cages were driven into the sediment 15 to 20 cm so that the base of the cage was flush with the ground. Each cage had a removable lid for access to the cage interior (Figure 4).

Prior to the start of the experiment (September 13, 1987) the area of the marsh within each cage was cleared of all snails. Cages were placed within a zone

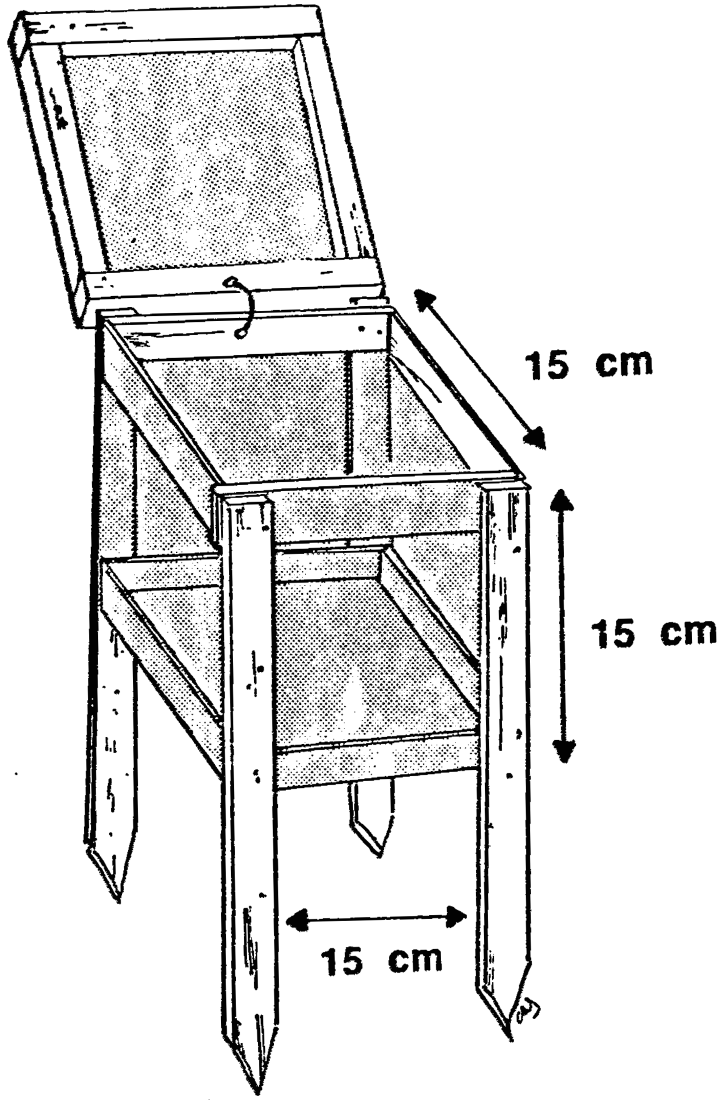

FIGURE 4. Cage design for the competition and the reciprocal transplant experiments.

of the marsh in which all three species were found to co-occur. Treatments were assigned to cages randomly. Snails were counted and cages were cleaned once a week.

Replicates (n = 3) of each of the 3 possible pairwise combinations of species consisted of 15 individuals of each species per cage in the following groupings: *Littorina* with *Assiminea*, *Littorina* with *Ovatella*, and *Assiminea* with *Ovatella*. Control treatments consisted of 30 of each species caged alone. The experimental design thus included a total of 18 cages.

After one month (October 14, 1987) the snails were removed from their cages, returned to the laboratory and growth was measured using a microscope and ocular micrometer for lip increments. Variance in this data set was homogenized by log transformation prior to statistical analysis.

Transplant Experiments

In order to examine the role that physical factors might play in determining the vertical distribution of the three study species, two reciprocal transplant experiments were conducted at Metcalf Marsh (July 12, 1987 through July 27, 1987 and October 11, 1987 through November 1, 1987). Both experimental treatments used cages at high (n = 9) and low (n = 9) marsh locations (Figure 2). Six treatments with 3 replicates each (18 cages total) were employed. In all treatments 10 animals were placed in each cage (Figure 4) at the start of the experiment. Experimental treatments were those in which *Ovatella* was transplanted from the high to low zone, and those in which *Littorina* and *Assiminea* were transplanted from the low to the high zone. Control treatments were those in which *Ovatella* was caged in the high zone, and those in which *Assiminea* and *Littorina* were caged in the low zone. All snails were marked with nail polish on the shell apex for future identification. Dead snails were removed daily and replaced with differentially marked individuals.

Removal Experiments

In order to determine whether the numbers of *Assiminea* or *Littorina* would increase in the absence of *Ovatella*, *Ovatella* were removed on a daily basis from a further set of experimental quadrats from July 9, 1987 through July 23, 1987. These *Ovatella* removal experiments were in the high zone of Metcalf Marsh centered between the transect lines (Figure 2). The subsequent numbers of *Assiminea* and *Littorina* observed in these quadrats were then compared to the control quadrats located on transect lines themselves.

Laboratory Studies: Experiments

Starvation

All three snail species were examined for their ability to withstand starvation. Thirty animals of each species were collected from the Metcalf Marsh site. These animals were returned to the lab where their shells were cleaned with acetone to remove any bacterial or algal material present on the shell. Snails were then placed in clean culture dishes with a small amount of 3 micrometer filtered seawater. These culture dishes were kept in a darkened portion of an outside water table. Culture dishes were replaced and animals were cleaned with filtered seawater daily.

Agregative Behavior

In single species and pairwise groupings the behavior of adult *Assiminea* and both adult and juvenile *Ovatella* were studied with particular attention to gregarious associations and potential avoidance behaviors. *Littorina* was not used because it would often remain dormant in its shell for the entire duration of pre-experimental trials. Juvenile Assiminea were not available at the time of the experiments.

Experiments were conducted using 10 cm diameter by 2 cm height culture dishes, with a layer of the filamentous green alga Percusaria covering the bottom of each dish. During the trials all dishes were placed on a platform just above water level in outdoor (but well shaded) water tables.

There were 8 treatments of 5 trials each, except for juvenile Ovatella when only sufficient numbers for 3 trials could be obtained. All trials lasted for seven days. The 3 control treatments all contained 20 individuals and were as follows: Assiminea, adult Ovatella and juvenile Ovatella. The 5 experimental treatments were as follows: (1) 10 Assiminea and 10 adult Ovatella, (2) 10 Assiminea and 10 juvenile Ovatella, (3) 20 Assiminea and 10 adult Ovatella, (4) 20 Assiminea and 10 juvenile Ovatella, (5) 20 adult Ovatella and 10 Assiminea. At the end of each experiment a careful map was made of the location of each snail within the container.

CHAPTER III

RESULTS

Study Site

The three transect lines were similar in slope and tidal heights (Table 1, Figure 5). The three transect lines show four distinct zones; three zones on the basis of average tidal height (Table 1) and the fourth ("Mudflat") based upon the lack of vegetative cover (Figure 9).

TABLE 1. Heights above datum for the four tidal zones at the Metcalf Marsh study site.

Zone	Number of Observations	Mean Tidal Height (cm)	Standard Deviation
Terrestrial	3	274.03	11.55
High Marsh	16	207.69	10.40
Low Marsh	6	179.49	6.15
Mudflat	3	167.69	6.75

Population Estimates

From May 15, 1987 through May 17, 1988 snail populations at Metcalf Marsh were monitored over three transect lines. Metcalf marsh shows clear vertical

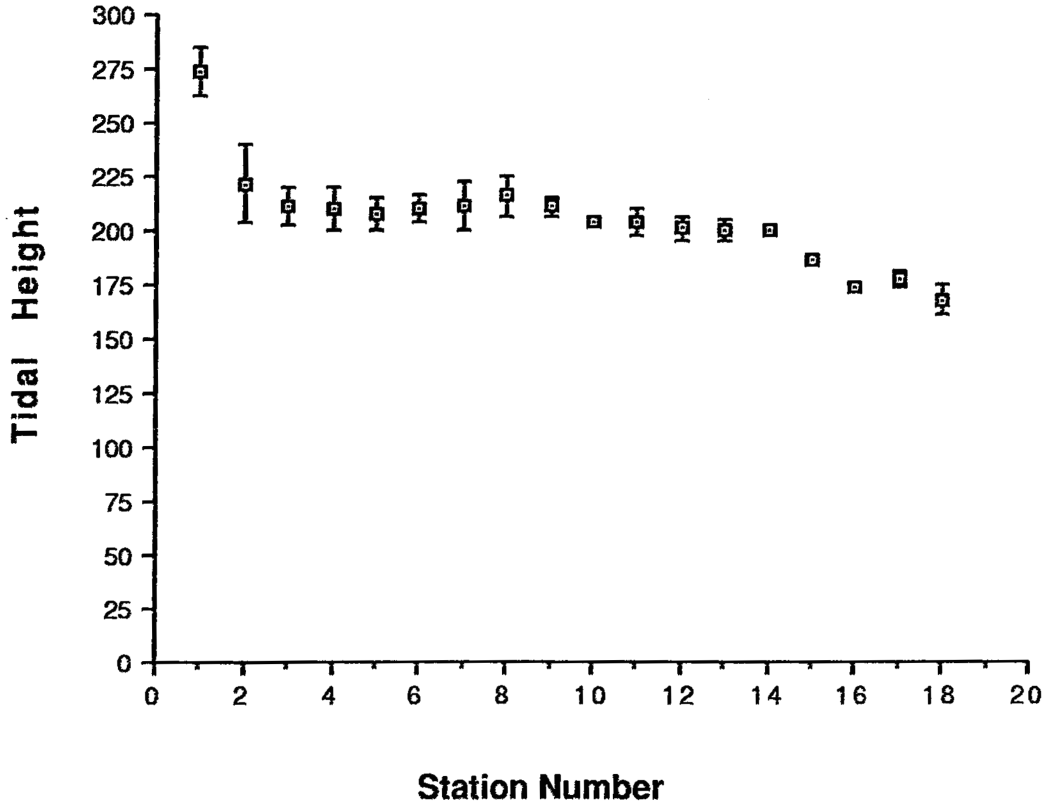

FIGURE 5. Mean slope profile of the three transect lines at the Metcalf Marsh site. Station number 1 is the terrestrial zone, stations 2 - 14 are the high marsh, stations 15 - 17 are the low marsh and station 18 is the mudflat zone.

zonation with respect to gastropod species (Figures 6 - 8). In the high marsh, Ovatella is the most common species with Littorina subrotundata and Assiminea californica present occasionally. In the low marsh, only Assiminea and L. subrotundata occur in abundance, with L. subrotundata becoming increasingly more abundant toward the lower limit of the vegetation. Over the course of the year only two snails were found in either the mudflat or terrestrial zones (one Assiminea in the mudflat zone and one Ovatella in the terrestrial zone). These two tidal levels were therefore excluded from further analysis.

Sod was excavated for the first six sampling dates of the study. A total of five more snails were found in the lab than in the field sampling trials (Table 2). Based upon these results no correction was made to the field counts obtained during the course of the study.

