Title

The Effects of the Introduced Mussel, Musculista senhousia, and Other Anthropogenic Agents on Benthic Ecosystems of Mission Bay, San Diego

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UNIVERSITY OF CALIFORNIA, SAN DIEGO

The Effects of the Introduced Mussel, *Musculista senhousia*, and Other Anthropogenic Agents on Benthic Ecosystems of Mission Bay, San Diego

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Oceanography

by

Jeffrey A. Crooks

Committee in charge:

Professor Lisa Levin, Chair
Professor Paul Dayton
Professor James Enright
Professor John Largier
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1998

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1998

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This dissertation is composed of chapters that represent papers prepared for publication in the scientific literature. The text of Chapter 2 is being prepared for submission to Conservation Biology, and I am the primary researcher and sole author of this paper. The text of Chapter 3 has been submitted for publication to Marine Ecology Progress Series, and I am the secondary researcher and have co-authored the paper with Deborah Dexter . The text of Chapter 4 is in press for the book Invasive Species and Biodiversity Management, and I am the primary researcher and have co-authored the paper with Michael Soulé. The text of Chapter 5 has been published in Marine Ecology Progress Series, and I am the primary researcher and sole author of that paper. The text of Chapter 6 has been submitted to Journal of Experimental Marine Biology and Ecology, and I am the primary researcher and have co-authored the paper with Hugh Khim.

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ABSTRACT OF THE DISSERTATION

The Effects of the Introduced Mussel, *Musculista senhousia*, and other Anthropogenic Agents on Benthic Ecosystems of Mission Bay, San Diego

by

Jeffrey A. Crooks

Doctor of Philosophy in Oceanography

University of California, San Diego, 1998

Professor Lisa A. Levin, Chair

Over the past 150 years, Mission Bay, San Diego, has undergone a variety of changes that have affected benthic ecosystems. River diversion, dredging, filling, over-harvesting, pollution, and the introduction of exotic species have greatly altered bivalve assemblages in the bay. A gradient of flushing and organic enrichment also has been established by patterns of circulation and input of urban runoff. This results in relatively depauperate macrofaunal communities in the poorly-flushed back bay, peaks of abundance mid-bay, and high species richnesses in the mid-bay and nearer the mouth.

One of the most striking changes in Mission Bay has been the invasion of a small, Asian mussel, *Musculista senhousia*. This mytilid, which often forms byssal mats on intertidal and soft sediments, was first found at least two decades before it came to dominate portions of the bay, highlighting that a lag may exist between the invasion and subsequent population explosion of invasive species. The invasion of *M. senhousia* can be viewed both as a consequence and a cause of ecological change. As is often observed in urbanizing systems, anthropogenic changes, coupled with increases in the global movement of species, probably have made Mission Bay more vulnerable to invasion and may account for an increased rate of appearance of exotics over the last two decades.

Musculista senhousia can cause ecological changes by its physical alteration of the benthos. A variety of small macrofauna are found within natural mussel mats at higher densities than adjacent, mat-free sediments. Manipulative experiments using artificial mussel mats, living mussels, and mussel mimics suggest that the presence of the physical structure alone can explain much of this facilitation, although the biological activities of living mussels do affect some taxa. The effects of the mats are scale-dependent, however. Competition experiments demonstrate that the growth and survivorship of large, surface-dwelling, suspension-feeding clams are inhibited by *M. senhousia*. These experiments suggest that *M. senhousia* may have contributed to observed changes within a remnant salt marsh system (Northern Wildlife Preserve). Rapid colonization of a newly-created mitigation site could affect ongoing restoration efforts in this marsh.

CHAPTER I

INTRODUCTION

The estuarine ecosystems of San Diego County, which include bays, lagoons, and true estuaries, are potentially rich biological environments that exist at the interface of marine, freshwater, and terrestrial habitats. These are naturally variable systems that experience a wide range of physical conditions, and because they occur in a densely populated region, they are subjected to a variety of anthropogenic threats. Habitat loss and modification have been widespread, and many intertidal wetlands have been lost (Marcus 1989; Zedler 1996). This is especially true in the highly modified coastal lagoon, Mission Bay. Relatively high pollution loads also characterize the region. San Diego Bay represents one of the most polluted embayments in the nation, with high levels of toxic chemicals, pesticides, and heavy metals, although conditions are improving (O'Connor and Beliaeff 1995). Mission Bay and Tijuana Estuary, as well as San Diego Bay, also can receive high loads of organic pollution (Marcus 1989). One of the most serious threats to the biotic integrity of San Diego's coastal systems is the invasion of non-indigenous species.

A preliminary literature survey indicates that at least 58 marine species have invaded San Diego County (Table 1-1). These species span a wide variety of taxa, and can be found in benthic, fouling, and water column habitats. Most species appear to be confined to the coastal embayments and lagoons, although several species (e.g., the nudibranch *Catriona rickettsi* and the algae *Sargassum muticum*) can be found on the outer coast. The rate of introduction of these exotic species into San Diego appears to be increasing, with almost half of the known invaders appearing since 1970 (Fig. 1-1). Although this pattern, which is quite similar to that found for San Francisco Bay, may be partially accounted for by a recent interest in studying invasions by non-native species, there can be little doubt that there are higher rates of invasion in these systems due to global increases in the volume and efficiency of vectors of introduction (Cohen and Carlton 1998). In addition to the marine exotics, a number of exotic species of non-marine origin are found in San Diego's coastal wetlands. These include mammals (e.g., rats, house mice, opossums, and cats), fish (e.g., carp, threadfin shad, and golden shiner), and a host of upland transition zone plants (e.g., ice plant, brass buttons, and sea rockets).

The study of exotic species has ecological relevance from two broad perspectives. First, a biological invasion is a natural process, and the study of invasions and the role of invasive species can provide insight into the structure and function of ecological communities (Moyle and Light 1996; Vitousek et al. 1997). With this increased interest in introduced species, the emerging field of invasion biology is making advances and contributing to our understanding of ecological systems (Lewin 1987; Lodge 1993). However, the field is still in its infancy (Townsend 1991; Kareiva 1996; Vermeij 1996), and many of the general ideas that are developing have a decidedly terrestrial bias (e.g., DiCastri 1990; Caughley and Gunn 1996; Hunter 1996; Meffe and Carroll 1997). Examination of invaders in marine systems can therefore help to generalize the field of invasion biology. The second perspective involves the conservation concerns that arise when considering exotic species. There is currently an unprecedented movement of species around the world (Cairns and Bidwell 1996; Vitousek et al. 1997). The effects of some invaders are obviously negative (e.g., zebra mussels and Africanized bees), while some appear to have neutral or even positive effects. However, for the vast majority of invaders we know very little (Williamson 1996; Ruiz et al. 1997; Vitousek et al. 1997).

This thesis explores synecological dynamics and changes occurring in soft-bottom benthic macrofaunal communities of Mission Bay, San Diego, emphasizing the invasion of the exotic, mat-forming mussel *Musculista senhousia*. In the thesis, consideration of patterns and processes in the bay progresses from relatively large spatial (bay-wide) and temporal scales (decades) to small-scale interactions that take place in a matter of weeks in small patches on a tidal flat. Chapter 2 describes the historical ecology of Mission Bay and examines long-term changes in that ecosystem in relation to changes in the bivalve fauna. In addition, interspecific interactions between the invasive mussel *M. senhousia* and three native clam species are examined using manipulative experimentation. On shorter-time scales, Chapter 3 describes how the subtidal benthic community of Mission Bay has varied over the course of the past 20 years along a gradient of flushing. One of the most striking changes in the soft sediment habitats in the bay has been the invasion of *M. senhousia*. Although this species was first recorded in the 1960's (MacDonald 1969), it was not until the 1990's that extremely high densities of the mussel were reported. This general issue of lag times related to biological invasions is addressed in Chapter 4. The synecological effects of *M. senhousia* on smaller spatio-temporal scales (one tidal flat examined over four years) are assessed in Chapter 5 by comparing areas with and without naturally occurring mats as well as by comparing the same tidal flat at times when mats are present to times when mats are absent. The effects of physical structure created by the mussel are assessed by comparing infaunal colonization of plots with and without artificial mats. The interactions between mussels, their mats, and colonizing biota are expanded upon in Chapter 6, which compares the relative effects of physical habitat creation by *M. senhousia* to the effects of biological activities of living mussels.

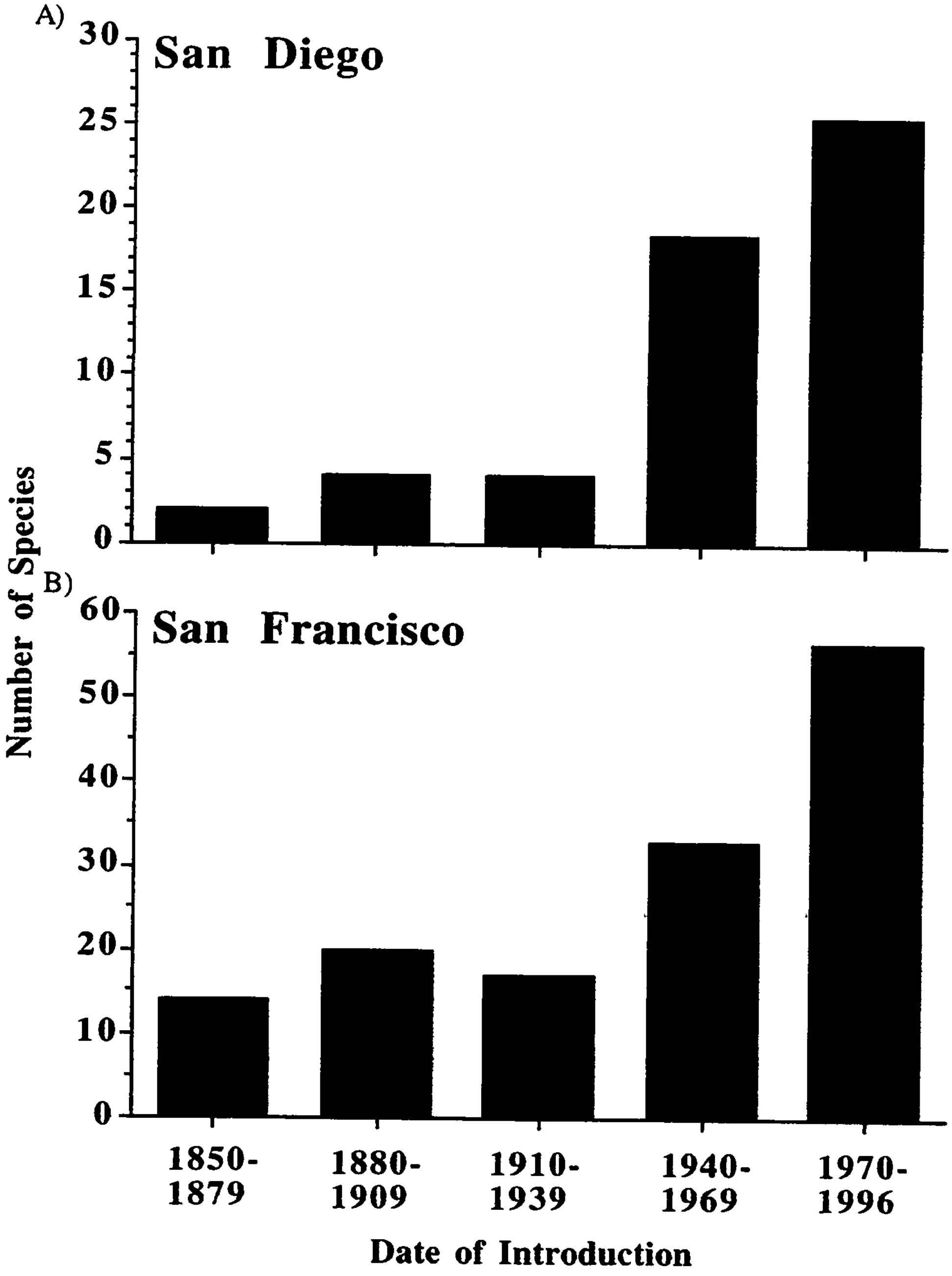

Figure 1-1. Date of first record of exotic marine species in a) San Diego and b) San Francisco. See also Table 1-1. San Francisco data from Cohen and Carlton (1995).

Table 1-1. Marine exotic species reported in San Diego. Sources include Carlton 1979, Fleminger and Kramer 1988, MacDonald et al. 1990, Takahashi 1992, Cohen and Carlton 1995, SCAMIT 1996, Sewell 1996, Zedler 1996, Fairey et al. 1997, and Lambert and Lambert 1998.

Species	Source Region
Plants	
Avicennia marina	New Zealand
Algae	
Sargassum muticum	Japan
Ciliates	
Lobochona prorates	?
Cnidarians	
Anemones	
Bunodeopsis sp.	Gulf of California?
Diadumene lineata	Japan
Hydrozoans	
Tubularia crocea	NW Atlantic
Annelids	
Oligochaetes	
Tubificoides brownea	N Atlantic
Polychaetes	
Hydroides elegans	Indo-Pacific
Lycatopsis pontica	?
Neanthes acuminata (= *caudata*)	?
Pseudopolydora paucibranchiata	Japan ?
Streblospio benedicti	Atlantic
Crustaceans	
Copepods	
Pseudodiaptomus marinus	E. Asia
Ostracods	
Aspidoconcha limnoriae	?
Redekea californica	?
Amphipods	
Corophium acherusicum	?
Corophium heteroceratum	China
Corophium uenoi	Japan
Grandidierella japonica	Japan
Jassa marmorata (= *falcata*)	NW Atlantic
Stenothoe valida	?
Isopods	
Iais californica	Australasia
Limnoria tripunctata	?
Limnoria quadripunctata	?
Sphaeroma quoyanum	Australasia
Sphaeroma walkeri	N Indian Ocean
Barnacles	
Balanus amphitrite	Indian Ocean
Decapods	
Palaemon macrodactylus	E. Asia
Molluscs	
Gastropods	
Babakina festiva	Japan
Catriona rickettsi	Japan
Bivalves	
Lyrodus pedicellatus	?
Mercenaria mercenaria	US East Coast
Musculista senhousia	Japan
Mytilus galloprovincialis	Mediterranean
Teredo navalis	?
Theora fragilis (= *lubrica*)	Asia, Indo-Pacific
Bryozoans	
Bugula "neritina"	?
Cryptosula pallasiana	Atlantic
Watersipora "subtorquata"	NW Pacific
Watersipora arcuata	?
Zoobotryon verticillatum	subtropical
Tunicates	
Ascidia sp.	?
Ascidia zara	Japan
Bostrichobranchus pilularis	US East Coast
Botryllus schlosseri	Europe
Ciona intestinalis	N Atlantic
Ciona savigny	Japan
Microcosmus squamiger	Australia
Polyandrocarpa zorritensis	Peru
Styela canopus	US East Coast?
Styela clava	W Pacific
Styela plicata	?
Symplegma brakenhelmi	?
Symplegma reptans	Japan
Vertebrates	
Fish	
Acanthogobius flavimanus	Japan
Poecilia latipinna	E. North America
Tridentiger trigonocephalus	Japan, NW Pacific

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CHAPTER II

THE HISTORICAL ECOLOGY AND ASSOCIATED CHANGES IN THE BIVALVE FAUNA OF AN URBANIZED SOUTHERN CALIFORNIA BAY

> "The transformation of Mission Bay Park from a little used, unnavigable backwater made up of tidal basins, sand dunes, salt marshes, swamps, and salt flats into a major recreational resource serving millions of people yearly is one of the foremost examples of what can be accomplished through City, State, and Federal cooperation."
>
> City of San Diego 1978

Abstract

Mission Bay is a small coastal lagoon situated in the densely populated City of San Diego. This ecosystem contains sensitive wetland habitats and is home to several endangered species. Qualitative historical records show that the bivalve assemblage that existed in the bay 100 years ago is dramatically different from the assemblage that is now present. Changes in the bivalve fauna of the bay indicate that a suite of anthropogenic effects, including over-exploitation of edible species, dramatic habitat modification, pollution, altered interspecific interactions, and the invasion of exotic species have all played a role in shaping the community present in the bay. Quantitative comparisons of the bivalves currently present in a tidal creek of a remnant salt marsh with those present 30 years ago reveal that an exotic mussel, *Musculista senhousia*, has become overwhelmingly dominant in the system while native surface-dwelling clams have become less common. Comparisons of bivalves in a one-year old restored marsh with those in the adjacent natural marsh show that two exotic mussels have rapidly colonized the area. Experiments were conducted in order to investigate the role of interspecific interactions in giving rise to observed changes in the bivalve community. These demonstrated that the growth and survivorship of surface-dwelling cockles (*Chione* spp.) can be significantly inhibited by *Musculista senhousia*, while a deeper-dwelling, deposit-feeding clam (*Macoma nasuta*) showed no such inhibition. This historical ecology of the bivalve fauna of Mission Bay establishes baseline information necessary to evaluate anthropogenic effects and set goals for conservation and restoration efforts.

Introduction

Biota in urbanized ecosystems are subject to a variety of threats due to the activities of humans, including habitat destruction, resource over-exploitation, pollution, and introduction of exotic species (Adams 1994; McNeely et al. 1995; Mooney et al. 1995). In many systems the onset of such effects often predates thorough study of the flora and fauna of the area. This is particularly true for near-shore marine habitats (e.g. bays, estuaries, and the continental shelf), where there is often a lack of information on historical conditions and very few appropriate, pristine reference sites (Dayton 1998; Dayton et al. 1998). However, information in the form of species lists and natural history observations is sometimes available for large or conspicuous taxa, and these can be used to generate comparative benchmarks for these groups and determine some major processes acting in these urbanized ecosystems. Such historical ecology is necessary to better assess the consequences of human actions, such as evaluating anthropogenic impacts or judging of the efficacy of restoration or mitigation efforts.

The long-term evaluation of marine communities can provide insights into both anthropogenic and natural forces acting in ecosystems over ecological time scales (Dayton et al. 1998). For example, long-term monitoring of changes in the marine communities of the northern Pacific has revealed a substantial decrease in the biovolume of zooplankters (Roemmich and McGowan 1995). Comparisons of rocky shore organisms currently present in Monterey Bay with those present in the 1930's have demonstrated a relative shift in community composition toward warmer-climate species (Barry et al. 1995). Long-term data sets have been used to assess the effects of a variety of natural and anthropogenic alterations of soft-sediment ecosystems in areas such as San Francisco Bay, Puget Sound (Nichols 1985), and Europe (Pearson and Barnett 1987). Comparisons over decadal time scales demonstrate the impact of organic enrichment (e.g., Caspers 1981; Weigelt 1991; Tsutsumi 1995) and fishing activities, including dredging and trawling (Reise and Schubert 1987), on benthic macroinvertebrates.

In attempting to understand the relationship between human activities and biotic alterations in aquatic systems, bivalve communities provide good bases for historical comparisons. These relatively conspicuous taxa are often collected by naturalists and have a good fossil record. Compositional changes in bivalve assemblages can be used to assess patterns and processes operating in ecosystems, including the invasion of exotic species. In San Francisco Bay, for example, the number of exotic bivalves introduced into the system has continually risen over the last 100 years (Nichols and Pamatmat 1988; Cohen and Carlton 1998). This change provides an indication of increased levels of inoculation of non-native species and also suggests the possibility that the bay is becoming more vulnerable to invasion over time (Cohen and Carlton 1998). In addition, molluscs are well suited for assessment of causal mechanisms of changes within communities because of their amenability to experimental manipulation.

The goals of this paper are to describe the historical ecology of bivalve assemblages in Mission Bay, San Diego, using qualitative and quantitative descriptive information as well as experimental manipulations to help determine potential causal mechanisms giving rise to observed changes. I will (1) review historical hydrological and habitat changes in Mission Bay, (2) qualitatively and quantitatively assess long-term changes in the bivalve community of the bay, (3) examine the dynamics of bivalve colonization of a newly-created Mission Bay wetland, and (4) experimentally examine the potential role of interspecific interactions in shaping bivalve assemblages. Manipulations were conducted using an exotic, mat-forming mussel (*Musculista senhousia*) and three native clam species. Two of the clams are shallow-dwelling suspension feeders (*Chione undatella* and *C. fluctifraga*) and one is a deep-living deposit feeder (*Macoma nasuta*). Possible causal mechanisms giving rise to observed long-term changes in the bivalve fauna are then evaluated.

Mission Bay, San Diego, California

Mission Bay is a coastal lagoon located ca. 10 km north of the larger San Diego Bay and 23 km north of the United States / Mexico border. Mission Bay, located in the urbanized city of San Diego, has been highly modified by the activities of man, yet is considered an important biological resource as it contains some remnant wetland ecosystems that have supported a variety of scientific research efforts (e.g., ZoBell and Feltham 1942; Levin 1983, 1984, 1986; Phleger and Cary 1983; Crooks 1996; Levin et al. 1998). The bay and its wetlands are one of a number of southern California's coastal ecosystems that have been particularly affected by increased urbanization. In this region, 80 to 90 % of the coastal wetlands have been destroyed, and those fragmented systems remaining are home to several endangered species (Zedler 1996).

When first explored by the Spanish in 1662, False (Mission) Bay

> "was a good port, although it had at its entrance a bar of a little more than two fathoms depth, and ... there was a very

> large grove at an estuary which extended into the land, and
> many Indians" (Pourade 1960).

The bay has been highly modified over the last 140 years. Historically, the San Diego River emptied through extensive wetlands into either Mission Bay and/or neighboring San Diego Bay (Fig. 2-1). In order to prevent San Diego Bay, which provides an excellent harbor, from filling with sediment, the San Diego River was diverted into Mission Bay in the 1850's (Chapman 1963). This caused some deeper parts of the bay to fill with sediments, resulting in increased shallow water, eelgrass, and tidal flat areas.

From 1945 to 1963, there was a major physical restructuring of the bay to create a multi-purpose recreational park. This involved dredging to create deep-water habitat, filling to create islands and parkland, and again altering the course of the San Diego River so that it bypassed both bays and emptied directly into the Pacific through an artificial flood control channel (Fig. 2-1). Also, there has been periodic dumping of sand on the many of the beaches in the bay (Herring 1991). Freshwater input to the bay is limited to two small tidal creeks and numerous storm drains. Because the two creeks (particularly Tecolote Creek) empty into areas of sluggish flushing, a gradient of organic enrichment has been established (Marcus 1989; Chapter 3). In the back bay, sediments are richer in organics and muddier than those nearer the mouth of the bay (Fairey et al. 1997).

Following major alteration of the bay in the 1940's and 1950's, a small remnant (30 hectares) of salt marsh and mudflat habitat remained in the northeast corner of the Bay (Northern Wildlife Preserve and Kendall Frost Reserve). In December 1995, a 2.8 hectare plot of filled land adjacent to this remnant salt marsh was returned to intertidal depths for the creation of new salt marsh and tidal creek habitats (the Crown Point Mitigation Site). Cordgrass (*Spartina foliosa*) and pickleweed (*Salicornia virginica*) were planted along creek banks in March 1996. Natural colonization by annual pickleweed (*Salicornia bigelovii*) occurred on the tidal flat, and eelgrass (*Zostera marina*) colonized the tidal creeks during the first year that the marsh was open to tidal flushing (Levin pers comm).

Several historical studies of the marine mollusc fauna of Mission Bay exist. The first qualitative list was published in 1885 (Orcutt and Dall 1885), and there have been periodic studies since that time. (e.g., Fry and Croker 1934; Morrison 1952a,b, 1954, 1957; Chapman 1963). The most extensive survey of the mollusc fauna of the bay to date was conducted in the late 1920's (Morrison 1930), prior to the major physical reconstruction of the bay. In the mid-1960's, a quantitative survey of the tidal creek mollusc fauna in the northeast portion of the bay was conducted (MacDonald 1967, 1969a,b). These studies provide information against which the current bivalve assemblage in Mission Bay will be compared.

Methods

Qualitative Comparisons

Historical records, coupled with personal observations and communications, were used to construct a species list of Mission Bay bivalve fauna and assess relative changes over time. Taxonomy and biogeography of bivalve species were determined using primarily Bernard (1983), as well as Oldroyd (1924), Fitch (1953), Abbott (1954), Keen (1971), Keen and Coan (1974), McLean (1978), Carlton (1979b), Abbott and Dance (1986), Turgeon (1988), Bernard et al. (1991), and Cohen and Carlton (1995). Biogeographic provinces were considered to extend ± 3 ° beyond the latitudinal boundaries in Bernard et al. (1991).

Quantitative Comparisons

Quantitative sampling of the tidal creek bivalve community at the Northern Wildlife Preserve was conducted in April 1994, September 1994, July 1995, and December 1996. On each date, six to ten stations along the length of the tidal creek were sampled. I used the sampling methods described by MacDonald (1967, 1969a,b), so direct comparisons of the composition and abundances of members of the bivalve community are possible (although only means are reported in the earlier study so no statistical tests were done). Sediment from a surface area of 0.0625 m^2 was excavated to a depth of approximately 25 cm, sieved in the field through 1 mm mesh, and preserved in buffered formalin. All bivalves were identified to species and their shell length measured with a digital caliper. The tidal creek at the Crown Point Mitigation Site was sampled during December 1996. 12 samples were taken: 9 in the 11-month old tidal creek, and 3 in the adjacent natural creek (Fig. 2-1).