All three snail species show a pattern of abundance characterized by winter lows and summer highs (Figures 6 - 8). These patterns of change correlate well with seasonal changes in the environment (Table 3). The environmental parameter of most importance in determining these changes in abundance is probably precipitation levels, as the

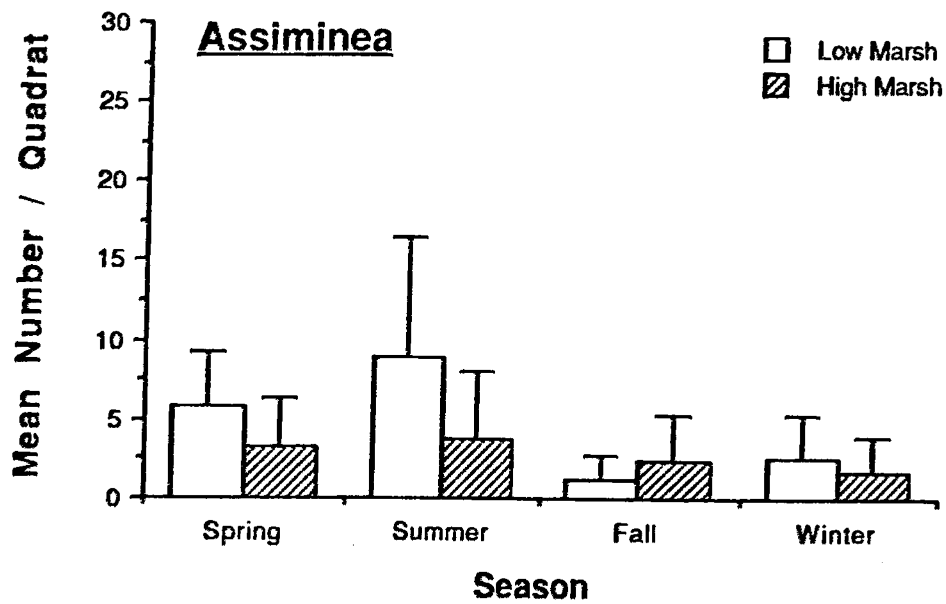

FIGURE 6. Seasonal patterns in the vertical distribution of <u>Assiminea</u> <u>californica</u> at the Metcalf Marsh site from May 15, 1987 through May 17, 1988.

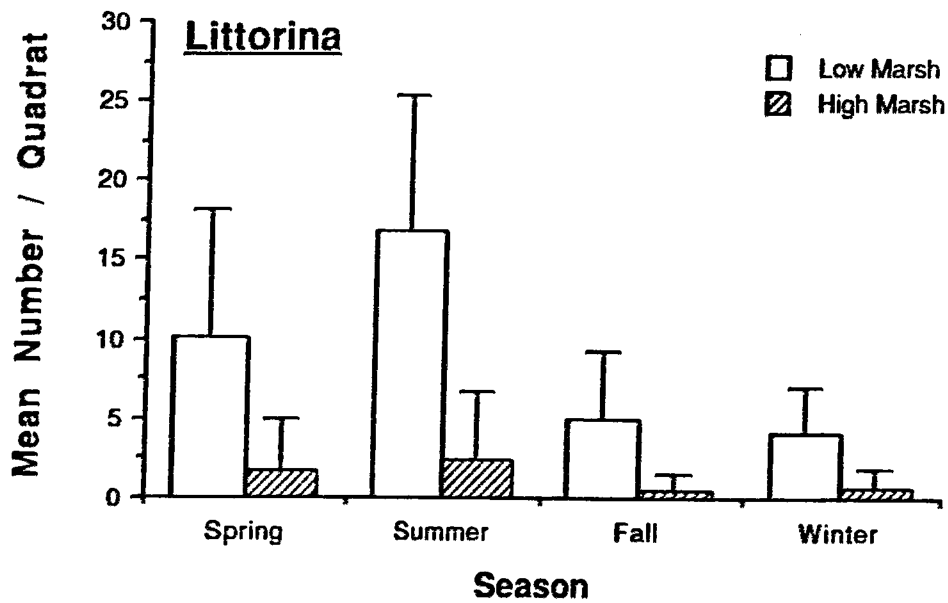

FIGURE 7. Seasonal patterns in the vertical distribution of Littorina subrotundata at the Metcalf Marsh site from May 15, 1987 through May 17, 1988.

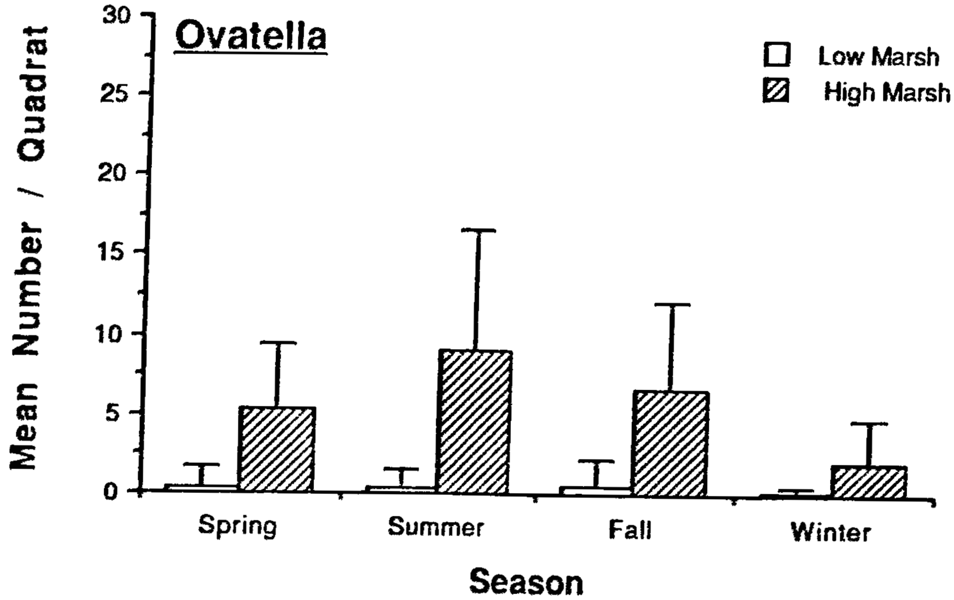

FIGURE 8. Seasonal patterns in the vertical distribution of <u>Ovatella myosotis</u> at the Metcalf Marsh site from May 15, 1987 through May 17, 1988.

TABLE 2. Results of excavation trials in which field counts of snail density was compared to the numbers obtained by removing the sod and completely dissecting it in the laboratory. Values are given for *Littorina* (L), *Assiminea* (A) and *Ovatella* (O). Lab counts are shown in parenthesis only when they differed from those counts obtained in the field.

	Field Count (Lab Count)			Difference			Daily
Date	L	A	O	L	A	O	Total
5-15-87	2	1(2)	8(9)	0	+1	+1	+2
5-25-87	1	5(6)	6	0	+1	0	+1
6-12-87	13	5	1	0	0	0	0
6-25-87	19(20)	3(4)	2	+1	+1	0	+2
7-9-87	15	4	0	0	0	0	0
7-23-87	10	12	1	0	0	0	0
			Total	+1	+3	+1	+5

fall and winter months far exceed the spring and summer.

TABLE 3. Seasonal climatic averages in Coos Bay, Oregon given in monthly averages. Precipitation is in inches and temperatures are in Celsius. Data was compiled from United States Weather Bureau records and the National Oceanic Data Center's Water Temperature Guide to the Pacific Coast of North America.

	Jan. - March	April - June	July - Sept.	Oct. - Dec.
Air temperature	8.10	12.60	15.00	10.50
Water temperature	10.10	11.50	12.80	11.30
Precipitation	8.48	2.78	0.81	8.33
Number of days with more than 1/100 inch precipitation	19	12	5	17

A two way ANOVA testing the effect of tidal height on seasonal abundance for each species (Table 4) was conducted. Results indicate that there was a significant ($p < 0.001$) interaction between tidal height and season (Figures 6 - 8). For all species of snails at almost all seasons, the numbers of snails remain similar in the zone of low density while they rise and fall with the seasons in the zone of higher density.

TABLE 4. Results of the two way ANOVA comparing tidal height and seasonal abundance values for *Assiminea*, *Littorina* and *Ovatella*.

Species & Source	SS	DF	MS	F	P
Assiminea					
Tidal	379.050	1	379.050	28.660	0.001
Season	1489.424	3	496.475	37.808	0.001
Interaction	603.882	3	201.294	15.329	0.001
Error	7406.060	564	13.131		
Littorina					
Tidal	6649.561	1	6649.561	377.203	0.001
Season	3652.948	3	1217.649	69.072	0.001
Interaction	1911.728	3	637.243	36.148	0.001
Error	9942.537	564	17.629		
Ovatella					
Tidal	3310.311	1	3310.311	156.933	0.001
Season	654.189	3	218.063	10.338	0.001
Interaction	602.803	3	200.834	9.521	0.001
Error	11896.933	564	21.094		

Vegetation Sampling

Vegetation was sampled at both Metcalf Marsh and South Slough in order to determine comparability between sites, whether the quadrats were representative of the marsh, whether there were seasonal variations in the percent cover patterns and to determine any zonation patterns in vegetative cover which might exist at Metcalf Marsh (Figures 9 - 13). In all cases, statistical tests were performed upon arcsine transformed data. The results were as follows:

1. At both the Metcalf and South Slough study sites the marshes are dominated by Salicornia virginica and Distichlis spicata with a few other species. Pairwise t-tests conducted on the five most common species indicate that there was no significant difference in the overall vegetative characteristics of the two sites.

2. A Chi-Square test comparing percent cover values obtained in the large vs small pin frame analyses showed no difference. The quadrats are therefore assumed to be representative of the sites as a whole.

3. A series of ANOVA tests were conducted in order to determine whether the relative abundance of any item changed seasonally. Only "bare space" showed

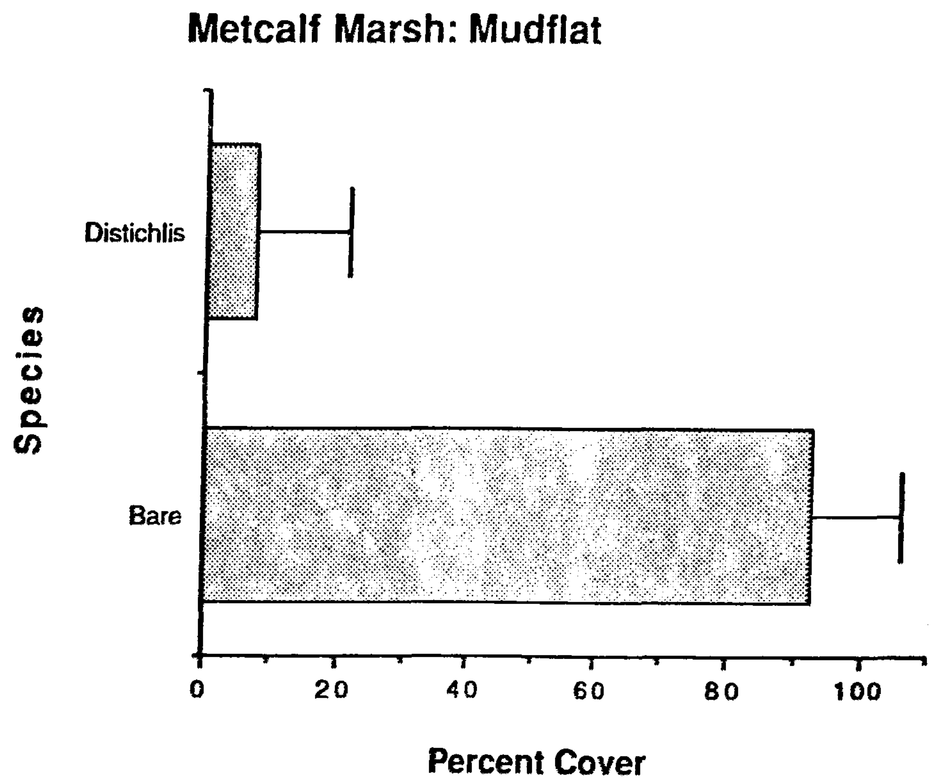

FIGURE 9. Large rake estimates of percent cover of vegetation by tidal height at the Metcalf Marsh site: Mudflat zone. Sampling dates were August 4, 1987, November 11, 1987, February 2, 1988, and May 19, 1988.