Quantitative subtidal data for Mission Bay were collected in conjunction with a Biological Oceanography class at San Diego State University (Chapter 3). From 1977 to 1996, seven back-bay stations were sampled using an orange-peel grab (surface area = approx. 0.1 m^2) deployed from a boat. Four to seven replicate grabs were taken at each station. Samples were sieved through a 750-micron mesh and sorted under a dissecting microscope. The data from these samples were used to determine spatial distribution of bivalves in the bay and investigate temporal patterns of abundance of two dominant species, *Musculista senhousia* and *Solen rosaceus*. Regression analyses were used to investigate temporal trends in these species.

Manipulative experiments

Two experiments were conducted that examined the growth and survivorship of three native clam species in the presence of the exotic, mat-forming mussel, *Musculista* *senhousia.* These experiments were all conducted on the unvegetated tidal flat on Northern Wildlife Preserve, at a tidal elevation of approximately 0.25 m above Mean Lower Low Water.

Experiment 1 - *Musculista senhousia* vs. *Macoma nasuta*

In this experiment, growth and survivorship of the deposit-feeding clam, *Macoma nasuta*, was assessed in the presence and absence of *Musculista senhousia.* The experiment was arranged as a Randomized Complete Block design with 12 blocks. The experimental units were topless mesh enclosures (10-cm in diameter and 14-cm deep) that received one of two treatments: (1) *Macoma nasuta* with *Musculista senhousia*, or (2) *Macoma nasuta* without *Musculista senhousia.* At the beginning of the experiment, clams and mussels were collected from intertidal flats of east Mission Bay. At the experimental site, holes were excavated and enclosures placed in the sediment. The enclosure was then filled with the natural sediment removed from the plot and 3 *Macoma nasuta* were added to each enclosure. Mussels in their mats, at densities encountered in the field (approx. 60 / plot), were then transplanted to one plot in each of the 12 blocks. Each enclosure was then covered with a sideless cage with coarse mesh (1 cm) on top to prevent shorebird predation. The experiment began in December 1996 and ran until June 1997. During the course of the experiment, plots were occasionally cleared of algae and, in the control plots, of obvious clumps of naturally recruiting mussels. At the end of the experiment, sub-samples of the mussels were counted and their shell lengths measured, and the length-weight regressions in Crooks (1996) were used to determine biomass of mussels in the plots.

The response variables in the experiment were percent survivorship and percent mortality of *Macoma nasuta*. Survivorship was determined as the number of clams found alive (out of the original three) in each plot at the end of the experiment. Growth in clams was to be assessed using a phosphorescent tag, Calcein (Rowley and MacKinnon 1995). Prior to the experiment, clams were immersed in a bath of Calcein for 24 hours, and any shell added during this period fluoresced under UV light. However, in addition to tagging the shell, this procedure also caused a growth check that was visible with the naked eye. Distance from this check to outer margin of the shell was used as the measure of shell growth. Randomized Complete Block ANOVA's were used to test for statistical differences in survivorship and growth in the two treatments.

Experiment 2 - *Musculista senhousia* vs. *Chione undatella* and *Chione fluctifraga*

In this experiment, growth and survivorship of two suspension-feeding clams, *Chione undatella* and *C. fluctifraga*, were measured in the presence and absence of *Musculista senhousia.* The experiment was arranged as a Randomized Complete Block design, with 18 blocks for *C. undatella* and 18 for *C. fluctifraga.* The experimental units were topless mesh enclosures (10-cm in diameter and 8-cm deep) that received one of two treatments: 1) one clam and no mussels, or 2) one clam and mussels in their mats in ambient densities (approx. 40 / plot). The blocks were then covered with mesh to prevent shorebirds from predating upon mussels. During the course of the experiment, which ran from August to December 1997, plots were occasionally cleared of macroalgae and mussel clumps removed from control plots. At the conclusion of the experiment, clams were collected for assessment of survivorship and growth. Survivorship was determined as the number of clams found alive at the end of the experiment (out of the 18 original clams in each treatment). Prior to the experiment, the clams were measured and growth was assessed as the increase in length, measured from the posterior to the anterior margin of the shell. Chi-squared analyses were conducted to detect statistical differences in mortality and Randomized Complete Block ANOVA's were conducted for measures of growth. Samples of mussels in the treatment and control plots were also counted and measured for shell length.

Results

The Bivalve Fauna of Mission Bay

Since the first description of the bivalve fauna of False (Mission) Bay (Orcutt and Dall 1885), over 100 species in 33 Families have been reported (Table 2-1). Many of these species typically are associated with bays (e.g., *Chione* spp., *Macoma* spp., and *Tagelus* spp.), although species more often found on exposed coasts also were represented (e.g., the pismo clam *Tivela stultorum*). Six species, *Mytilus galloprovincialis, Musculista senhousia, Theora fragilis, Crassostrea gigas, Mercenaria mercenaria*, and *Ruditapes phillipinarum*, are considered introduced, although the latter three species have been reported infrequently and appear not to be established. In addition, the winged oyster *Pteria sterna*, may be non-native (Kelsey 1907; Hanna 1966; Carlton 1979b), although it is possible that this more southerly species naturally recruits in the bay during warm-water periods (C. Gramlich pers. comm.). Also, it is possible that exotic shipworms (*Teredo* spp. and *Lyrodus pedicellatus*), which have been found in San Diego Bay (Carlton 1979b), have been present in Mission Bay although they do not appear on species lists for this area.

Species with both warm-water and cold-water affinities are represented in Mission Bay. Among the native species, three biogeographic provinces are represented. Twenty-three of the species are primarily of the Californian province (from Point Conception, California to Bahía Magdalena, Baja California, Mexico). Twenty-three of the species are found in the Panamic and Californian provinces, thirty-five of the species are found in the Oregonian and Californian, and ten are found in all three provinces.

Two species are considered to be primarily Panamanian in origin, while six were considered to be primarily Oregonian (Table 2-1).

Qualitative Comparisons

One hundred years ago, Mission Bay supported a relatively rich bivalve fauna that contained several large, edible species. Near the seaward margin of the bay was a stretch of rocky beach famous as a clam bed (Orcutt and Dall 1885). At this time, the sunset clam (*Gari californica*), the Washington clam (*Saxidomus nuttallii*), the littleneck clam (*Protothaca staminea*), and other species were reported to be common. Another species, the naked clam *Chlamydoconcha orcutti*, was described from this area (Dall 1884; Williams 1949; Carlton 1979a). This remarkable and rare clam possesses a much reduced, internal shell, to which may be attached a dwarf male (Morton 1981). In the early 20th century, some common species were reported to be "cockles" (*Chione* spp. and/or *Protothaca* spp.), the scallop *Argopecten vestalis* (= *A. aequisulcatus*), the Washington clam, the flat clam (*Semele decisa*) as well as the gaper (*Tresus nuttallii*), which was considered "particularly abundant" (Orcutt 1909; Weymouth 1921). In 1940, the scallop (*A. vestalis*), the hard-shell cockles (*Chione* spp.), the Washington clam, the razor clam (*Tagelus californianus*), the bent-nosed clam (*Macoma nasuta*), and the gaper were reported to be the common edible species (Bonnot 1940). In 1962, the common edible species were the heart cockle, blue mussel (*Mytilus edulis*), and California mussel, *M. californianus* (Chapman 1963). Formerly common species such as the gaper and Washington clams were no longer considered abundant.

Currently, the Washington, sunset, purple, flat, and gaper clams appear to be uncommon or absent in the intertidal, although some may be found occasionally in the subtidal (C. Gramlich pers. comm.). Some of the common clams present today that were also abundant historically include cockles (*Chione undatella* and *C. fluctifraga*), the razor clam, the scallop (*A. vestalis*), the bent-nosed clam, and the littleneck clam. Some of the most conspicuous changes in the bay have resulted from the invasion of exotic species. Three exotics, *Theora fragilis*, *Musculista senhousia*, and *Mytilus galloprovincialis*, are now common and often abundant in Mission Bay.

Theora fragilis is an Asian species that was first recorded on this coast in Newport Bay in late 1960's (Seapy 1974), and was probably introduced via ballast water from Japan (Cohen and Carlton 1995). The small, thin-shelled species was first reported in Mission Bay in 1978 (D. Dexter pers. comm.). It appears to be tolerant of high levels of organic enrichment (Tsutsumi and Kikuchi 1983; Tsutsumi et al. 1991), and can be common in the subtidal back bay as well as intertidal areas (Crooks pers. obs.).

An important change in the molluscan assemblage began in the 1960's with the invasion of the Asian mussel, *Musculista senhousia*. This mytilid was first reported on the Pacific coast of North America in Washington in the 1920's, where it was probably introduced with Japanese oyster seed. In the 1940's it was reported in San Francisco Bay, and in the 1960's it was first found in Mission Bay (Carlton 1979b; Crooks 1996). Introduction to the San Diego region was probably through ballast water or ship fouling. Intermittent intertidal records in Mission Bay between 1971 and 1992 indicate that the mussel could be found in densities of 500 to 5,000 m^{-2} (Levin unpub data; Crooks 1996). In 1995, densities of *M. senhousia* in the shallow subtidal of Mission Bay averaged 160,000 m^{-2}, which are among the highest ever reported for a marine bivalve. This small, soft-sediment dwelling species often forms dense mats on the surface of intertidal and subtidal soft sediments. The mussels and their mats serve to alter the physical structure of the benthic habitat, and as such, it can have marked effects on benthic macrofauna (Chapters 5 and 6) and flora (Reusch and Williams 1998).

The status of the blue mussel (*Mytilus edulis* complex) in Mission Bay and San Diego appears considerably more confused. Reports of blue mussels in the fossil record are scarce in southern California (Cooper 1894; Grant and Gale 1931; Emerson and Chace 1959; Moore 1968; Hertlein and Grant 1972). Similarly, blue mussel shells appear absent from local native American shell middens (Shumway et al. 1961; Miller 1966). Early works on the molluscan fauna of the Pacific coast report that the southern extension of the mussel's range was Monterey, California (Cooper 1867). In 1885, a blue mussel, then called *Mytilus edulis*, was reported in San Diego Bay (but not Mission Bay) (Orcutt and Dall 1885; Dall 1921). Even then it was noted that this species was "probably introduced." In the 1940's, there was a sudden growth in the population of blue mussels in the San Diego area, and the species was called *M. edulis diegensis* (Coe 1946). In the 1980's and 1990's, genetic and morphological evidence suggested that the species that was in southern California was the Mediterranean mussel, *M. galloprovincialis* (Koehn et al. 1984; MacDonald and Koehn 1988; Seed 1992). Recent genetic work, however, has demonstrated that three taxa of blue mussels are present in San Diego: the more northern species of mussel, *M. trossulus* (which itself may be a ballast water transport from ports in San Francisco Bay northward), *M. galloprovincialis*, and hybrids of the two (Suchanek et al. 1997). More genetic, ecological, and historical research is needed to further clarify the status of the blue mussel in southern California.

Quantitative Comparisons – Intertidal

Quantitative sampling in the salt marsh tidal creek of the Northern Wildlife Preserve in the 1990's revealed the presence of 5 bivalve species: *Musculista senhousia*, the bent-nosed clam (*Macoma nasuta*), the cockle *Chione undatella*, the razor clam *Tagelus californianus*, and the littleneck clam *Protothaca staminea* (Fig. 2-2a). Similar sampling in the 1960's also revealed 5 species, although substantial differences in both species composition and abundances existed. *Chione undatella* and *M. nasuta* were not found in the quantitative samples in 1960's, while *Cryptomya californica* and *Chione fluctifraga* were absent in the 1990's. During the thirty years between the two sampling periods, *Musculista senhousia* increased in abundance by about two orders of magnitude, *Tagelus californianus* remained in approximately comparable densities, and *P. staminea* experienced about a three-fold decrease in abundance.