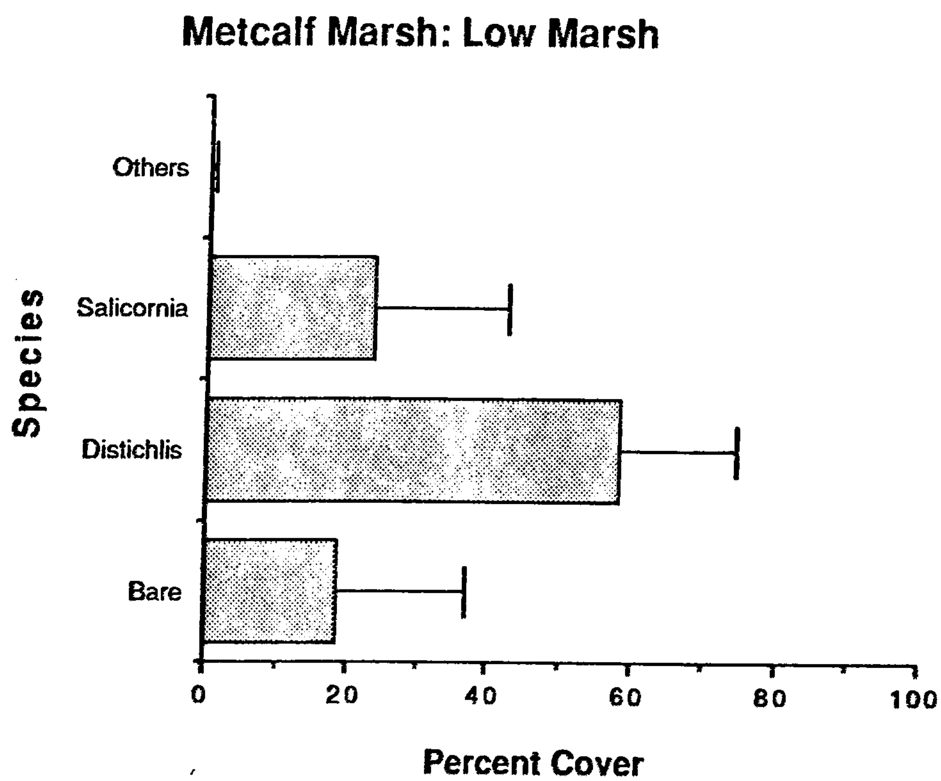

FIGURE 10. Large rake estimates of percent cover of vegetation by tidal height at the Metcalf Marsh site: Low Marsh zone. Sampling dates were August 4, 1987, November 11, 1987, February 2, 1988, and May 19, 1988.

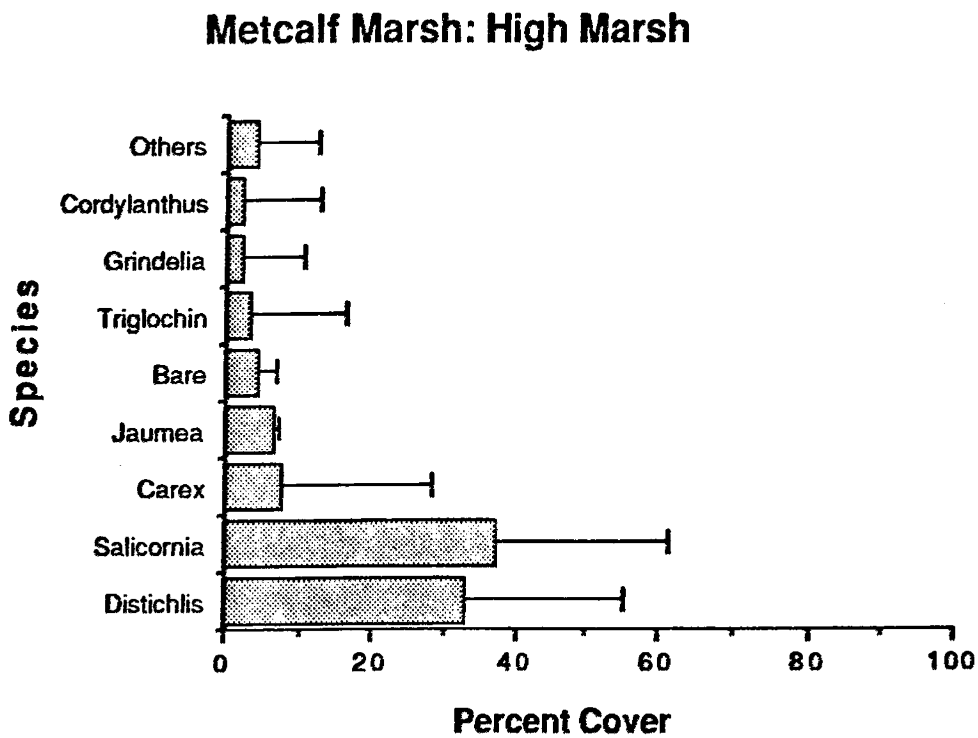

FIGURE 11. Large rake estimates of percent cover of vegetation by tidal height at the Metcalf Marsh site: High Marsh zone. Species included in the "others" category are Hordeum brachyantherum, Orthocarpus castillejoides and grasses. Sampling dates were August 4, 1987, November 11, 1987, February 2, 1988, and May 19, 1988.

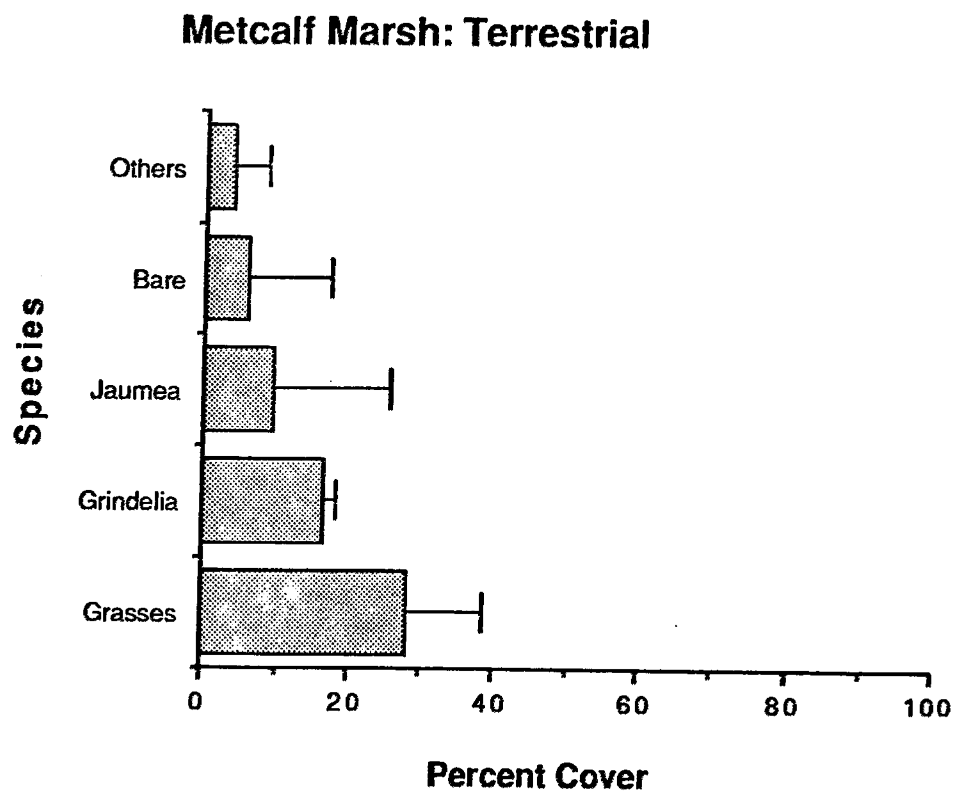

FIGURE 12. Large rake estimates of percent cover of vegetation by tidal height at the Metcalf Marsh site: Terrestrial zone. Species included in the "others" category are Rubus spectabilis, Oenanthe sarmentosa and Lathyrus species. Sampling dates were August 4, 1987, November 11, 1987, February 2, 1988, and May 19, 1988.

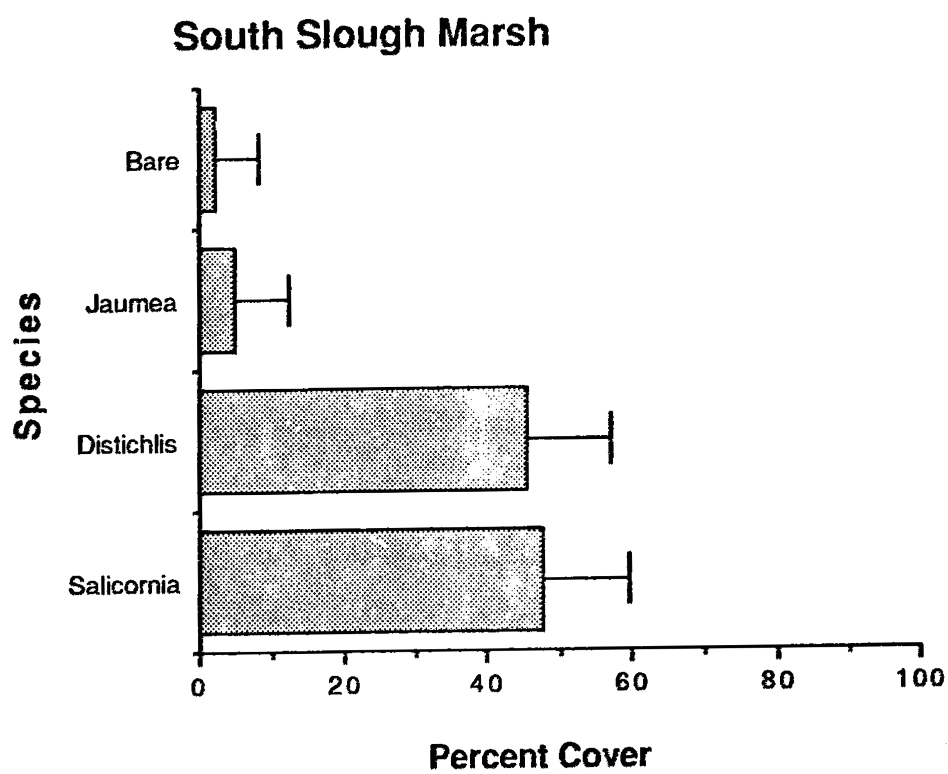

FIGURE 13. Large rake estimates of percent cover of vegetation at the South Slough site. Sampling dates were August 16, 1987, November 18, 1987, February 15, 1988, and May 14, 1988.

a significant effect of season upon relative abundance ($p < 0.001$), increasing in the winter as the halophytic plants were dying back. This effect was found at both sites, for both pin frame sizes (Table 5).

4. Pairwise t-tests on all plant species indicate that the two zones ("Mudflat" & "Terrestrial") which rarely contained snails were radically different than both the low and high marsh ($p < 0.001$). The most landward quadrats were dominated by grasses and other terrestrial vegetation (Figure 12). The lowest quadrats were predominently mudflat with a seasonal expansion of the marsh downward into the site (Figure 9). Pairwise t-tests indicated that the low and high marsh did not differ from each other in the relative proportion of the dominant plants Salicornia and Distichlis ($p < 0.05$). As is seen in most salt marshes, these two tidal heights did differ in the percent cover of minor species; with the high marsh containing a higher number of species than the low marsh (Figures 10 & 11).

Growth Rates

From September 13, 1987 through October 14, 1987 a series of pairwise competition experiments were conducted at South Slough. While all species showed measurable growth, t-tests conducted on all possible

TABLE 5. Results of the ANOVAs comparing, by season, arcsine transformed large and small rake estimates of percent cover of bare space at both the Metcalf Marsh and South Slough study sites.

Site, Rake & Source	SS	DF	MS	F	P
Metcalf Marsh: Small Rake					
Season	4.369	3	1.456	9.716	0.001
Error	152.280	996	0.153		
Metcalf Marsh: Large Rake					
Season	5.564	3	1.855	13.393	0.001
Error	137.923	996	0.138		
South Slough Marsh: Small Rake					
Season	1.861	3	0.620	26.478	0.001
Error	5.528	236	0.023		
South Slough Marsh: Large Rake					
Season	1.498	3	0.499	20.748	0.001
Error	5.680	236	0.024		

combinations indicated that there appeared to be no significant differences ($p < 0.001$) in growth rate with each species whether it was caged alone, caged with native species or caged with the introduced species (Table 6).

Transplant Experiments

Results of the summer and fall reciprocal transplant experiments were quite striking. For all species in both trials the experimental treatments had between 0.0 and 53.3 percent survival and the control treatments had between 76.6 and 96.6 percent survival, indicating a strong effect of tidal height on survival of all three species (Figures 14 - 16). A two way ANOVA conducted on each species by treatment and season showed clearly that there was a strong interactive effect between tidal height and season, with the transplants conducted in the summer showing significantly lower survival than their fall counterparts ($p < 0.001$) (Table 7). Two experimental protocols were used in order to answer the alternative hypothesis that starvation in the reciprocal transplant cages was responsible for the observed results: starvation experiments and field diet analysis.

TABLE 6. Results of competition experiments conducted at South Slough Marsh from September 13, 1987 through October 14, 1987. Data include the log transformed mean and standard deviation of lip growth in millimeters, as well as the results of independent paired t-tests performed on all possible treatment comparisons.

Species & Treatment Comparison	Mean	Standard Deviation	Probability
Ovatella:			
Ovatella control	1.110	0.040	
Ovatella & *Littorina*	1.115	0.023	0.867
Ovatella control	1.110	0.040	
Ovatella & *Assiminea*	1.087	0.041	0.521
Ovatella & *Littorina*	1.115	0.023	
Ovatella & *Assiminea*	1.087	0.041	0.428
Assiminea:			
Assiminea control	0.703	0.493	
Assiminea & *Littorina*	0.440	0.082	0.414
Assiminea control	0.703	0.493	
Assiminea & *Ovatella*	0.419	0.020	0.375
Assiminea & *Littorina*	0.440	0.082	
Assiminea & *Ovatella*	0.419	0.020	0.600
Littorina:			
Littorina control	0.157	0.031	
Littorina & *Assiminea*	0.138	0.068	0.690
Littorina control	0.157	0.031	
Littorina & *Ovatella*	0.151	0.027	0.825
Littorina & *Assiminea*	0.138	0.068	
Littorina & *Ovatella*	0.151	0.027	0.777

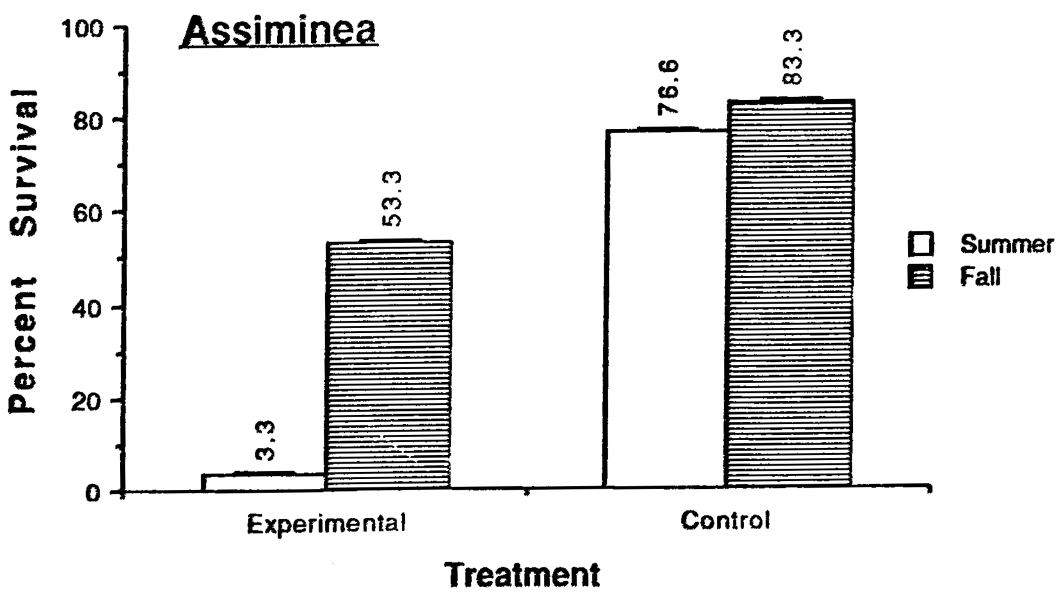

FIGURE 14. Percent survival of <u>Assiminea californica</u> in the summer (7/12/87 through 7/27/87) and fall (10/11/87 through 11/1/87) reciprocal transplant trials at the Metcalf Marsh site.

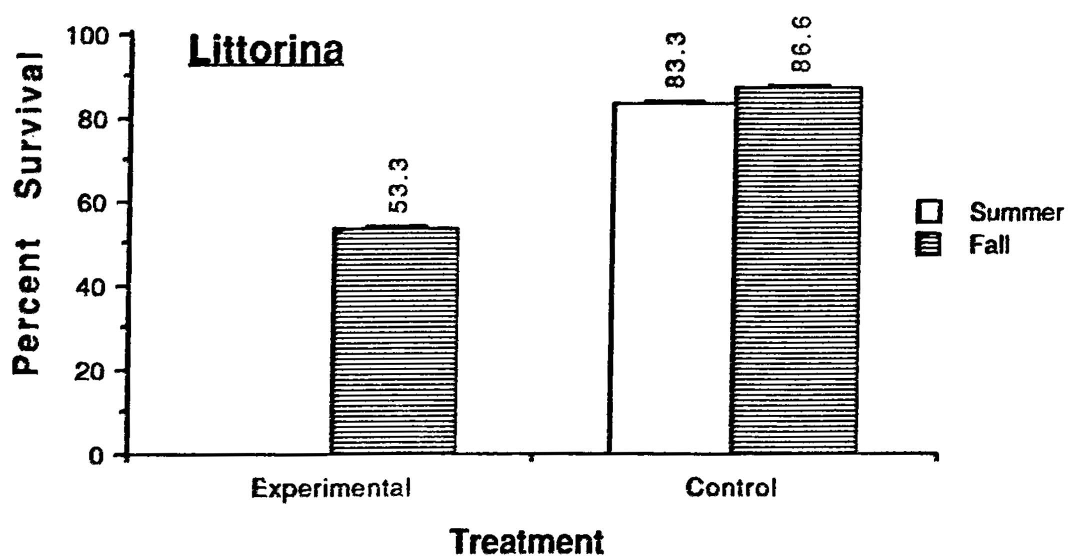

FIGURE 15. Percent survival of <u>Littorina subrotundata</u> in the summer (7/12/87 through 7/27/87) and fall (10/11/87 through 11/1/87) reciprocal transplant trials at the Metcalf Marsh site.

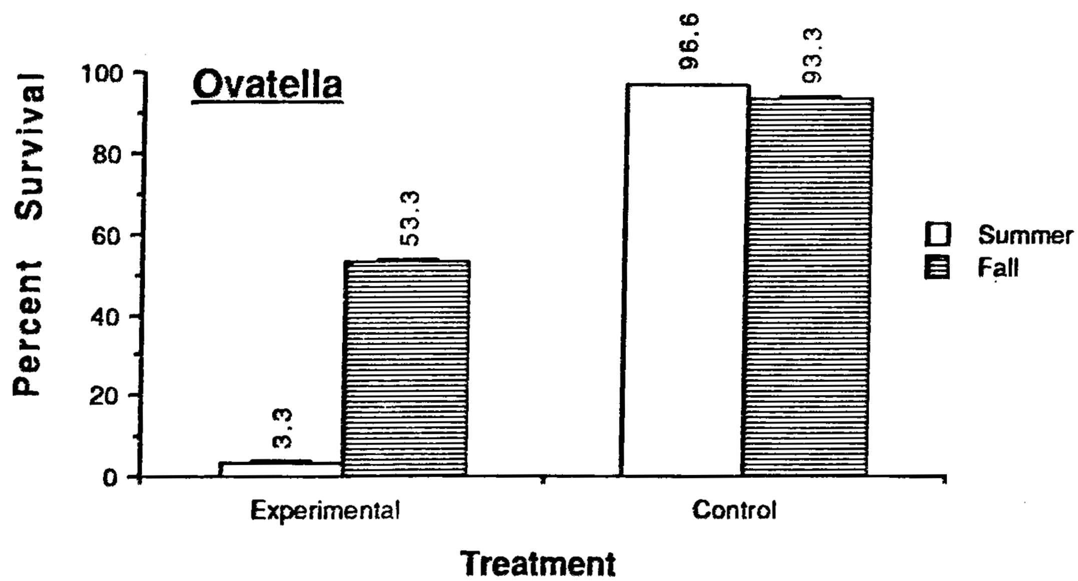

FIGURE 16. Percent survival of Ovatella myosotis in the summer (7/12/87 through 7/27/87) and fall (10/11/87 through 11/1/87) reciprocal transplant trials at the Metcalf Marsh site.

TABLE 7. Results of the two-way ANOVA comparing mean percent survival in the experimental and control treatments of both the summer and fall reciprocal transplant experiments.

Species & Source	SS	DF	MS	F	P
Assiminea					
Treatment	80.083	1	80.083	137.286	0.001
Season	24.083	1	24.083	41.286	0.001
Interaction	14.083	1	14.083	24.143	0.001
Error	4.667	8	0.583		
Littorina					
Treatment	102.083	1	102.083	204.167	0.001
Season	24.083	1	24.083	48.167	0.001
Interaction	18.750	1	18.750	37.500	0.001
Error	4.000	8	0.500		
Ovatella					
Treatment	114.083	1	114.083	342.250	0.001
Season	24.083	1	24.083	72.250	0.001
Interaction	30.083	1	30.083	90.250	0.001
Error	2.667	8	0.333		

Starvation

Thirty snails of each species were starved in the laboratory. All 90 snails remained alive at the end of three weeks (5 days longer than the caging experiments). Starvation therefore does not seem to be a viable hypothesis to explain the results of the reciprocal transplant experiments.

Field Diets

Field diets of the three species were examined in order to determine if they consumed the same food items and whether these food items varied in their availability in the high and the low marsh study areas. Chi-Square tests were performed on the results of the field diet analysis (Table 8) in order to determine whether there were significant differences between any of the species at either tidal height, within a species between tidal heights or between the habitat (mud and vegetation) samples at either tidal height. No significant differences were found. Similar statistical tests were conducted in order to determine whether the snails' diets differed significantly from the array of items available in the habitat. No significant differences were found.