Quantitative sampling in the tidal creek of the newly created marsh (CPMS) revealed the presence of four bivalve species (Fig 2-2b). *Musculista senhousia* was by far the most abundant species; densities in the restored creek were about 4 times higher than in the natural creeks (Fig. 2-2). The next most abundant species was *Mytilus galloprovincialis.* Both mussel species quickly recruited into the creek and grew rapidly, as relatively large individuals were found of both species. The largest *Mytilus galloprovincialis* was 21 mm in the quantitative samples and animals of 51 mm in length were collected from other sites in the creek. The maximum length for the species is approximately 75 mm (Morris et al. 1980). The largest *Musculista senhousia* collected in the quantitative samples was 24 mm, which is approximately two-thirds its maximum size (Crooks 1992). Two new recruits of other species, a juvenile pholad and *Protothaca staminea*, also were present. In the natural creeks at the same time, *Musculista senhousia*, *Tagelus californianus*, and *Macoma nasuta* were present (Fig. 2-2b).

Quantitative comparisons - Subtidal

Sampling in the subtidal sediments of Mission Bay from 1977 to 1996 has revealed the presence of 18 bivalve species. Like the wetland locations, the most dramatic trend in these subtidal populations has been the increasing abundance of the introduced mussel *Musculista senhousia* (Fig. 2-3a). This invasive species has significantly increased in abundance over the two decades in which the populations have been monitored ($F_{1,14} = 27.61$, $P < 0.001$). In the same time frame, the jack-knife clam (*Solen rosaceus*), which was one of the most abundant clams in the early years of the study, has declined in abundance ($F_{1,14} = 8.98$, $P = 0.010$). The density of the other bivalves found varied over the course of the study but remained relatively low and showed no temporal trends ($F_{1,14} = 0.02$, $P = 0.894$). The number of species of other bivalves, however, has declined over the sampling period ($F_{1,14} = 5.04$, $P = 0.041$).

The distribution of subtidal bivalve species in Mission Bay appears to reflect a general pattern of decreased flushing away from the mouth of the bay. Densities of all bivalves are relatively low in the extreme back of the bay, near the entrance of Tecolote Creek (Fig. 2-1), but increase further away from this area of low flushing and organic input (Fig. 2-4a). At the site nearest the mouth of the bay, densities again decrease. If *Musculista senhousia* is excluded from the analyses, the decrease in abundance near the mouth is less obvious, as the mussel is rare at this site (see Chapter 3). Species richnesses in the bay show somewhat similar patterns, with relatively low numbers of species in the back bay and higher species richnesses towards the mouth (Fig. 2-4b).

Effects of *Musculista senhousia* on clams (Cockles and Mussels alive, alive O?)

In both experiments, the transplants of *Musculista senhousia* in their mats persisted well over the four- to six-month courses of the experiments. In the experiment with the deep-dwelling, deposit-feeding clam (*Macoma nasuta*), the final densities (± 1 s.e.) of mussels in the mussel treatment were 58.3 ± 6.6 per plot, and the average estimated total biomass was 1.9 ± 0.2 g dry flesh weight (dfw) per plot. In the control plots, the final density of mussels was 33.8 ± 4.5 per plot due to a recruitment event. However, these mussels were smaller (modal length of 14 mm compared to a modal length of 22 mm in the treatment plots), their average biomass was lower (0.6 ± 0.1 g dfw per plot), and they had not formed extensive mats. Thus their effect was considered to be small in relation to that of the mussels in the plots containing dense mats. In the experiment with the surface-dwelling, suspension-feeding cockles (*Chione undatella* and *Chione fluctifraga*), the average final densities in the mussel transplant and control plots were 55.0 ± 6.6 and 2.0 ± 1.4 mussels per plot, respectively. The average total biomass in the treatment and control plots were respectively 1.1 ± 0.1 and 0.02 ± 0.2 g dfw per plot.

The results of these experiments suggest that the effects of the *Musculista senhousia* depended on the lifestyles of the clams. *Macoma nasuta*, which has increased in abundance along with *Musculista* in the Northern Wildlife Preserve (Fig. 2-2a), was not significantly inhibited by the mussel. Average percent survivorship was high (over 70%) in both the treatment and control, and no significant differences were found (Fig. 2-5A). Similarly, growth was rapid and no significant differences were found between the treatment and control (Fig. 2-5C). The average initial lengths of the clams in the treatment and control plots were respectively 7.0 ± 0.4 and 6.9 ± 0.2 mm. Average final sizes were respectively 11.1 ± 0.2 and 11.7 ± 0.1 mm in the treatment and control plots.

Unlike *Macoma nasuta*, *Chione undatella* and *Chione fluctifraga* were significantly inhibited by the presence of the mussel and its mats. Survivorship of these clams in the presence of mussel mats was less than 50% than that in plots without mats (Fig. 2-5b). Of those clams surviving the duration of the experiment, growth in the mussel treatments was less than 25% of that in the control plots (Fig. 2-5d). The average initial lengths of the *Chione undatella* in the treatment and control plots were respectively 17.5 ± 0.8 and 17.1 ± 0.7 mm., and average final sizes were 18.3 ± 1.2 and 19.6 ± 0.7 mm . For *Chione fluctifraga*, average initial lengths in the treatment and control plots were respectively 17.1 ± 0.6 and 17.3 ± 0.5 mm., and average final sizes were 17.0 ± 0.6 and 19.5 ± 0.6 mm .

Discussion

Despite the somewhat sparse and often qualitative nature of the record of bivalve communities in Mission Bay, it is clear major changes in the bivalve communities have occurred. There has been a demise of the rich clam beds, and the large, commercially important species, such as the flat and gaper clams, have largely disappeared from the bay. Additionally, there has been a dramatic increase in the representation of exotic species, especially *Musculista senhousia* and *Mytilus galloprovincialis*, and a recent decline in species richness in the subtidal of Mission Bay. Within the last remnant of salt marsh in Mission Bay, there also have been major changes in the composition and abundances of bivalve species. By reconstructing historical trends in the Bay and examining species interactions experimentally it is possible to recognize several interacting mechanisms that may be responsible for changes in bivalve assemblage. These include over-harvesting of bivalves, habitat modification, pollution, interspecific interactions, and invasion of exotic species. Because of the data resolution, however, it is possible that some changes, such as those due to long-term effects of global warming, remain undetected.

Over-exploitation

The earliest anthropogenic effect on local bivalve communities was collecting by native Americans, which is evidenced by large numbers of shells in middens along the coast of San Diego (Shumway et al. 1961; Miller 1966). These activities may date back eight thousand years, but it is difficult to assess what impact this gathering had on local bivalve populations. However, it is almost certain that the intensity of exploitation increased with the growth of the city of San Diego from a small town of 2287 in 1850 to a major city with over 1 million residents 140 years later. In 1909, long-time San Diego naturalist C. Orcutt stated that bivalves that were once abundant from the rock bed inside the entrance to Mission Bay were nearly exterminated. In 1930, it was noted that "collectors who have collected in Mission Bay for years report the entire disappearance of certain forms from the regions wherein they had previously found them common" (Morrison 1930). Bivalve species that appear to have been collected in large numbers were the Washington, sunset, flat, and gaper clams (Orcutt 1909; Keep and Bailey 1935; Weymouth 1921; Bonnot 1940). In addition to bivalves, large, attractive, and now locally uncommon gastropods, such as the chestnut cowry (*Cypraea spadicea*) and California frog shell (*Bursa californica*), were also heavily collcted (Orcutt 1909; Reish 1995).

In addition to direct effects of collection, there may have also been indirect effects such as disturbance of habitat in search of game species. For example, collecting for the ghost shrimp (*Neotrypea* (=*Callianassa*) spp.), which typically involves suction pumping or digging, can disrupt the small clam, *Cryptomya californica*, a frequent commensal in ghost shrimp burrows. In recent years, collecting for clams appears to have abated due to low abundances and pollution concerns, but a bait fishery for ghost shrimp still persists (Crooks pers. obs.).

Habitat Loss and Degradation

Habitat modification in Mission Bay has been extensive, and this probably represents one of the over-riding forces of change in the bay. In fact, the alteration of the physical nature of Mission Bay pre-dates its first intensive study, with the "permanent" diversion of the San Diego River into the southern bay in 1852. This diversion caused portions of the southern bay to fill to intertidal depths at the expense of deeper water habitats (Fig. 2-1). Since no good data exist for the composition of the bivalve community before 1885, it is difficult to assess accurately the effects of this river diversion. It is likely that the bivalve composition of the bay before and after this change to the system were fairly similar, as the San Diego River naturally flowed into the bay on a semi-regular basis (Pourade 1961). Changes associated with river diversion were almost certainly quite small compared to the effects of the major alterations of the bay that involved the creation of the recreational park.

The dramatic restructuring of the bay that began after World War II has had major effects on the quantity and quality of habitats, circulation, and biota in the bay (Morrison 1957; Chapman 1963). Morrison (1957) noted that "since 1949 the dredging and upheaval of the shore line of Mission Bay has destroyed many shells and their habitats." Much of the intertidal habitat, such as tidal flats and salt marshes, has since been converted to deeper water or filled to above the high-tide mark. Even those regions where intertidal habitat still exists have been modified, as the dumping of sand on beaches and subsequent movement of this material has altered sedimentary regimes. For example, the Northern Wildlife Preserve appears considerably sandier than it was previously (Morrison 1930; Herring 1991). This may explain the shift in *Chione* species seen in the Northern Wildlife Reserve over the last 30 years (Fig. 2-2). *Chione fluctifraga*, which is more typical of back-bay, muddy habitats, has been replaced by *C. undatella*, which usually is found in sandier habitats nearer the mouth of bays (Morris et al. 1980; Crooks pers. obs).

Urban run-off coupled with flushing patterns in the bay have established a gradient of pollution and organic enrichment that can affect benthic communities (Marcus 1989; Fairey et al. 1995; Chapter 3). The patterns observed in the bivalve assemblages tend to resemble patterns in the benthic macrofaunal communities as a whole. The back bay is relatively depauperate, while areas closer to the mouth exhibit peaks in abundances and relatively high species richness. Nearer the mouth of the bay, abundances drop due to decreased densities of opportunistic organisms, but species richness remains high. This pattern appears to be fairly characteristic for assemblages along an organic enrichment gradient and has been reported in a number of systems worldwide (Pearson and Rosenberg 1978). The distribution of *M. senhousia* in the bay also reflects another general pattern, that of prevalence of exotics in disturbed or polluted areas (Elton 1958; Kowarik 1995). This invasive mussel is abundant in moderately-polluted areas and virtually absent in less polluted areas, although sediments nearer the mouth exhibit properties that are well within the range reported for the species (Crooks 1992; Chapter 3).

Interspecific Interactions

The bivalve competition experiments demonstrate that interactions between bivalves may be very important for shaping community patterns (Fig. 2-5). For example, although *M. senhousia* may facilitate smaller biota such as small gastropods, amphipods, and insect larvae through the construction of structurally complex mats (Chapters 5 and 6), some surface-dwelling, suspension-feeding bivalves can be severely inhibited by the mussel. In this study, both suspension-feeding cockles (*Chione undatella* and *C. fluctifraga)* were negatively affected by *M. senhousia* in the field experiments (Fig. 2-5). An earlier experiment examining effects of *M. senhousia* on suspension-feeding clams under laboratory conditions also produced similar results (Crooks 1992). Qualitative observations in areas where the mussel is native as well as regions where it is exotic also have suggested inhibitory effects of the mussel on other suspension-feeding bivalves, including *Meretrix lusoria, Mactra chinensis, Mactra veneriformes, Ruditapes phillipinarum, Xenostrobus pulex*, and scallops (Sugawara et al. 1961; Uchida 1965; Willan 1987; Creese et al. 1997). Also, the decline of the deep-dwelling suspension feeder, *Solen rosaceus*, in the subtidal may be linked to the increased abundances of *Musculista senhousia*, although experiments would be necessary to determine this definitively (Fig. 2-3). The negative effects of *M. senhousia* on suspension-feeding clams may be mediated by competition for food and/or space, both of which have been suggested to be important under some circumstances in soft-sediment systems (Peterson 1977, 1982; Peterson and Andre 1980; Kammermans 1993). The high density of *M. senhousia* may cause a reduction in the food supply in near-bottom waters, while the structure of mussel mats may physically inhibit these clams.

In contrast to the effects on *Chione* spp., *M. senhousia* had no significant effect on *Macoma nasuta* in the field experiment. This species appears to be primarily a deposit feeder (although it may facultatively feed on suspended particles; Rae 1979), and has increased in abundance along with *Musculista senhousia* in the tidal creeks of the Northern Wildlife Preserve (Fig. 2-2). This feeding mode, coupled with the different depth horizon in which the species lives, may ameliorate negative effects of the mussel and its mats. Similarly, the small deposit-feeding bivalve *Nucula hartvigiana* has been suggested to be facilitated by the presence of mussel mats, perhaps by the provision of food resources (Willan 1987).