TABLE 8. Results of the field diet analysis (both tidal heights combined) conducted at Metcalf Marsh in October 1987. Data presented includes the percentage of *Assiminea* (A), *Littorina* (L), and *Ovatella* (O) which contained the food item as well as an estimate of the item's total relative abundance. For all three species the sample size was forty.

Item	Number of Snails Containing Item			Total Relative Abundance		
	A	L	O	A	L	O
Bacteria:						
Rods	40	40	40	20.0	20.0	20.0
Cocci	40	40	40	20.0	20.0	20.0
Cyanophyceae:						
Nostoc	12	13	13	10.0	10.8	10.8
Gloeocapsa	15	7	12	12.5	5.8	10.0
Bacillariophyceae:						
Navicula 1	22	25	28	50.8	60.0	59.2
Navicula 2	25	25	29	60.8	40.0	62.5
Navicula 3	12	18	11	29.2	39.2	21.2
Nitschia	22	20	24	23.3	18.3	22.5
Melosira	22	17	20	22.5	18.3	19.2
Closterium	2	7	4	1.7	5.8	3.3
Pleurosigma	3	5	3	2.5	4.2	2.5
Diatom Parts	20	20	20	95.8	92.5	95.0

TABLE 8. (Continued) Results of the field diet analysis (both tidal heights combined) conducted at Metcalf Marsh in October 1987. Data includes the percentage of Assiminea (A), Littorina (L), and Ovatella (O) which contained the food item as well as an estimate of the item's total relative abundance. For all three snail species the sample size was forty.

Item	Number of Snails Containing Item			Total Relative Abundance		
	A	L	O	A	L	O
Chlorophyceae:						
Cladophorales	11	12	13	9.2	10.0	10.8
Chlorocococean	9	9	9	7.5	7.5	7.5
Enteromorpha	7	3	4	5.8	3.3	3.3
Miscellaneous:						
Macro Algae	22	19	21	34.2	20.0	47.5
Higher Plants	26	15	31	52.5	19.2	71.7
Unidentified Material	20	20	20	94.2	99.2	98.3

Aggregative Behavior

Results of the population censusing (for September 13, 1987 through May 17, 1988) indicate that *Assiminea* and *Ovatella* have a high degree of overlap (Table 9). Results show that 60.67 percent of *Assiminea* and 82.98 percent of *Ovatella* were found in heterogeneous quadrats (quadrats containing both native and introduced species). In contrast, on these sampling dates only 16.12 percent of all groups containing *Littorina* were found in heterogeneous quadrats.

TABLE 9. Mean percent of individuals in each quadrat found on the soil surface in both quadrats which contained only either native or introduced species (homogeneous) and those which contained both native and introduced species (heterogeneous).

Species	Homogeneous Quadrats N	Mean	(SD)	Heterogeneous Quadrats N	Mean	(SD)
Littorina	116	45.46	(28.82)	41	39.24	(35.16)
Assiminea	94	49.27	(29.15)	145	54.03	(30.41)
Ovatella	33	59.39	(31.21)	161	57.66	(27.59)

In addition, all population censuses contained notations as to whether the snails were located on the soil or on the vegetation. The percent of individuals found on the soil was calculated for quadrats which contained either native or introduced species (homogeneous) and those which contained both native and introduced species (heterogeneous). In all associations all three species seemed to be found in either microhabitat approximately fifty percent of the time (Table 9).

In order to test adult-adult avoidance in the field, Ovatella were removed from five experimental quadrats in the high zone at the Metcalf Marsh site during two weeks in July of 1987. In the control treatments, a total of 1,190 Ovatella were observed yielding a mean number of 86 (SD = 11.07) snails observed per day. After the initial removal of 88 snails in the five experimental quadrats, a total of 64 Ovatella were removed from these quadrats over the next fourteen days. This yielded a mean density of Ovatella, for all quadrats combined, of 4.57 (SD = 1.45) snails per day.

A total of 17 Assiminea were found in the control quadrats with a daily mean of 1.21 (SD = 0.68). Nineteen Assiminea were found in the experimental quadrats yielding a daily mean of 1.33 (SD = 0.90). There was no tendency towards increase in numbers of Assiminea observed in the experimental quadrats over time. No _Littorina_ were found in either the control or the experimental quadrats.

In order to further examine whether _Assiminea_ and _Ovatella_ actively avoid one another, a series of experiments were conducted in the laboratory. These experiments yielded the following results:

First, both _Ovatella_ and _Assiminea_ tend to cluster. Clusters outnumber solitary individuals with a maximum ratio of 5.8:1 and a minimum ratio of 3.17:1 (Table 10).

Second, in equal density treatments, the number of individuals in heterogeneous groupings outnumbered those in homogeneous or solitary groupings by a minimum of 3.8:1 and a maximum of 19:1. In unequal density treatments the number of snails found in heterogeneous groupings outnumbered either solitary or homogeneous groupings by a minimum of 1.5:1 and a maximum of 10:1 (Table 11).

Third, Chi-Square analysis showed that, of the 90 heterogeneous groups formed, there were no significant differences between the number of instances in which the number of one species was greater than, less than, or equal to the number of individuals of the other species in the same grouping (Table 12).

TABLE 10. Results of laboratory behavioral trials showing the total number of individuals in each of the group types formed per treatment. In all treatments except Ovatella juveniles the number of replicates was 5. In the case of Ovatella juveniles the number of replicates was 3. In treatments with no number of individuals indicated the number used was 10, and in those treatments with no age indicated, individuals tested were adults.

Treatment	Solitary	Clustered
Control Treatments:		
Assiminea (20)	21	79
Ovatella (20)	19	81
Ovatella (juveniles) (20)	17	83
Equal Density Treatments:		
Assiminea & Ovatella	17	83
Assiminea & Ovatella (juveniles)	17	83
Unequal Density Treatments:		
Assiminea (20) & Ovatella	22	128
Assiminea (20) & Ovatella (juveniles)	25	125
Assiminea & Ovatella (20)	36	114

TABLE 11. Results of laboratory behavioral trials showing the numbers of individuals in each association type. In treatments with no number of individuals indicated, the number used was 10, and with no age indicated, the individuals tested were adults.

Treatment & Species	Solitary	Clustered Homogeneous	Clustered Heterogeneous
Assiminea & *Ovatella*			
Assiminea	10	2	38
Ovatella	7	4	39
Assiminea & *Ovatella* (juveniles)			
Assiminea	10	4	36
Ovatella	7	2	41
Assiminea (20) & *Ovatella*			
Assiminea	18	26	56
Ovatella	4	7	39
Assiminea (20) & *Ovatella* (juveniles)			
Assiminea	20	29	51
Ovatella	5	9	36
Assiminea & *Ovatella* (20)			
Assiminea	17	3	30
Ovatella	19	32	49

TABLE 12. Results of laboratory behavioral trials showing whether one species contributed more individuals to the heterogeneous groups observed. Groups were designated as to whether they contained more *Assiminea* than *Ovatella* (A > O), more *Ovatella* than *Assiminea* (O > A) or equal numbers of both species (A = O). In treatments with no number of individuals indicated, the number was 10. An asterisk (*) indicates trials in which the *Ovatella* were juveniles.

Treatment	A > O	O > A	A = O
Assiminea & *Ovatella*	6	6	4
Assiminea & *Ovatella**	4	8	5
Assiminea (20) & *Ovatella*	9	3	9
Assiminea (20) & *Ovatella**	9	3	8
Assiminea & *Ovatella* (20)	3	8	5
Total	31	28	31

CHAPTER IV

DISCUSSION

Transect sampling at Metcalf Marsh revealed both vertical and seasonal patterns of abundance in Assiminea, Littorina and Ovatella. All species were characterized by approximately equal densities, with summer highs and winter lows. The native snails, Assiminea and Littorina, displayed higher densities in the low marsh while the introduced species, Ovatella, was more common in the high marsh. This pattern of vertical distribution indicates a negative correlation between native and introduced species. Two hypotheses were tested to explain this pattern. The first was that interspecific interactions between native and introduced species regulate the intertidal distribution of the snails. The second was that physiological constraints limit the intertidal distributions of the three snail species.

In order to test the hypothesis that interspecific interactions were responsible for the observed patterns of zonation, the following experiments were conducted:

1. Observations were made in the field and the laboratory to determine whether there were avoidance

Field observations indicated that Assiminea and Ovatella had a high degree of overlap. From September, 1987 through May, 1988, less than twenty percent of the Littorina were found in quadrats with Ovatella, while approximately sixty percent of the Assiminea were found in quadrats which contained Ovatella. Within all of these heterogeneous quadrats, co-occurrence of the native and introduced snails within one shell length were common.

In order to examine in more detail the apparent lack of avoidance of Ovatella by Assiminea these species were examined in experimental mixtures in the laboratory. Both species are gregarious, and the number of individuals in mixed species groupings outnumbered both solitary individuals and those in single species groupings by an average ratio of 4:1. Neither Assiminea nor Ovatella had a greater tendency to contribute to these mixed species associations. These data, in concert with field observations, provide strong evidence that there is no avoidance between Assiminea and Ovatella.

In similar studies conducted on the east coast of North America, it has been documented that the native snail Ilyanassa obsoleta avoids the introduced Littorina littorea (Brenchley, 1982a, 1982b; Brenchley & Carlton, 1983). Littorina littorea preys heavily upon the eggs of Ilyanassa (Brenchley, 1982a, 1982b; Brenchley & Carlton, 1983). Ilyanassa requires hard substrates upon which to lay eggs; however, many hard substrate areas are densely populated with L. littorea (Brenchley, 1982a, 1982b). An avoidance of Littorina could aid in increased survival of young Ilyanassa.

2. In order to further examine the manner in which the native snails reacted to the presence of introduced snails, field census data were analysed in order to determine the relative proportion of snails on the vegetation versus on the soil surface. In those quadrats containing native species only, as well as those which contained both native and introduced species, all three species were found with equal frequency on the soil surface.

These data indicate that the presence of more than one species type in a quadrat is not correlated with shifts in microhabitat utilization. However, it remains possible that these species are dividing these resources in a more fine-grained manner than these methods would detect. As stated earlier, however, co-occurrence of native and introduced snails is common, and thus spatial separation seems unlikely. These results are similar to those of Fowler (1977a) who was unable to define areas of allopatry between Assiminea and Ovatella at his study site in San

Francisco Bay.

3. In order to determine whether the numbers of native snails increased in the high marsh upon the removal of the introduced species, Ovatella were removed from quadrats in the high marsh zone. Neither Assiminea nor Littorina increased in the high marsh when Ovatella was removed. ALthough this experiment was short term, the results indicate that the presence of Ovatella does not preclude the native species from inhabiting the high marsh.

Perelli (1984) studied interactions between the introduced Littorina littorea and the native L. saxatilis on the east coast of North America. Vertical migrations of the native species in response to the removal of the introduced species were examined. Littorina saxatilis migrated in response to high densities of conspecifics, but not in response to high numbers of L. littorea. Perelli's data provide evidence that there is no strong interaction between these two species.

4. Pairwise T-tests indicate that there were no significant differences in the growth rates within species when placed in single species or pairwise associations with either a native or introduced species. Two potential explanations for these results are that the three species have different diets or that

there is no resource limitation.

5. In order to directly test the hypothesis that the three species showed differences in diets and therefore did not compete for food, I examined the field diets of the three species in both the low and high marsh zones. Chi-Square tests conducted indicate that there was no significant difference between any of the species at either tidal height, within a species between tidal heights or between food availability and its relative abundance in the snail's diet. It therefore appears that the snails are generalists and do not partition this resource.