Invasions

Invasive species in Mission Bay demonstrate that exotics may be thought of as both a cause and consequence of abiotic and biotic changes in invaded ecosystems. As this and other research on *M. senhousia* has demonstrated (Creese et al. 1997; Reusch and Williams 1998; Chapter 5), invasive species can have major effects on resident species. This can occur both through alteration of the ecosystem-level properties such as habitat modification (Chapters 5 and 6) as well as through interspecific interactions such as competition (this study). Furthermore, environmental changes that are occurring in coastal ecosystems worldwide, such as pollution and habitat loss and degradation, may increase the vulnerability of ecosystems to invasions (Elton 1958; Orians 1986; Hobbs 1989; Kowarik 1995). The distribution of *M. senhousia* in the subtidal of Mission Bay (Fig. 2-3) is suggestive of this relationship. Increased invasibility of coastal habitats, coupled with increased inoculation of species through vectors such as ballast water, may be causing the increased rates of invasion observed in recent years (Lambert and Lambert 1998; Cohen and Carlton 1998).

Given these considerations, it is almost certain that other bivalves will continue to be introduced into San Diego. Likely invaders are exotics already present on this coast, such as the Japanese clam (*Potamocorbula amurensis)*, the gem clam (*Gemma gemma)*, the ribbed mussel (*Arcuatula demmisa)*, or the Manila clam (*Ruditapes phillipinarum*). Other potential invaders include species that have shown a propensity for synanthropic movement beyond their native range, like the green mussel (*Perna viridis*) (Asakura 1992). These invaders could be relatively innocuous, or have very large effects like *Potamocorbula amurensis* in San Francisco Bay, which has been suggested to hinder spring blooms of plankton by its filter-feeding activities and depress zooplankton populations (Alpine and Cloern 1992; Kimmerer et al. 1994). Non-bivalve species that consume bivalves will also likely invade. Of particular concern is the predatory European shore crab (or green crab), *Carcinus maenas*. This species is currently expanding rapidly northward from its initial focus of invasion in San Francisco. Southward movement appears more gradual, but San Diego is within the projected range for this destructive species (Grosholz and Ruiz 1995).

The results of the studies in the Crown Point Mitigation Site demonstrate that exotics such as *Musculista senhousia* can rapidly colonize and dominate restored systems. Similar differences in abundances of *M. senhousia* in restored and natural systems were also observed in San Diego Bay (Scatolini and Zedler 1996). Such patterns may be fairly general, and relate in broad terms to the opportunistic nature of some exotics as well as the physical conditions in the restored systems (Elton 1958; Hedgpeth 1980; Orians 1986; Williamson 1996). Within these systems, *Musculista senhousia* could affect success of restoration efforts by inhibiting other larger bivalves, such as *Chione* spp., attempting to colonize the sites. Also, *M. senhousia* actually may impede the species targeted for restoration, such as has occurred with eelgrass (*Zostera marina*) in San Diego Bay (Reusch and Williams 1998). Given the ever-increasing numbers of invaders appearing in estuarine ecosystems, the vulnerability of these novel habitats to invasion, and the increasing need for mitigation sites in these ecosystems, exotic species must be incorporated into planning and assessment of restoration efforts (Hedgpeth 1980).

Implications

These results help identify some of the major factors that have affected bivalves, and probably many other taxa, in Mission Bay, and provide a better impression of what the bivalve assemblages in the bay were like at a time before major human intervention. From this, it is clear that the communities currently present are distinctly different from those present over one hundred years ago. Generation of baseline information such as this is not merely an academic exercise. For example, if one of the goals of restoration efforts, such as that in the Crown Point Mitigation Site, is to create a "natural" system, then contemporaneous comparisons to a much modified reference site (e.g., Northern Wildlife Preserve) should be viewed with caution. As a matter of practice, it may be impossible to return a site to its condition prior to human intervention, due to irreversible changes such as habitat fragmentation, species extinctions, or biological invasions, as well as compromises concerning environmental, recreational, and economic issues that are often made in urban areas. It is highly desirable, however, to have some knowledge about the system in a pre-intervention state. Such information may also help alleviate biases in our assessment of current anthropogenic impacts in urbanized systems, as it will indicate what potential consequences of human actions have already occurred. Such considerations highlight the need to balance our view of contemporary dynamics with historical insight.

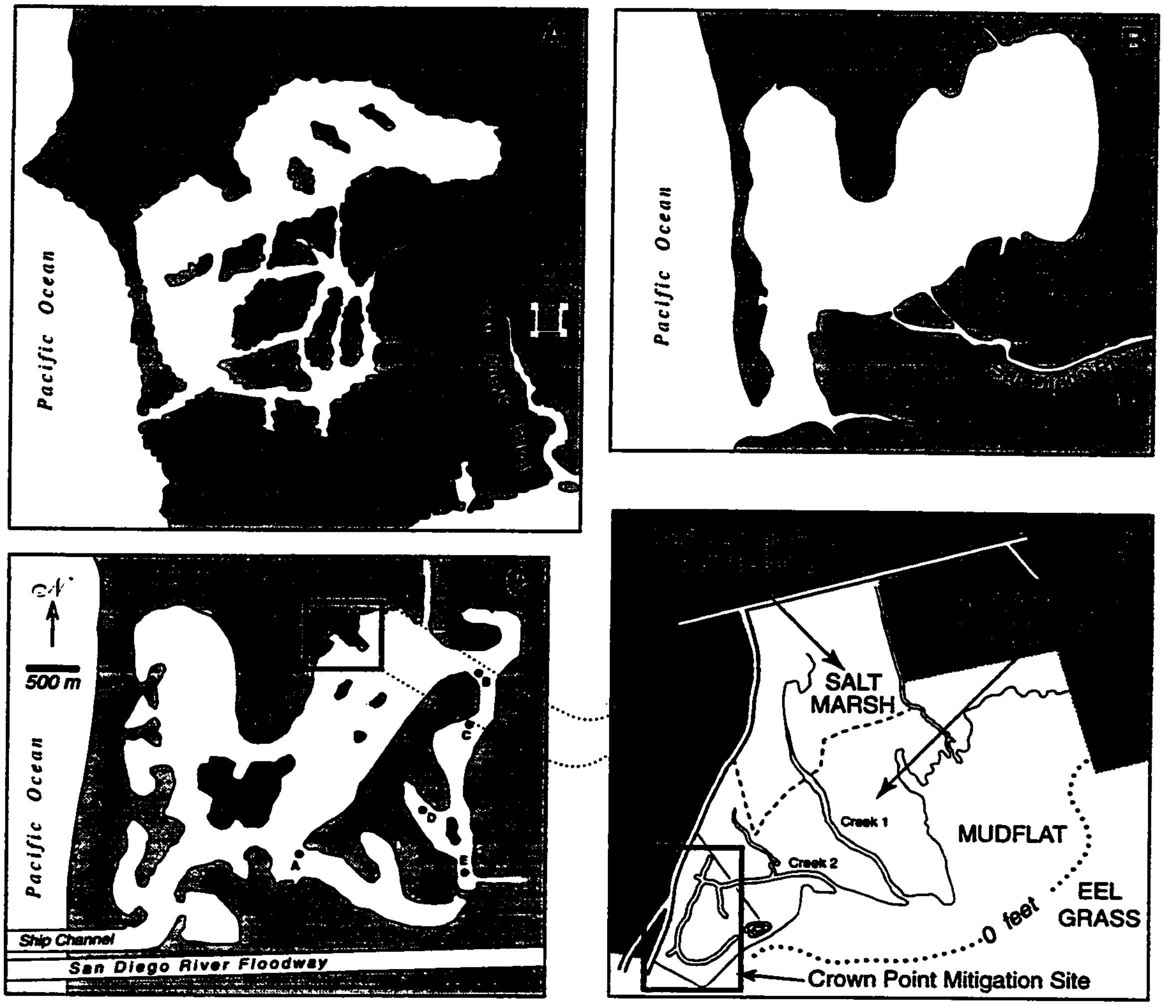

Figure 2-1. Mission Bay, San Diego, California. A) Spanish map from 1782 by pilot Juan Pantoja (Pourade 1960). B) The bay as it appeared in 1931. Note the location of the San Diego River and the filling in of the south bay. The northeast portion of the bay was also very shallow (Chapman 1963). C) Mission Bay as it appears now, after the post-World War II dredging and filling operations. Also shown are the location of the subtidal sites. D) Close-up of the Northern Wildlife Preserve and Crown Point Mitigation Site.

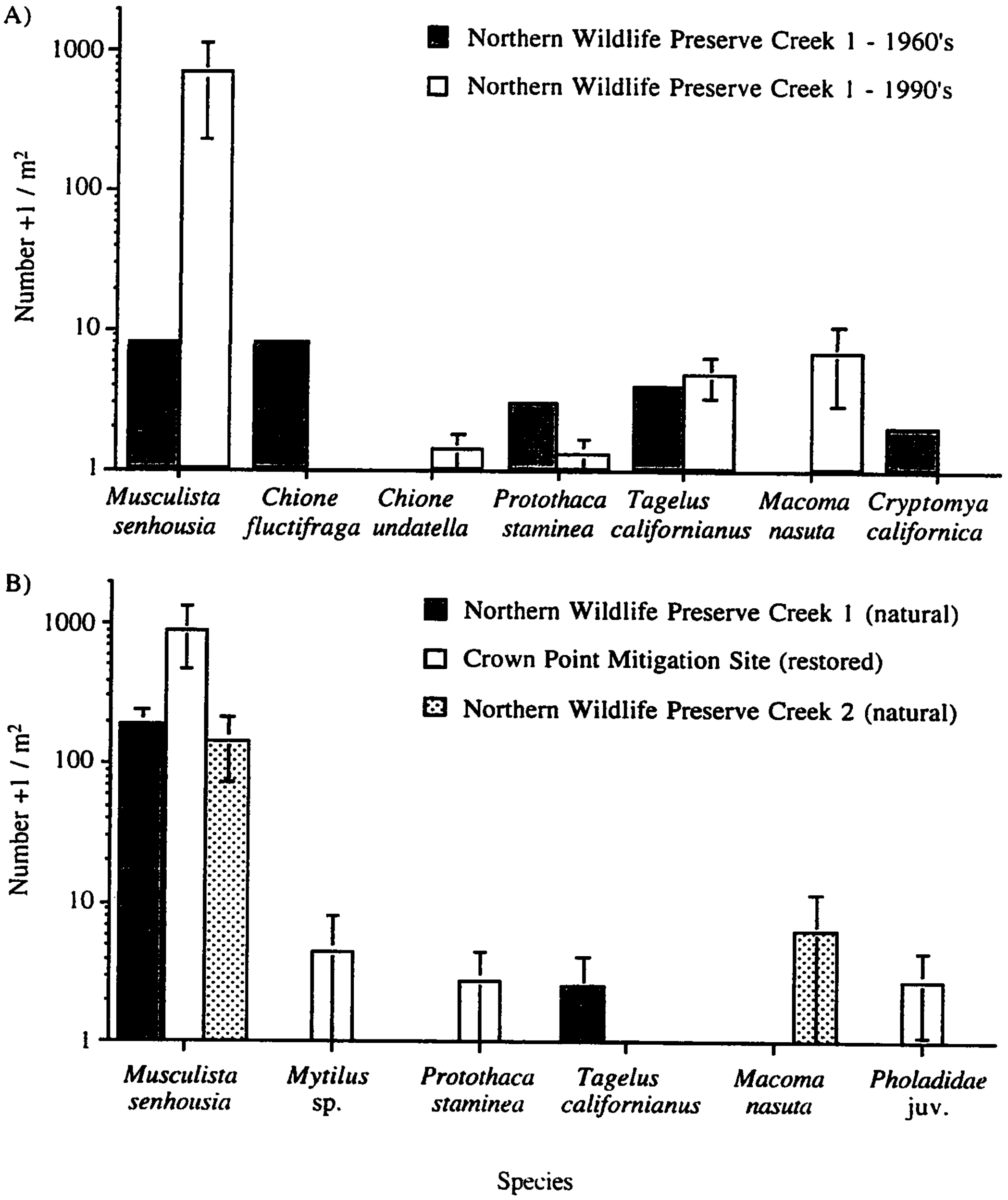

Figure 2-2. A) Comparison of the tidal creek bivalve fauna of the Northern Wildlife Preserve in the mid-1960's and mid-1990's (historical data from MacDonald 1969). B) Comparisons of the bivalve fauna in a one-year old created marsh (CPMS) to two natural tidal creeks (see Fig. 2-1).

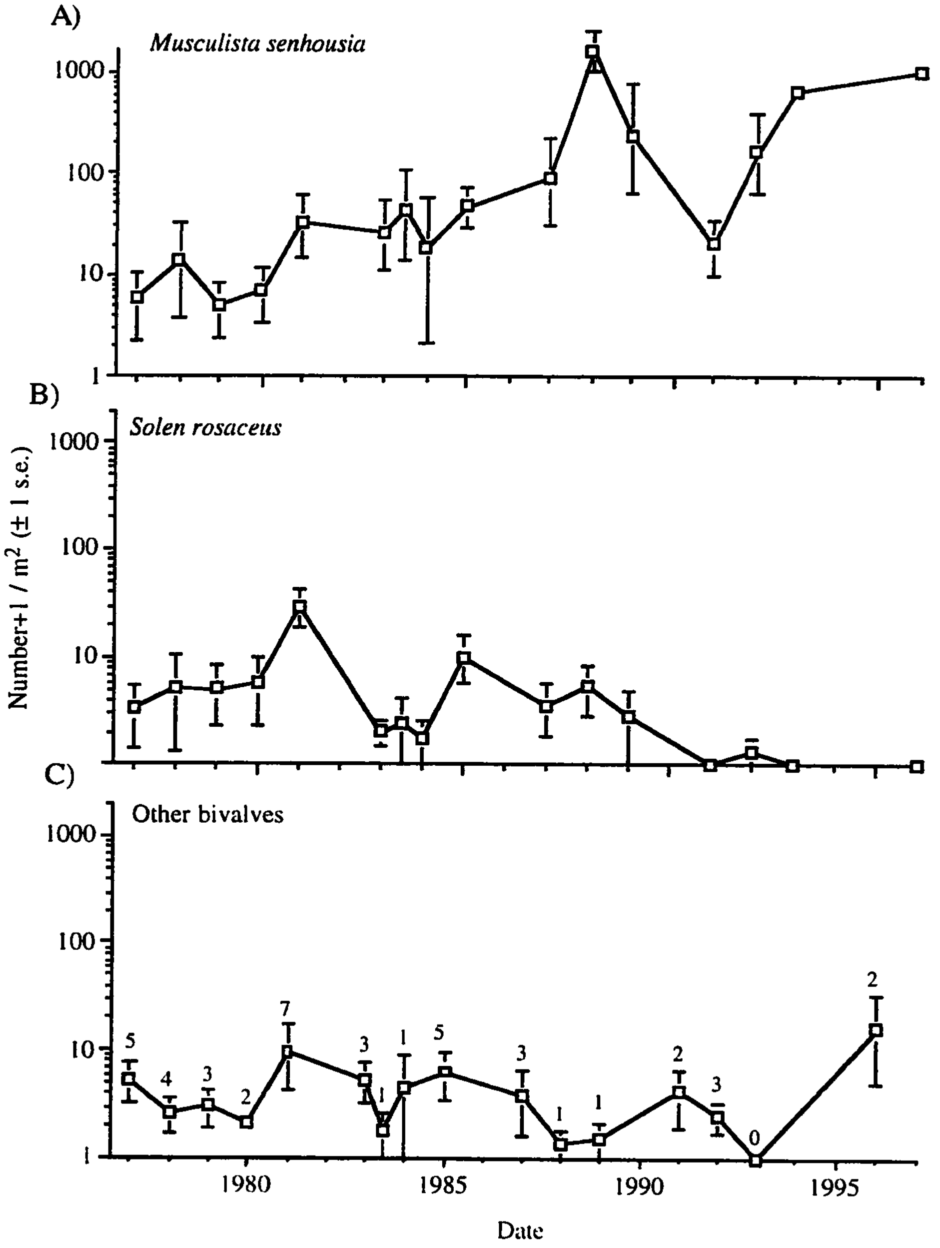

Figure 2-3. Historical trends in subtidal bivalve populations in Mission Bay. Panels represent A) the introduced mussel, *Musculista senhousia*, B) the native jack-knife clam *Solen rosaceus*, and C) other bivalves (the number of species collected is also shown).

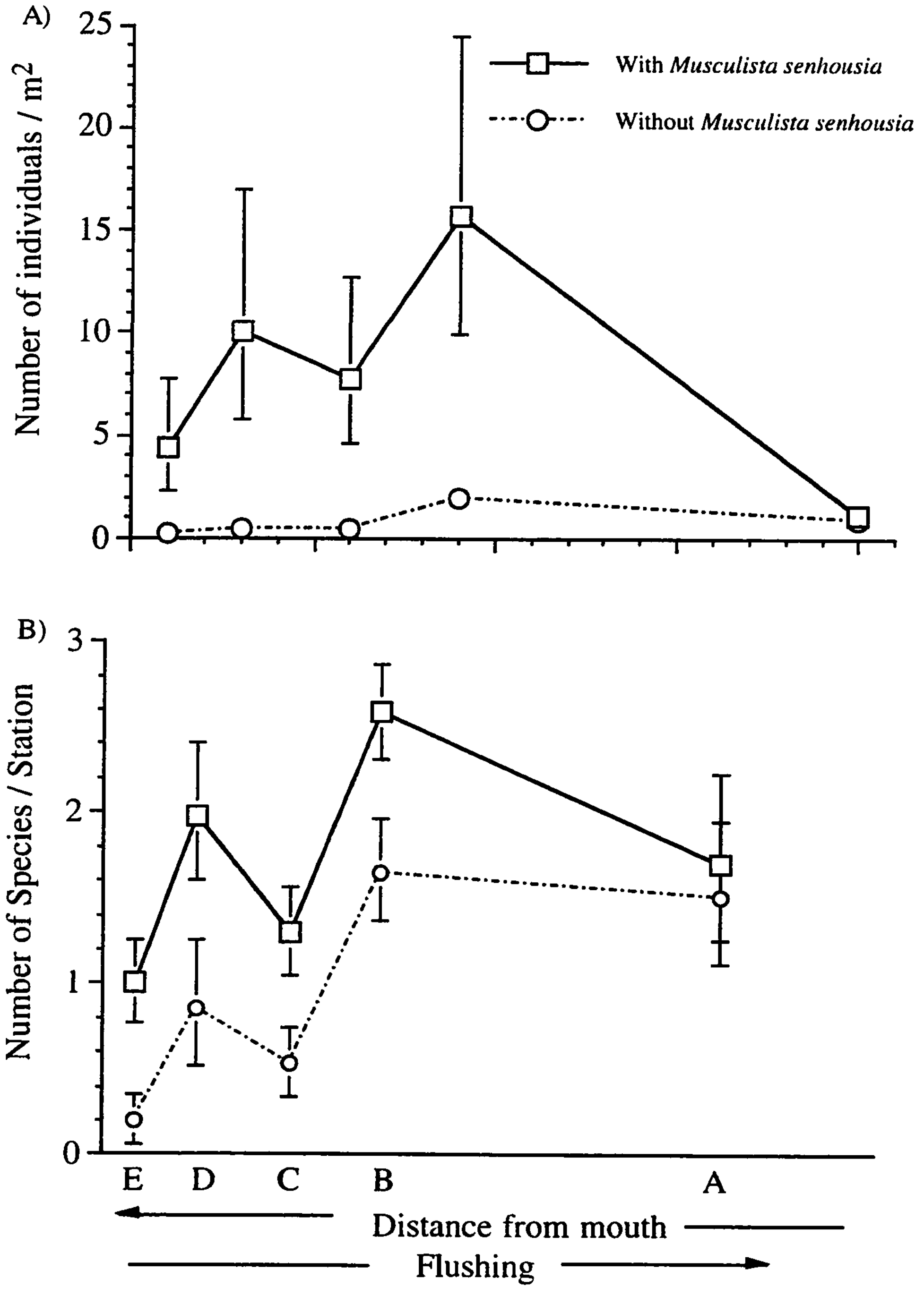

Figure 2-4. Densities (A) and species richnesses (B) of bivalves along a transect in Mission Bay. Letters represent location of subtidal stations (see Fig. 2-1).

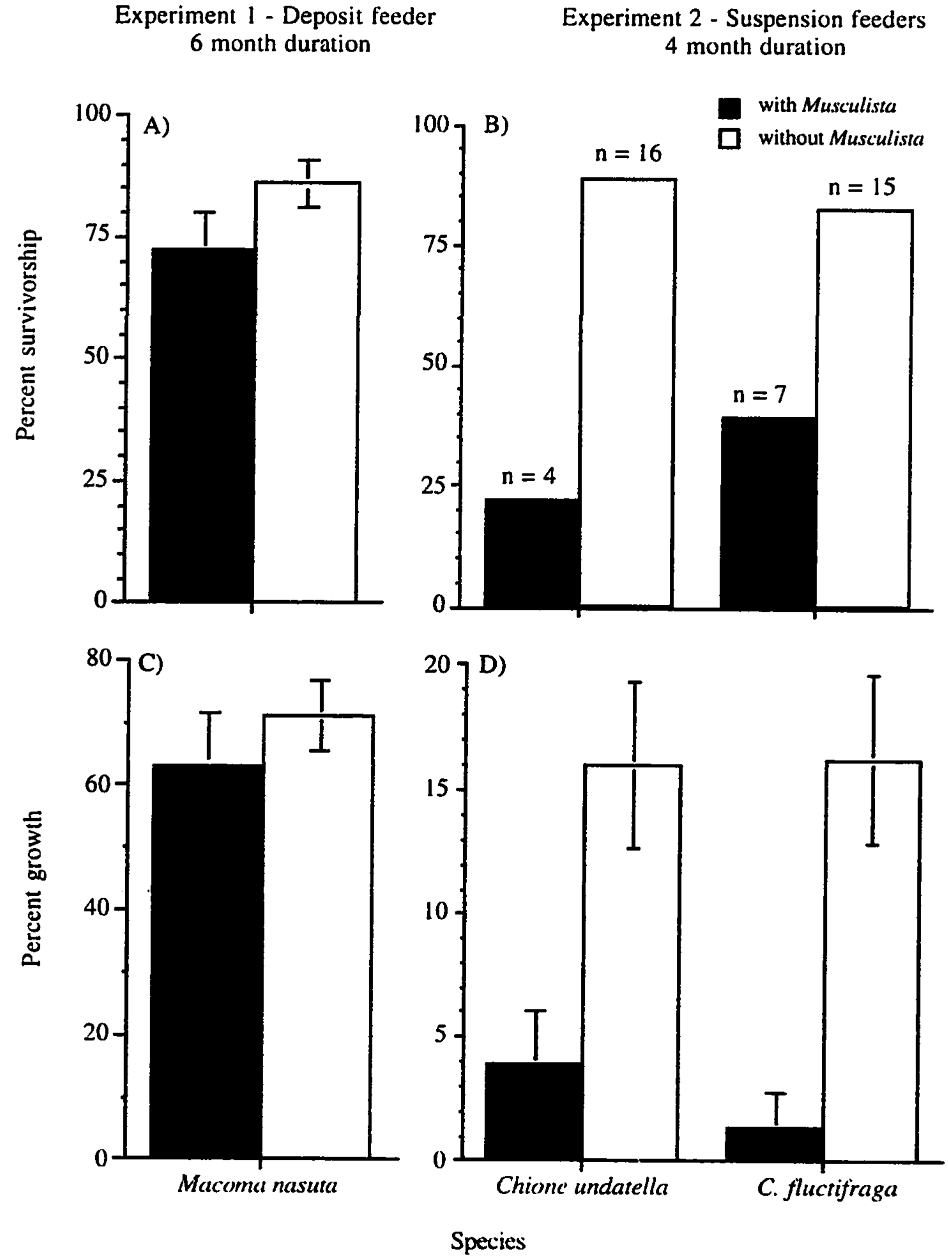

Figure 2-5. Results of experiments testing the effects of *Musculista senhousia* on the survivorship and growth of a deep-dwelling, deposit-feeding clam, *Macoma nasuta* (A and C), and two shallow-dwelling, suspension-feeding clams, *Chione undatella* and *C. fluctifraga* (B and D). n = the number of *C. undatella* or *C. fluctifraga* surviving.