There are however, limits to this as an estimation of dietary overlap. The data was collected only in one season and may vary intraannually. Further, specific sizes of all dietary items were not measured. However, these results parallel those of Fowler (1977a). He found that the stomach contents and fecal material of Assiminea and Ovatella were virtually identical, except that Ovatella consumed more mud than Assiminea.

Previous studies focusing on deposit feeding gastropods have provided conflicting results as to whether competition occurs (Hairston et al., 1960; Beukema, 1976; Levin et al., 1985; Reise, 1985). Fenchel and Kofoed (1976) examined resource partitioning between large and small species of mud snails. They found that the species may select different size diatoms by choosing to forage in areas with different grain size. Therefore the snails were selecting for sand grain size and a shift in the mean size of diatoms consumed is a result of that selection. Similarly, it has been shown that species can interfere with the feeding of non-conspecifics in a number of ways. First, repeated contact between snails may reduce their ability to forage effectively (Levinton, 1979). Second, differences in size between the species may create situations in which with larger species has the same impact as several of the smaller conspecifics (Levinton, 1979). Third, it has been shown that species differ in the degree to which they turn over the sediments, and that these differences correspond to shifts in microalgal availability and therefore can have an effect of species interactions (Levinton, 1985).

Behrens (1971) studied L. sitkana and L. scutulata on the west coast of North America. She conducted caging experiments and found decreases in growth rate only in the summer and only in those cages which contained numbers of snails which far exceeded normal field densities. Behrens also determined that Littorina feeds on benthic diatoms, and shelter in the same places, and concluded that resource partitioning does not appear to play a role in the coexistence of these species.

Behrens (1974) later studied the intertidal gastropods Littorina scutulata and L. planaxis on the west coast of North America. Littorina planaxis is found higher in the intertidal than its congener L. scutulata. In caging experiments L. planaxis inhibited L. scutulata from living higher in the intertidal; Behrens concluded that this inhibition was probably a result of resource limitation. Littorina scutulata did not prevent L. planaxis from living lower on the shore; other factors likely limit its lower distribution.

Yamada and Mansour (1987) examined the relationship between L. saxatilis and L. littorea. Littorina saxatilis lives higher in the intertidal than L. littorea. They conducted mixed and single species cages at three tidal heights and found that both species grew better in the low zone cages. Littorina littorea decreased the growth rate of L. saxatilis, but L. littorea grew better in the presence of L. saxatilis than when caged with conspecifics. Yamada and Mansour determined that the upper limit of L. littorea seemed to be determined by food scarcity.

In order to examine the alternative hypothesis that physical factors played a critical role in maintaining the vertical distribution patterns observed, two sets of reciprocal transplants were conducted at Metcalf Marsh. For all species in both trials, survival in the control treatments was dramatically higher than those in the experimental treatments.

One alternative explanation for the observed results are that transport and handling of the experimental group was the cause of death and not the new location (Underwood & Denley, 1984). However, both the control and the experimental snails used in this experiment were handled in an identical manner, so this criticism is not likely to be valid.

Another alternative explanation for the higher death rates in the experimental cages was that those animals starved during the 16 day experiment (Underwood & Denley, 1984). Although this has been shown to be important in other systems (Behrens, 1974; Menge 1978a, 1978b; Underwood & Denley, 1984), it is unlikely that it was the major factor contributing to decreased survival in the experiment treatments. Animals starved in the laboratory remained alive for 21 days.

Therefore, the results suggest that some type of physical factor plays a critical role in determining the patterns of distribution of these three snail species in the marsh. The role of physical factors in establishing patterns of vertical distributions is widely discussed (Doty, 1946; Doty & Archer, 1950; Lewis, 1964; Stephenson & Stephenson, 1972; Connell, 1975; Connell & Slatyer, 1977; Underwood, 1979; Menge & Sutherland, 1987).

It appears that the introduced snail, *Ovatella myosotis*, has not altered the distribution or abundance of the native snails, *Assiminea californica* and *Littorina subrotundata*. There is vertical zonation of these species, and physical factors play a critical role in establishing and maintaining these patterns. There is no evidence for interspecific avoidance, or that the native species change their patterns of microhabitat utilization or patterns of vertical zonation when the introduced snail is removed.

There is no evidence that the native and introduced species compete for spatial or trophic resources. All three species are gregarious and large spaces are often covered with snails while other areas are virtually free from these animals (Fowler 1977a; pers. obs.). Diet analyses indicate that resource partitioning does not appear to be present among the species.

It therefore appears that the success of

Ovatella as an introduced species on the Pacific Coast of North America may lie in its ability to tap resources not utilized by the native gastropod species. These resources are space (living higher intertidally than the native gastropod species are able to) and food (which occurs in these high marsh regions).

How can an introduced species be successful if communities are as tightly knit as co-evolutionary theory would suggest (Elton, 1930, 1958; Birch, 1957; MacArthur, 1958, 1972; Hairston, 1959; Connell, 1975; Abrams, 1983)? The answer seems to be that communities, many of them anyway, are not as closely linked as we have come to believe. Some invading species can enter and find non-utilized or underutilized resource axes and can be added to the community matrix without necessarily altering it (Birch, 1979; Simberloff, 1981; Roughgarden, 1986b).

Two major mechanisms have been proposed to explain the coexistence of species. The first is that in order to avoid competitive exclusion species will divide the limiting resources in a fine grained manner (niche separation) (MacArthur, 1958; Macarthur & Levin, 1967; Grant, 1972; Lawlor & Smith, 1976). The second is that anything which interferes with competition contribute to the coexistence of species. Both of these theoretical views may be pertinent to the present study.

The evidence for niche separation among these species comes from two sources. Fowler (1977a) suggested that differences in the structure of the the radula and radular mass is evidence for niche separation between _Assiminea_ and _Ovatella_. The radulae of the two species are similar in tooth number and tooth shape, but not in radular size. The radula of _Assiminea_ is much narrower than that of _Ovatella_. Fowler postulated that _Ovatella_, having a wide radula, scrapes food from broader areas, missing smaller crevices and pits which _Assiminea_ would be able to utilize. It is also possible that the reason _Ovatella_ has had such a small impact upon _Assiminea_ is that these families co-occur throughout the world, and they may therefore be "pre-adapted" for coexistence because of their prior evolutionary history.

There are a number of ways in which different species may use the same resources with little or no effect on the other's distribution and abundance (Connell, 1975; Underwood & Denley, 1984; Roughgarden & Diamond, 1986):

1. The density of one or more of the species may be kept below that at which resources become limiting and that the point at which the effects of

competition would start. Some examples are predation (Paine, 1966; Caswell, 1978; Birch, 1979; Reise, 1985), parasites and pathogens (Birch, 1957, 1979), weather (Birch, 1979; Weins, 1985), and disturbance (Dayton, 1971, 1973, 1975; Egerton, 1973; Connell & Slatyer, 1977; Birch, 1979; Connell & Sousa, 1983; Paine & Levin, 1984; Sousa, 1984, 1985; Denslow, 1985; Weins, 1985; Chesson & Case, 1986).

2. One species may effect the chances that the other species will survive and reproduce; however, the second species has a refuge from which it can recolonize depopulated places (Caswell, 1978; Birch, 1979; Sousa, 1984).

3. One species can effect the probability that the other species will survive and reproduce. However, one species is at an advantage at one time or under certain conditions while the other is at an advantage at another, and therefore the advantages balance out (Connell, 1961, 1975; Birch, 1979; Brenchley & Carlton, 1983; Underwood & Denley, 1984).

Several of the factors outlined above may play a role in the coexistence of these three species. First, the native and introduced species have physical refugia from which they can re-colonize areas from which they have been removed. There is also strong evidence that these species are not resource limited and therefore are likely not subject to the competition-driven mechanisms which often shape community structure and species abundance.

This study of introduced species has shed light on the mechanisms by which invading species are able to succeed in their new environments. How introduced species succeed has been shown to vary between species and between habitats. A large number of generalities, however, have been drawn from a relatively few examples. Most well-known invasions are those pests, which by definition, have a measurable deleterious impact (Elton, 1958; Laycock, 1966; Moyle, 1976; Hedgepeth, 1980; Case et al., 1984). As shown here, however, an introduced species may be successful without leading to major alterations in the existing community.

As the introduction of species into new, and often protected, habitats continues, it seems particularly important to continue studies of introduced species in order to ascertain whether or not a pattern exists which enables certain species to be successful invaders (Baker, 1965; Lewontin, 1965) and other habitats to be susceptible to invasion (Paine & Levin, 1981; Diamond & Case, 1986b; Fox & Fox, 1986;

Orians, 1986; Moutlton & Pimm, 1986; Vitousek, 1987; Pimm, 1987). Discerning this pattern should prove important not only to ecological theory, but also to conservation and management questions alike (Regier, 1968; Lachner et al., 1970; Hocutt, 1984; Kohler & Stanley, 1984; Fox & Fox, 1986). Without improved information we can neither understand nor reliably predict what the result of future human impacts on the natural world will be.

APPENDIX A

Measurements of tidal height of transect lines at Metcalf marsh. Measurements were taken at three meter intervals along the transect lines and values are in Cm above datum. Values marked with an asterisk are those in which the sample was 2, in all others the sample size was 3.

Zone	Station Number	Mean Tidal Height	Standard Deviation
Terrestrial	1	274.03	11.56
High Marsh	2	221.83	18.02
	3	211.66	8.92
	4	209.97	10.26
	5	207.43	7.60
	6	209.97	6.39
	7	210.82	11.07
	8	215.90	9.16
	9	210.82	4.34
	10	204.04	1.47
	11	204.04	6.39
	12	200.66	5.08
	13*	199.81	5.29
	14*	199.39	1.80
Low Marsh	15	186.69	1.80
	16	173.99	1.80
	17	177.84	3.59
Mudflat	18	167.69	6.75

APPENDIX B

Mean number of snails observed per quadrat at each tidal height. Number of observations (quadrats) for terrestrial (Land) was 3, for the high marsh (High) 16, for the low marsh (Low) 6 and for the mudflat (Mud) 3. Standard deviation values are given in parentheses.

Date	Tidal Level	Littorina	Assiminea	Ovatella
5/15/87	Land	0	0	0
	High	0.7 (1.1)	2.1 (2.7)	5.4 (5.1)
	Low	15.2 (12.1)	4.5 (3.4)	0.7 (1.6)
	Mud	0	0	0
5/28/87	Land	0	0	0
	High	1.3 (2.5)	2.6 (2.6)	4.1 (3.6)
	Low	13.2 (9.0)	5.7 (3.7)	1.2 (2.9)
	Mud	0	0	0
6/13/87	Land	0	0	0
	High	0.9 (1.5)	1.8 (2.2)	6.5 (7.9)
	Low	15.1 (9.6)	4.3 (3.8)	1.3 (2.9)
	Mud	0	0.3 (0.6)	0
6/25/87	Land	0	0	0
	High	1.5 (2.2)	2.0 (2.2)	4.8 (3.9)
	Low	12.3 (4.9)	2.3 (1.2)	0.2 (0.4)
	Mud	0	0	0
7/9/87	Land	0	0	0
	High	1.2 (2.1)	2.2 (2.5)	8.6 (6.1)
	Low	12.3 (4.9)	8.7 (6.4)	0
	Mud	0	0	0
7/23/87	Land	0	0	0
	High	2.6 (4.2)	4.4 (4.4)	10.9 (8.3)
	Low	18.5 (6.1)	15.8 (4.2)	0
	Mud	0	0	0
8/4/87	Land	0	0	0
	High	5.4 (7.0)	7.4 (6.9)	14.5 (9.6)
	Low	25.5 (12.4)	18.7 (7.2)	0
	Mud	0	0	0
8/20/87	Land	0	0	0
	High	2.9 (4.5)	4.4 (3.7)	9.6 (4.9)
	Low	17.7 (4.4)	1.2 (1.7)	0
	Mud	0	0	0

APPENDIX B

(Continued) Mean number of snails observed per quadrat at each tidal height. Number of observations (quadrats) for terrestrial (Land) was 3, for the high marsh (High) 16, for the low marsh (Low) 6 and for the mudflat (Mud) 3. Standard deviation values are given in parentheses.