Table 2-1. Bivalve species reported from three different time periods in Mission Bay, San Diego, California. Data are from Orcutt and Dall (1885), Hemphill (1891), Kelsey (1907), Orcutt (1909), Smith (1909), Weymouth (1921), Morrison (1930, 1957), Bonnot (1940), McDonald (1966), Dexter (1983), Hertz and Hertz (1992, pers. comm.), C. Gramlich pers. comm., B. Kubitz pers. comm., S. Rugh pers. comm., and Crooks (pers. obs.). PAN = Panamic province, CAL = Californian province, ORE = Oregonian province. * *Mytilus edulis* complex

Species	1885 - 1919	1920 - 1957	1969 - present	Synonyms	Biogeographic Province
Anomiidae					
Anomia peruviana		x	x	*Anomia lampe*	PAN, CAL
Pododesmus macroschisma		x	x		ORE
Arcidae					
Anadara multicostata		x		*Arca multicostata*	PAN, CAL
Anadara tuberculosa			x		PAN, CAL
Arca mutabilis		x			PAN
Barbatia gradata	x	x		*Arca reticulata*	PAN, CAL
Cardiidae					
Americardia biangulata		x	x	*Trigoniocardia biangulata*	PAN, CAL
Laevicardium elatum	x			*Cardium elatum*	PAN, CAL
Laevicardium substriatum	x	x	x	*Cardium substriatum*	CAL
Trachyardium quadragenarium		x	x	*Cardium quadrigenarium*	CAL
Carditidae					
Glans carpenteri	x	x	x	*Cardita subquadrata* ?	CAL, ORE
Chamidae					
Chama arcana		x	x		CAL
Pseudochama exogyra	x	x	x		ORE
Chlamydoconchidae					
Chlamydoconcha orcutti	x		x		CAL, ORE
Cooperellidae					
Cooperella subdiaphana	x	x	x	*C. scintillaeformis*	CAL, ORE
Corbulidae					
Corbula luteola			x		CAL
Corbula sp.	x				
Cuspidariidae					
Cuspidaria apodema			x		ORE
Donacidae					
Donax californica	x	x	x	*D. flexuosus*	PAN, CAL
Donax gouldii		x	x		CAL
Erycinidae					
Lasaea subviridis			x		CAL, ORE
Hiatellidae					
Hiatella arctica		x	x	*Saxicava arctica*	PAN, CAL, ORE
Panope abrupta		x	x	*Panopea generosa*	CAL, ORE
Leptonidae					
Kellia suborbicularis	x	x	x	*K. laperousii*	PAN, CAL, ORE
Mysella tumida			x		ORE
Thecodonta oblongus			x		CAL
Limidae					
Limaria hemphilli	x	x		*Lima dehiscens*	PAN, CAL

Table 2-1 (cont.)

Lucinidae					
Here richthofeni	x			*Phacoides richthofeni*	CAL
Lucinoma annulata		x		*Phacoides annulata*	ORE
Lucina californica	x	x		*Phacoides californica*	PAN, CAL, ORE
Lucina nuttalli	x	x	x	*Phacoides nuttalli*	CAL
Lucina tenuisculpta			x	*Parvilucina tenuisculpta*	CAL, ORE
Lyonsiidae					
Entodesma pictum			x		PAN, CAL
Lyonsia californica	x	x	x	*L. gouldii*	PAN, CAL, ORE
Mactridae					
Mactra californica		x	x	*Mactrotoma californica*	PAN, CAL
Mactra nasuta	x	x		*Mactra falcata*	PAN, CAL
Spisula hemphillii			x		CAL
Spisula planulata		x		*Mactrotoma planulata*	CAL
Tresus nuttalli	x	x	x	*Schizothareus nuttallii*	CAL, ORE
Myacidae					
Cryptomya californica	x	x	x		PAN, CAL, ORE
Mytilidae					
Adula diegensis		x	x	*Botula diegensis ?*	CAL, ORE
Adula falcata			x		CAL
Brachidontes adamsianus			x		PAN, CAL
Gregariella chenuana	x			*Modiolaria denticulata*	PAN, CAL
Lithophaga plumula			x		PAN, CAL, ORE
Modiolus capax	x	x	x		PAN, CAL
Modiolus flabellatus		x			CAL, ORE
Modiolus rectus	x	x			PAN, CAL
Musculista senhousia			x		Exotic
Mytilus californianus		x			PAN, CAL, ORE
Mytilus edulis *		x	x		
Mytilus galloprovincialis *			x		Exotic
Septifer bifurcatus	x	x	x	*Mytilus bifurcatus*	CAL, ORE
Ostreidae					
Crassostrea gigas		x		*Ostrea laperousii*	Exotic
Ostreola conchaphila	x	x	x	*Ostrea lurida*	ORE
Pectinidae					
Chlamys gigantea	x	x	x	*Hinnites multirugosus*	CAL, ORE
Argopecten vestalis		x	x	*Pecten circularis aequisulcatus*	PAN, CAL
Pecten diegensis		x			CAL, ORE
Leptopecten latiauritus	x	x		*P. monotimeris* (sub-species)	CAL, ORE
Periplomatidae					
Periploma discus			x		CAL
Petricolidae					
Petricola carditoides	x	x			CAL, ORE
Petricola californiensis			x		CAL
Petricola denticulata		x			PAN, CAL
Pholadidae					
Barnea subtruncata			x		PAN, CAL, ORE
Penitella gabbi		x		*Zirfaea gabbi*	CAL, ORE
Penitella penita		x		*Pholadidea penita*	CAL, ORE
Zirfaea pilsbryi		x	x		CAL, ORE

Table 2-1 (cont.)

Psammobiidae					
Gari californica	x	x		*Psammobia rubroradiata*	CAL, ORE
Heterodonax pacificus	x	x	x	*Heterodonax bimaculata*	PAN, CAL
Nuttallia nuttallii		x	x	*Sanguinolaria nuttallii*	CAL, ORE
Tagelus californianus	x	x	x	*Solecurtus californianus*	CAL, ORE
Tagelus subteres	x	x	x	*Solecurtus subteres*	CAL
Pteriidae					
Pteria sterna		x	x		Exotic?
Semelidae					
Cumingia californica			x		CAL, ORE
Cumingia lamellosa		x	x		PAN
Semele decisa	x	x	x		CAL
Semele pulchra		x			PAN, CAL
Semele rubropicta		x			CAL, ORE
Semele rupicola		x	x		CAL, ORE
Theora fragilis			x	*Theora lubrica*	Exotic
Solenidae					
Ensis myrae		x		*E. californicus*	CAL
Siliqua lucida		x	x		CAL, ORE
Solen rosaceus	x	x	x		CAL
Tellinidae					
Leporimetis obesa	x	x		*Metis alta, Lutricola alta*	CAL
Macoma indentata	x	x	x		CAL, ORE
Macoma inquinata	x		x		CAL, ORE
Macoma nasuta		x	x		CAL, ORE
Macoma secta	x	x	x		CAL, ORE
Tellina bodegensis	x		x		CAL, ORE
Tellina carpenteri		x	x		PAN, CAL, ORE
Tellina idae			x		CAL
Tellina modesta		x	x	*T. buttoni*	CAL, ORE
Thraciidae					
Cyathodonta dubiosa		x			PAN, CAL
Thracia curta		x			CAL, ORE
Thyasiridae					
Thyasira sp.			x		
Ungulinidae					
Diplodonta orbella		x	x		PAN, CAL, ORE
Veneridae					
Amiantis callosa		x			CAL
Chione californiensis	x	x	x	*C. succinta*	PAN, CAL
Chione fluctifraga	x	x	x		CAL
Chione undatella	x	x	x	*C. simillima*	PAN, CAL
Irusella lamelliffera		x		*Venerupis lamelliffera*	CAL, ORE
Mercenaria mercenaria			x		Exotic
Protothaca laciniata	x	x	x	*Paphia laciniata, Tapes laciniata*	CAL
Protothaca staminea	x	x	x	*Paphia staminea*	CAL, ORE
Protothaca tenerrima			x		CAL, ORE
Ruditapes phillipinarum			x		Exotic
Saxidomus nuttallii	x	x	x	*S. aratus*	CAL, ORE
Tivela stultorum	x	x		*T. crassetelloides*	CAL

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CHAPTER III

BENTHIC COMMUNITIES AND THE INVASION OF AN EXOTIC MUSSEL ALONG A GRADIENT OF FLUSHING IN AN URBANIZED BAY: A LONG-TERM HISTORY

Abstract

Mission Bay is a highly modified lagoon in the densely populated city of San Diego, California. As gradients of flushing and organic enrichment have been reported in the bay, data on benthic invertebrate populations from long-term sampling were viewed in the context of the Pearson and Rosenberg Model (PRM), which relates flushing and organic enrichment of sediments to species diversity, abundance of individuals, and total biomass. These results reveal that communities in the back of the bay are characterized by low diversities and abundances, while those nearer the mouth have higher diversities and abundances. Communities near the middle of the bay have high densities of opportunistic species. In general, the patterns of species richness and abundance of individuals in the bay are similar to other locations having gradients of flushing and organic enrichment as described by the PRM. One departure from model predictions, however, is the dominance of suspension-feeding organisms in the back bay. This can primarily be attributed to the increased dominance of an exotic, suspension-feeding mussel, *Musculista senhousia*. This small Asian mytilid has become particularly abundant in the middle portions of the bay at a point corresponding with the peak of opportunists in the PRM. It is suggested that such areas may be particularly vulnerable to invasion and that the PRM might be used to predict the success of exotic species in other systems.

Introduction

Estuarine benthic communities exposed to gradients of flushing and organic enrichment, established by patterns of estuary – ocean exchange and input of organic-rich material in the form of point-source outflows or urban runoff, often respond similarly (Pearson and Rosenberg 1978; Bonsdorff 1980; Heip 1995). A model for the relationship between organic enrichment and benthic community structure, in terms of species richness, abundance and biomass, has been developed (Pearson and Rosenberg 1978). The Pearson Rosenberg Model (PRM) predicts that areas with low flushing and high organic enrichment tend to have relatively depauperate communities, with low abundances and diversities. Sites with intermediate levels of flushing are characterized as having high densities of opportunistic species. In well-flushed sites, abundances drop but species richness increases.

Mission Bay is a 1862-ha, highly altered coastal lagoon in San Diego, California (Fig. 3-1). The physical and hydrographic characteristics of the bay establish a gradient of flushing and organic enrichment (Taylor 1982; California Coastal Commission 1987; Marcus 1989; Largier et al. 1997). Near the mouth, flushing is relatively vigorous (San Diego City Planning Department 1957; San Diego Water Utilities Department 1978). In the back bay, flushing is sluggish and waters tend to be more turbid because of increased distance from the mouth and the presence of a large, artificial island (Fiesta Island) which creates two narrow, dead-end channels (San Diego Water Utilities Department 1978). Drift tube and fluorescene dye studies also suggest higher retention times for this region (Levin 1983). Mission Bay is seasonally hypersaline, with warmer waters and higher salinities in the back bay during the summer months, which serves to further reduce bay-ocean mixing (Levin 1983; Largier et al. 1997). Compounding the effects of low flushing in the back bay is the input of organic-rich urban runoff from two creeks (San Diego Water Utilities Department 1978; Marcus 1989). Although quantitative sedimentary data for the bay are limited, recent data are characteristic of the different flushing regimes (Fairey et al. 1997). In the back bay, combustible organic matter is high (2.5 - 2.6%) and sediment grain sizes are small (78 - 93% fine sediments < 63µm). Nearer the entrance of the bay, there is less organic matter (0.61%) and grain sizes are larger (33% fines).

Within Mission Bay, regular sampling of the subtidal, soft-bottom benthos, conducted in conjunction with a course in biological oceanography at San Diego State University, began in 1970. During the first 8 years, sampling was carried out close to the entrance of Mission Bay (Dexter 1983). Beginning in 1977, sampling began around Fiesta Island at sites situated increasing distances from the mouth and ending at the dead-ends of the two passages (Fig. 3-1). In this paper, we will determine if the faunal communities at these stations are indicative of the reported flushing regimes. Specifically, we will describe 1) the benthic communities (including total densities, total biomass, and species richnesses) at the stations, evaluated in the context of the PRM, 2) changes in the macrofaunal communities over time, 3) correlations among dominant macrofaunal species, with an emphasis on an exotic mussel, *Musculista senhousia*, and 4) the changes in the *M. senhousia* population over time.

Methods

Sampling was conducted on 16 dates from 1977 to 1996 (primarily in the late summer or winter). On each sampling date, four to seven replicate grab samples of approximately 0.1 m^2 surface area were taken within a 3-6 m radius at each station, which ranged in depth from 3.8 to 5 m. The Hayward orange-peel grab used for sampling penetrated approximately 15 cm into the substrate. A total of 463 grabs were collected, and the mean sample volume was 4.50 l. Sampling was conducted at 7 stations, one of which (Station B) was an original station (Fig. 3-1). Stations A,B,C, and F were sampled on every date (16 times), Station E was sampled on 14 dates, and Stations D and G were sampled 11 times each.

Sediment was wet sieved through 750-µm mesh, and material retained on the sieve was stained with rose bengal and preserved in 5% buffered formalin. Samples were sorted under a dissecting microscope, and all macrofauna were transferred to alcohol, counted, and identified to the lowest taxonomic level possible. All collected specimens from each core were also wet-weighed together to provide a total weight. This information was used to characterize macrofaunal communities in terms of species richness, total density of individuals, densities of major macrofaunal taxa, and biomass. In addition, feeding modes of species were also determined (Fauchald and Jumars 1979; Morris et al. 1980).