Date	Tidal Level	Littorina	Assiminea	Ovatella
12/18/87	Land	0	0	0
	High	0.6 (1.3)	1.1 (1.3)	2.9 (2.6)
	Low	4.0 (2.3)	1.7 (1.7)	0
	Mud	0	0	0
1/1/88	Land	0	0	0
	High	0.2 (0.6)	0.7 (1.5)	0.1 (0.5)
	Low	4.8 (4.7)	4.2 (4.7)	0.2 (0.4)
	Mud	0	0	0
2/5/88	Land	0	0	0
	High	0.6 (1.3)	1.6 (2.1)	1.8 (2.5)
	Low	4.7 (3.1)	2.7 (2.7)	0.3 (0.8)
	Mud	0	0	0
2/18/88	Land	0	0	0
	High	1.2 (1.9)	2.8 (1.9)	4.1 (3.2)
	Low	3.5 (2.5)	3.2 (1.9)	0
	Mud	0	0	0
3/5/88	Land	0	0	0
	High	2.1 (4.9)	2.8 (2.3)	4.6 (4.7)
	Low	3.3 (1.5)	7.0 (4.3)	0
	Mud	0	0	0
3/19/88	Land	0	0	0
	High	2.9 (4.5)	4.9 (3.8)	5.3 (4.3)
	Low	5.7 (1.4)	6.0 (3.3)	0
	Mud	0	0	0

APPENDIX B

(Continued) Mean number of snails observed per quadrat at each tidal height. Number of observations (quadrats) for terrestrial (Land) was 3, for the high marsh (High) 16, for the low marsh (Low) 6 and for the mudflat (Mud) 3. Standard deviation values are given in parentheses.

Date	Tidal Level	Littorina	Assiminea	Ovatella
4/3/88	Land	0	0	0
	High	2.3 (4.2)	4.9 (3.6)	5.4 (3.8)
	Low	7.8 (1.7)	7.7 (4.5)	0
	Mud	0	0	0
4/14/88	Land	0	0	0
	High	1.9 (3.6)	4.0 (4.1)	6.3 (4.0)
	Low	6.8 (1.6)	4.0 (1.4)	0.5 (1.2)
	Mud	0	0	0
5/1/88	Land	0	0	0
	High	0.9 (1.5)	2.1 (1.6)	5.0 (4.0)
	Low	13.3 (11.4)	4.2 (3.4)	0.5 (1.2)
	Mud	0	0	0
5/27/88	Land	0	0	0
	High	0.9 (1.9)	2.7 (2.5)	6.3 (4.2)
	Low	16.2 (6.0)	7.5 (1.6)	0.5 (1.2)
	Mud	0	0	0

APPENDIX C

Mean number of snails per quadrat examined by tidal height and season. Standard deviation values are given in parentheses.

Season	N	Tidal Height	Littorina	Assiminea	Ovatella
Spring	128	High	1.6 (3.3)	3.2 (3.1)	5.3 (4.1)
	48	Low	10.1 (7.9)	5.8 (3.4)	0.4 (1.3)
Summer	95	High	2.4 (4.2)	3.7 (4.3)	9.1 (7.5)
	37	Low	16.8 (8.4)	8.8 (7.5)	0.2 (1.3)
Fall	112	High	0.4 (1.1)	2.3 (3.0)	6.6 (5.6)
	42	Low	4.9 (4.3)	1.1 (1.6)	0.5 (1.7)
Winter	80	High	0.6 (1.2)	1.7 (2.1)	2.1 (2.7)
	30	Low	4.1 (2.9)	2.6 (2.6)	0.1 (0.4)

APPENDIX D

Comparison of arsine transformed percent cover estimates between large (1 meter) rakes used outside quadrats and small (15 centimeter) rakes used within sampling quadrats and cages. Standard deviation values are given in parentheses.

Species	Site	Tidal Level	Arcsine Percent Cover Large Rake	Arcsine Percent Cover Small Rake
Salicornia virginica	Metcalf	Land	0	0
		High	0.6 (0.3)	0.6 (0.3)
		Low	0.4 (0.2)	0.4 (0.2)
		Mud	0	0
	S. Slough		0.7 (0.1)	0.7 (0.1)
Distichlis spicata	Metcalf	Land	0	0
		High	0.6 (0.3)	0.6 (0.3)
		Low	0.8 (0.2)	0.8 (0.2)
		Mud	0.1 (0.2)	0.0 (0.1)
	S. Slough		0.7 (0.1)	0.7 (0.1)
Grindelia integrifolia	Metcalf	Land	0.4 (0.2)	0.4 (0.2)
		High	0.0 (0.1)	0.0 (0.1)
		Low	0	0
		Mud	0	0
	S. Slough		0	0
Jaumea carnosa	Metcalf	Land	0.2 (0.2)	0.2 (0.1)
		High	0.1 (0.2)	0.1 (0.2)
		Low	0	0
		Mud	0	0
	S. Slough		0.1 (0.1)	0.1 (0.1)
Triglochin maritima	Metcalf	Land	0	0
		High	0.1 (0.2)	0.0 (0.2)
		Low	0	0
		Mud	0	0
	S. Slough		0	0

APPENDIX E

Plant species found in the Metcalf and South Slough marshes. If the plant does not occur at the site it is marked with an asterisk if it does occur at the site, it is weighted as rare (> 1 percent cover), common (1 to 10 percent cover) or abundant (< 10 percent cover).

Scientific Name	Common Name	Metcalf Marsh	South Slough
Atriplex patula	Salt Bush	R	R
Carex lyngbei	Lyngby's Sedge	C	R
Cordylanthus maritima	Salt Marsh Bird's Beak	C	*
Cuscuta salina	Salt Marsh Dodder	C to A	C to A
Deschampsia caespitosa	Tufted Hairgrass	R	R
Distichlis spicata	Salt Grass	A	A
Enteromorpha sp.		C	C
Fucus sp.		C	R
Graminaceae	Grasses	C	C
Grindelia integrifolia	Gumweed	C	R
Hordeum brachyantherum	Meadow Barley	R	C
Jaumea carnosa	Fleshy Jaumea	C	C

APPENDIX E

(Continued) Plant species found in the Metcalf and South Slough marshes. If the plant does not occur at the site it is marked with an asterisk if it does occur at the site, it is weighted as rare (> 1 percent cover), common (1 to 10 percent cover) or abundant (< 10 percent cover).

Scientific Name	Common Name	Metcalf Marsh	South Slough
Juncus sp.	Rushes	R	R
Lathyrus sp.	Sweet Pea	R	*
Oenanthe sarmentosa	Water Parsley	R	R
Orthocarpus castillejoides	Owl's Clover	R	*
Percusaria		C	C
Plantago maritima	Seaside Plantain	R	R
Potentilla pacifica	Pacific Silverweed	R	R
Rumex sp	Dock	R	*
Ruppia maritima		R	R
Salicornia virginica	Pickleweed	A	A
Scirpus americanus	American Bulrush	R	R
Spergularia marina	Sand Spurry	R	R

APPENDIX E

(Continued) Plant species found in the Metcalf and South Slough marshes. If the plant does not occur at the site it is marked with an asterisk if it does occur at the site, it is weighted as rare (> 1 percent cover), common (1 to 10 percent cover) or abundant (< 10 percent cover).

Scientific Name	Common Name	Metcalf Marsh	South Slough
Triglochin maritima		C	C
Ulva sp.		C	C

APPENDIX F

Total number of *Littorina* (L), *Assiminea* (A) and *Ovatella* (O), found in the five experimental quadrats located in the high zone of Metcalf Marsh. In the experimental treatment the values from July 9 represent the density prior to any removal and are not included in the calculations.

	Control			Experimental		
Date	L	A	O	L	A	O
7/9/87	0	2	100	0	1	88
7/10/87	0	0	82	0	2	5
7/11/87	0	1	105	0	1	6
7/12/87	0	1	96	0	1	4
7/13/87	0	1	75	0	2	3
7/14/87	0	1	89	0	2	6
7/15/87	0	2	91	0	0	6
7/16/87	0	1	76	0	2	5
7/17/87	0	1	69	0	1	7
7/18/87	0	2	78	0	2	3
7/19/87	0	1	74	0	3	5
7/20/87	0	1	83	0	2	4
7/21/87	0	2	94	0	0	5
7/22/87	0	2	99	0	0	3
7/23/87	0	0	79	0	1	2

LITERATURE CITED

Abbott, R. 1958. The gastropod genus Assiminea in the Phillipines. Proc. Nat. Acad. of Sci. Philadelphia 110:213-278.

Abrams, P. 1983. The theory of limiting similarity. Ann. Rev. Ecol. System 14:359-376.

Allen, F. 1953. Distribution of marine invertebrates by ships. Aust. J. Mar. Freshwater Res. 4:307-316.

Baker, H. 1965. Characteristics and modes of the origins of weeds. In H. Baker and G. Stebbins (eds.), The Genetics of Colonizing Species. Academic Press, New York.

Baranowski, W. 1971. New northern extension of the range of Assiminea modesta. Nautilus 84:143-144.

Behrens, S. 1971. Distribution and abundance of the intertidal prosobranch snails Littorina scutulata and Littorina sitkana. Masters Thesis. University of British Columbia, Vancouver.

Behrens, S. 1974. Ecological interactions of three Littorines (Gastropoda Prosobranchia) along the western coast of North America. Ph.D. Diss. University of Oregon, Eugene.

Bertness, M. 1984. Habitat and community modification by an introduced herbivorous snail. Ecology 65:370-381.

Beukema, J. 1976. Biomass and species richness of the macrobenthic animals living in the tidal flats of the Dutch Wadden Sea. Nether. J. Sea Res. 10:236-261.

Birch, L. 1957. The meanings of competition. Amer. Natur. 91:5-18.

Birch, L. 1979. The effects of species of animals which share common resources on one anothers distribution and abundance. Fortschritte der Zooligie 25:197-221.

Carlton, J. 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean. Bull. Mar. Sci. 41:452-465.

Carlton, J. 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. Conserv. Bio. (In press).

Carlton, J. and B. Roth (1975). Phylum Mollusca: Shelled gastropods. In R. Smith and J. Carlton (eds.), Lights Manual. University of California Press, Berkeley.

Caswell, H. 1978. Predator-mediated coexistence: A non-equilibrium model. Amer. Natur. 112:127-154.

Chesson, P. and T. Case. 1986. Overview: Nonequilibrium community theories: Chance, variability, history and coexistence. In J. Diamond & T. Case (eds.), Community Ecology. Harper and Row, New York.

Clarke, B. et al. 1984. The extinction of endemic species by a program of biological control. Pac. Sci. 38:97-104.

Connell, J. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42:710-723.

Connell. J. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. In M. Cody and J. Diamond (eds.), Ecology and Evolution of Communities. The Belknap Press of Harvard University Press, Cambridge.

Connell, J. and R. Slayter. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Natur. 111: 1119-1144.

Connell, J. and W. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. Amer. Natur. 121:789-824.

Cooper, J. 1872. On new California pulmonata. Proc. Nat. Hist. Soc. Philadelphia 24:143-154

Cooper, J. 1886. On fossil and sub-fossil land shells of the United States with notes on living species. Bull. California Acad. Sci. 1:235-255.

Dayton, P. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Mono. 41:351-389.

Dayton, P. 1975. Experimental evaluation of ecological dominance in a rocky intertidal community. Ecol. Mono. 45:137-159.

Denslow, J. 1985. Disturbance-mediated coexistence of species. In S. Pickett and P. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Diamond, J. and T. Case. 1986b. Overview: Introductions, extinctions, exterminations and invasions. In J. Diamond and T. Case (eds.), Community Ecology. Harper and Row, New York.

Doty, M. 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific Coast. Ecology 27:315-328

Doty, M. and J. Archer. 1950. An experimental test of the tide factor hypothesis. Amer. J. Bot. 37:458-464.

Druehl, L. 1973. Marine transplantations. Science 179: 12.

Duggan, E. 1963. Report of non-indigenous marine shells collected in the state of Washington. Veliger 6:112.

Egerton, F. 1973. Changing concepts of the balance of nature. Quart. Rev. Biol. 48:322-350.

Ellis, A. 1926. British Snails: A Guide to the Non-Marine Gastropoda of Great Britain and Ireland. Clarendon Press, Oxford.

Elton, C. 1930. Animal Ecology and Evolution. Clarendon Press, Oxford.

Elton, C. 1958. The Ecology of Invasions by Animals and Plants. Chapman and Hall, London.

Fenchel, T. and L. Kofoed. 1976. Evidence for competition in mud snails (Hydrobiidae). Oikos 27:367-376.

Fortun, A. et al. 1981. The population structure of Assiminea grayana Fleming 1928 (Gastropoda: Assimineidae) in the southwest Netherlands. Basteria 45:73-78.

Fowler, B. 1976. Reproductive biology of Assiminea californica (Mesogastropoda: Rissoacea) in the salt marshes of Palo Alto. West. Soc. Natur. Ann. Rep. 9:40.

Fowler, B. 1977a. Biology and life history of the salt marsh snail Assiminea californica (Tryon 1865). Masters Thesis, San Jose State University, San Jose.

Fowler, B. 1977b. Reproductive biology of Assiminea californica (Tryon 1865). Veliger 23:163-168.

Fox, M. & B. Fox. 1986. The susceptablility of natural communities to invasion. In H. Mooney and J. Drake (eds.), The Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.

Fretter, V. and A. Graham. 1978. The prosobranch molluscs of Britain and Denmark. J. Moll. Stud. 5: 1-175.

Gould, A. 1870. Report on the Invertebrates of Massachussets, Second Edition, Composing the Mollusca. Wright and Potter, State Printers, Boston.

Grant, P. 1972. Interspecific competition among rodents. Ann. Rev. Ecol. System. 3:79-106.

Groves, R. and J. Burdon (eds.). 1986. Ecology of Biological Invasions. Cambridge University Press, Cambridge.

Hairston, N. 1959. Species abundance and community organization. Ecology 40:404-416.

Hairston, N. et al. 1960). Community structure, population control and competition. Amer. Natur. 94: 421-425.

Hanna, G. 1966. Introduced mollusks of western North America. Occas. Pap. California Acad. Sci. 48:1-108.

Hedgpeth, J. 1962. Introduction to Seashore Life of the San Francisco Bay Region and the Coast of Northern California. University of California Press, Berkeley.

Hedgpeth, J. 1980. The problem of introduced species in management and mitigation. Hegolander Meeresunters 33:662-673.

Hemphill, H. 1877. Presidents address. Proc. California Acad. Sci. 7:48-49.

Hocutt, C. 1984. Towards the development of an environmental ethic for exotic fishes. In S. Courtenay and J. Stauffer (eds.), The Distribution and Management of Exotic Fishes. The Johns Hopkins University Press, Baltimore.

Hoffnagle, J. et al. 1976. A Comparitive Study of Salt Marshes in the Coos Bay Estuary. (National Science Foundation Student Originated Studies). Oregon Institute of Marine Biology, Charleston, Oregon.

Jorgensen, N. 1971. En sjaelden landsnegl: Ovatella myosotis (Drapaurnaud 1805). Flora og Fauna 77: 113-115.

Keen, A. 1970. Western marine mollusks. Malacologia 10:51-52.

Kohler, C. and J. Stanley. 1984. A suggested protocol for evaluating proposed exotic fish introductions in the United States. In S. Courtenay and J. Stauffer (eds.), Distribution, Biology and Management of Exotic Fishes. The Johns Hopkins University Press, Baltimore.

Lachner, E. et al. 1970. Exotic fishes and other aquatic introductions into North America. Smith. Cont. Zoology 59:1-29.

Lasenby, C. et al. 1986. Theory, practice and effects of Mysis relicta introductions to North American and Scandanavian lakes. Can. J. Fish. Aqua. Sci. 43: 1277-1284.

Lawlor, L. and J. Smith. 1976. The coevolution and stability of competing species. Amer. Natur. 110:79-99.

Laycock, G. 1966. The Alien Animals. Natural History Press, Garden City.

Levinton, J. 1979. The effect of density on deposit-feeding populations: feeding and floating of Hydrobia ventrosa Montague (Gastropoda: Prosobranchia). Oecologia 43:27-39.

Levinton, J. 1985. Complex interactions of a deposit feeder with its resources. 2. Roles of density, a competitor, and detrital addition in the growth of the mud snail Hydrobia totteni. Mar. Ecol. Prog. Ser. 22:31-40.

Levinton, J. et al. 1985. Complex interactions of a deposit feeder with its resources. 2. Field and laboratory experiments on interference between Hydrobia totteni and Ilyanassa obsoleta (Gastropoda) and its possible relationship to seasonal shifts in zonation on mud flats. Mar. Ecol. Prog. Ser. 22: 53-58.

Lewis, J. 1964. The Ecology of Rocky Shores. English Universities Press, London.

Lewontin, R. 1965. Selection for colonizing ability. In H. Baker and G. Stebbins (eds.), The Genetics of Colonizing Species. Academic Press, New York.

Lidicker, W. and P. Anderson. 1962. Colonization of an island by Microtus californicus, analysed on the basis of runway transects. J. Anim. Ecol. 31:503-517.

Lidicker, W. 1966. Ecological observations on a feral house mouse population declining to extinction. Ecol. Mono. 36:27-50.

Little, C. and E. Andrews. 1977. Some aspects of excretion and osmoregulation in assimineid snails. J. Moll. Stud. 43:263-285.

MacArthur, R. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

MacArthur, R. 1972. Geographical Ecology: Patterns in the Distribution of Species. Princeton University Press, Princeton.

MacArthur, R. and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. Amer. Natur. 101:377-385.

MacDonald, K. 1969a. Quantitive studies of salt marsh mollusk faunas from the North American Pacific coast. Ecol. Mono. 39:33-60.

MacDonald, K. 1969b. Molluscan faunas of Pacific Coast salt marshes and tidal creeks. Veliger 11:399-405.

Menge, B. 1978a. Predation intensity in a rocky intertidal community: relation between predator foraging activity and environmental harshness. Oecologia 34: 1-16.

Menge, B. 1978b. Predation intensity in a rocky intertidal community: effect of an algal canopy, wave action and desiccation on predator feeding rates. Oecologia 34:17-35.

Menge, B. and J. Sutherland 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Amer. Natur. 30:730-757.

Meyer, K. 1955. Naturgeschichte der Strandschnecke Ovatella mysotis (Draparnaud). Archive fur Molluskenkunde 84:1-43.

Morgan, M. et al. 1978. Impact of the introduction of Kokanee (Oncorhynchus nerka) and opossum shrimp (Mysis relicta) on a subalpine lake. J. Fish. Res. Board Can. 35:1752-1579.

Moyle, P. 1976. Fish Introductions in California: History and impact on native fishes. Biol. Conserv. 9:101-118.

Moulton, M. and S. Pimm. 1986. Species introductions to Hawaii. In H. Mooney and J. Drake (eds.), Ecology of Biological Invasions of North America and Hawaii. Springer-Verglag, New York.

Nichols, F. and J. Thompson. 1985. Persistence of an introduced mudflat community in south San Francisco Bay, California. Mar. Ecol. Prog. Ser. 24:83-97.

Orians, G. 1986. Site characteristics favoring invasions. In H. Mooney and J. Drake (eds.) Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.

Paine, R. 1966. Food web complexity and species diversity. Amer. Natur. 100:65-75.

Paine, R. and S. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecology 51:145-178.

Paulson, E. 1957. Taxonomy of a salt marsh snail, Ovatella myosotis, in central California. Nautilus 71:4-7.

Perelli, L. 1984. Effects of Littorina littorea densities on growth and height distributions of L. saxatilis in the Great Sippewisset salt marsh. (Unpublished manuscript).

Pimm, S. 1987. Determining the effect of introduced species. Trends Ecol. Evol. 2:106-108.

Race, M. 1982. Competitive displacement and predation between introduced and native mud snails. Oecologia 54:337-347.

Regier, H. 1968. The potential misuse of exotic fish as introductions. Ontario Dept. Land Forest 82:92-111.

Reise, K. 1985. Tidal Flat Ecology: An Experimantal Approach to Species Intercations. Springer-Verlag, Berlin.

Roughgarden, J. 1986a. A comparison of food-limited and space-limited animal competition communities. In J. Diamond and T. Case (eds.), Community Ecology. Harper and Row, New York.

Roughgarden, J. 1986b. Predicting invasions and rates of spread. In H. Mooney and J. Drake (eds.), The Ecology of Biological Invasions in North America and Hawaii. Springer-Verlag, New York.

Roughgarden, J. and J. Diamond. 1986. Overview: the role of species interactions in community ecology. In J. Diamond and T. Case (eds.), Community Ecology. Harper and Row, New York.

Rudy, P. and Rudy, L. 1983. Oregon Estuarine Invertebrates: An Illustrated Guide to the Common and Important Invertebrate Animals. U.S. Fish and Wild. Serv. Cont. No. 79-111.

Seeleman, U. 1968. Zur Uberwindung der Biologischen Grenze Meer land durch Mollusken. Oecologia 1: 130-154.

Simberloff, D. 1981. Community effects of introduced species. In T. Nitecki (ed.), Biotic Crises in Ecological and Evolutionary Time. Academic Press, New York.

Smith, A. 1951. Assiminea grayana (Fleming) in the Humber. J. Conch. 23:134.

Sousa W. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65:1918-1935.

Stephenson. T. and A. Stephenson. 1972. Life Between Tidemarks on Rocky Shores. W.H. Freeman, San Francisco.

Talmadge, R. 1962. Random notes on Littorina newcombiana. Amer. Malacol. Union 29:29.

Taylor, D. 1981. Freshwater mollusks of California: A distributional checklist. California Fish Game 67:140-163.

Underwood, A. 1979. The ecology of intertidal gastropods. Adv. Mar. Bio. 16:111-210.

Underwood, A. and E. Denley. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In D. Strong, et al. (eds.), Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton.

Vitousek, P. et al. 1987. Introduced species in Hawaii: Biological effects and opportunities for ecological research. Trends Ecol. Evol. 2:224-227.

Weins, J. 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. In S. Pickett and P. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Yamada, S. and R. Mansour 1987. Growth inhibition of native *Littorina saxatilis* by introduced *L. littorea*. J. Exp. Mar. Biol. Ecol. 105:187-196.

Zaret, T. and R. Paine. 1973. Species introductions in a tropical lake. Science 182:449-455.