Certain species were identified as community dominants, and their distribution and abundances were selected for further analysis. The following criteria were applied to determine community dominants. The species 1) was present at one or more stations on at least 90% of the sample dates between 1977 through 1996, 2) comprised at least 5% of the individuals, and 3) was present on at least 40% of the sample dates at any single station.

In order to investigate the population dynamics of *M. senhousia*, lengths of the mussel were measured to the nearest 1 mm using vernier calipers on all intact specimens, unless very large numbers were collected. In these cases, a plankton splitter was used to subdivide large samples to obtain an unbiased representative subsample of 100-200 individuals.

In this study the sampling unit was considered to be a station, and station means were used for spatial and temporal comparisons. For calculations of means and standard errors, data were log (x+1) transformed and subsequently back-transformed for graphical presentations. In order to examine relationships between dominant species, Spearman rank correlations were calculated for all dates pooled (using station means). Because of the number of comparisons made, only those with a $P < 0.001$ were considered significant. Similarities of communities were calculated using the Bray-Curtis coefficients of community similarity (Krebs 1989). Both the spatial variation among replicates within a station (i.e., within-sampling unit variability) at any one time and temporal variation at a station over time also were examined.

In order to investigate general relationships between the communities at the sites, non-metric multi-dimensional scaling (MDS) was used (Clarke and Warwick 1994; ter Braak 1995). This technique provided the best two-dimensional configuration of samples using a Bray-Curtis similarity matrix comparing each station with all other stations. Two MDS plots were constructed. The first compared all stations, with data averaged across all years (only using dates in which all stations were sampled). The second compared the five most frequently sampled stations, using the averages of samples from summer months and the averages of samples from winter months. Data for MDS analyses were non-transformed and non-standardized.

Results

Dominant Species

The macrofauna of Mission Bay were primarily dominated by molluscs and polychaetes; the two groups combined accounting for 75 to 91% of all fauna at the stations (Table 3-1). Station A, closest to the mouth, had the most distinctive representation of these taxa, with relatively many polychaetes and few molluscs. Eight species (or species complexes) were identified as community dominants at the stations (Table 3-2). These included three suspension feeders (the exotic mussel *Musculista senhousia*, the sabellid polychaete *Euchone limnicola*, and the phoronid *Phoronis* sp.), one carnivorous polychaete (*Nereis arenaceodentata*), and four polychaete deposit feeders (*Lumbrineris* sp. (= *L. minima* in Dexter (1983)), the flabelligerid *Diplocirrus* sp., the cirratulid *Tharyx* sp., and the maldanid *Praxillella pacifica*).

In the early studies of Mission Bay, the deposit feeding polychaete *Lumbrineris minima* (Dexter 1983) was identified as the community dominant. In the current study, *Lumbrineris* sp. was still widely distributed throughout the bay, and population densities were consistently high at Station A (Fig. 3-2). The other deposit-feeding community dominants include *P. pacifica*, a large, head-down conveyor belt feeder, which was rare at most stations but attained high densities at Station A. *Tharyx* sp. was present at low densities at most stations, and reached highest densities at Stations D and F. The flabelligerid *Diplocirrus* sp. (= *Pherusa neopapillata* in Dexter (1983)) occurred at low densities at all stations except Station A. The suspension-feeding polychaete *E. limnicola* was present at all stations, although it occurred infrequently and at low densities at Stations D and E (Fig. 3-3). The populations of *Phoronis* sp. fluctuated widely; highest densities occurred at Station B, with moderate densities at Station C. It was rare at Station A. Densities of the predator *N. arenaceodentata* were generally the lowest of all the dominant species, but it was persistent throughout most stations, with less frequent occurrence at Station A.

Occasionally, other species were abundant in the benthos (i.e., comprising greater than 20% of the individuals at a specific station). These included the gastropod *Acteocina inculta* (Stations C and F in 1977; Station D in 1979), the polychaetes *Leitoscoloplos pugettensis* (= *Haploscoloplos elongatus* in Dexter (1983); Station E in 1980), *Chaetozone corona* (Stations F and G in 1980), and *Armandia brevis* (Station E in 1991), an unidentified turbellarian flatworm (Station E in 1981), the amphipod *Aoroides columbiae* (Station E in 1981), and the isopod *Paracerceis gilliana* (Station D in 1985).

Correlations Among Dominant Species

There were significant Spearman rank correlations ($P< 0.001$) among the distribution of some of the community dominants (Table 3-3). *Musculista senhousia* correlated negatively with one suspension-feeding polychaete (*Euchone limnicola*) and one deposit-feeding polychaete (*Diplocirrus* sp.), and positively with one predatory polychaete (*Nereis arenaceodentata*). These relationships may represent possible interspecific interactions as well as spatial or temporal differences in habitat utilization of the species . For example, the negative correlation between *Phoronis* sp. and *Praxilella pacifica* may represent different habitat preferences as the former was rare at Station A whereas the latter was most abundant there.

Spatial and Temporal Comparison of Communities

Although many of the common species in the bay could be found at all 7 stations, distinguishing features in the macrofaunal communities existed (Table 3-4). Three stations, in particular, could be recognized as relatively distinct. Station E, the poorly-flushed site at the mouth of Tecolote Creek, had the lowest averages of species richness, biomass, and density. Station A, which receives greater tidal flushing due to its proximity to the entrance channel of Mission Bay (Fig. 3-1), had the second highest average species richness, and relative abundance among the dominant species differed from all other stations. Biomass at this station was relatively low, and density intermediate. Station B, at the northern end of Fiesta Island, had the highest average biomass, macrofaunal density, and species richness.

MDS of the average species compositions at the stations provides another perspective on the general relationships between the communities (Fig. 3-4A). Stations A and E appear to be quite distinct from the other stations and each other. The remaining stations appear to cluster together, with Station B being most similar to

Station A. Stations G and D, which both reside in small coves on different sides of Fiesta Island, also appear relatively similar to each other. The analysis of five stations in summer and winter months reveals some seasonality in the faunal communities, as the summer and winter communities from a given station appear relatively distinct (Fig. 3-4B). Station A had the highest similarity between the summer and winter months, while Station E had the lowest similarity. The back-bay / front-bay gradient observed in the overall MDS (Fig. 3-4A) is also evident in both seasons. In both winter and summer, Station E is most similar to Stations F and C and least similar to Stations B and A.

Variability of the macrofaunal community composition at each station was examined from two perspectives: spatial variability of samples taken on any one sampling date and temporal variability at the station across years (Table 3-3). In general, the average within-year and between-year similarities tended to be correlated ($R^2 = 0.68$ using exponential regression), indicating that stations that tended to be spatially variable at any one time also tended to be variable over time. Of all stations, the highest heterogeneity (i.e., lowest similarity), for both within-year and between-year comparisons, was found at poorly-flushed Station E. Station A, near the front of the bay, was least variable over time, with the highest within-year (along with Station B) and between-year coefficients of similarities.

The densities of suspension and deposit feeders present at each site fluctuated considerably over time (Fig. 3-5). Suspension feeders showed relatively large temporal variability, with an average coefficient of variation across stations that was over 50% greater than that for deposit feeders ($P<0.001$; $t_6 = 9.68$, paired t-test). Differences also existed between the representation of suspension and deposit feeders at the stations. At Station A, deposit feeders consistently outnumbered suspension feeders. Station G also showed a trend for higher representation of deposit feeders (occurring on 7 out of the 11 dates), as well as a general trend for increased densities over time.

Species richness patterns at the stations also displayed temporal variability (Fig. 3-6). In general, there was an increase in the number of species per grab in the mid-1980's. This was followed by a decline and a subsequent increase in the 1990's. Station G appears to have had a relatively large increase in species richness over the course of the sampling.

Musculista senhousia

The exotic mussel, *M. senhousia* has become one of the most dominant species in the bay. This small, Asian mytilid was found at all stations, although it was very rare at Station A (Fig. 3-3). At stations B, C, D, E, and G, *M. senhousia* was on average the most abundant species collected, and at Station F it was the second most abundant (Table 3-2). Although typically displaying variable densities, *M. senhousia* has shown a general pattern of increased abundance within the bay. Densities reached a peak around 1988, but dropped off dramatically over the following three years. Similar to the patterns of species richnesses, densities have subsequently increased again in the 1990's.

M. senhousia in the subtidal of Mission Bay appears to be short-lived and fast-growing, as has been reported for intertidal Mission Bay populations (Crooks 1996). The size frequency histograms of *M. senhousia* display unimodal or bimodal distributions, suggesting the presence of only one or two year classes at any given time (Fig. 3-7). Modal sizes of mussels can change rapidly. For example, in January of 1983 there was a unimodal peak at 21.5 mm, with few small individuals present. Eight months later, the modal size of that cohort was 25.5 mm, and another cohort is evident with a mode 15.5 mm. Four months later, the modal size of this second cohort was

21.5 Growth in 1992 appears to have been less rapid, as the modal size did not change from January to June. The mean size of individuals, however, increased by 5 mm. There appears to be considerable variability of recruitment events of the population. Generally, the mean size of individuals is smaller in August and September, and larger in January and February.

To investigate relationships between the abundance of *M. senhousia* and the community parameters of species richness and total macrofaunal densities, regressions were performed on means of each station (excluding Station A, as the mussel was rarely found at this site) across all years (Fig. 3-8). Despite the increased dominance of *M. senhousia* in the bay, neither relationship was negative. There is no significant relationship between density of all other organisms combined and density of *M. senhousia* (Fig. 3-8A), and there is a significant positive relationship between number of other species present at a station and the density of the mussel (Fig. 3-8B).

Station B from 1970-1996

The benthos at Station B has been sampled on 21 dates between 1970 and 1996. In that time, there is no evidence of reduction in density or species richness (Fig. 3-9A). There has, however, been a shift in the feeding modes of the species present at the station. Prior to 1977, the community was dominated by deposit feeders (6 of 7 dates;. 3-9B). After 1977, suspension-feeders have been more abundant (9 of 12 dates). Much of this can be accounted for by the increased abundance of the suspension-feeding *M. senhousia* (Fig. 3-8A). In some years (e.g., 1985 and 1988), this invader can account for a large percentage of all fauna found at the station (Fig. 3-8A).

The abundant invertebrate macrofaunal organisms (e.g., *Lumbrineris* sp., *Diplocirrus* sp.) present in the early stages of invasion by this mussel are still present. The negative relationship between *M. senhousia* and *E. limnicola* (Table 3-1) is evident at this station, as the latter species is rare when the mussel is abundant (Fig. 3-3). Also, there is a possible negative relationship between the mussel and the deep-dwelling bivalve *Solen rosaceus*, which was identified as a dominant at this station in the early studies (Dexter 1983). Its average density between 1970 through 1987 (294 individuals collected) was $40/m^2$, but had declined to $2.5/m^2$ between 1988 through 1996 (6 individuals collected).

Discussion

The relationships between the faunal communities and flushing in Mission Bay (Fig. 3-10) correspond fairly well to general patterns of the PRM (Pearson and Rosenberg 1978; Long and Chapman 1985; Jensen 1986; Brown et al. 1987; Friligos and Zenetos 1988; Heip 1995), although a few differences from the general model were found. Station E appears to be a moderately polluted site, as number of species, biomass, and total abundance are all relatively low. Both the temporal and spatial variability exhibited here are high (Table 3-4B). Progressing to a less enriched areas, the model predicts a point called the "peak of opportunists" (Pearson and Rosenberg 1978). In this area, more species are found, and some of them are able to thrive, causing abundance to be very high. Typically, biomass does not greatly increase as these opportunists usually tend to be small in body size (Pearson and Rosenberg 1978). However, in Mission Bay, biomass is high at Station B, which appears to correspond with this point. Much of this can be attributed to the prevalence of the relatively large *M. senhousia*. As flushing increases and enrichment decreases, there is an ecotone and a transition to a "normal" community. Here, abundances drop, species richness remains high, and the community appears fairly stable over time. At Station A, there is a considerable drop in total density, due primarily to the loss of *M. senhousia*, but species diversities at the station are comparable to those at Station B (Table 3-4A). The pattern of gradual replacement of suspension feeders by deposit feeders along a gradient of increasing enrichment and decreasing grain size (Sanders 1958; Franz 1976; Pearson and Rosenberg 1978), the generality of which has been questioned (Snelgrove and Butman 1994), does not appear to hold in Mission Bay. Again, this appears to result at least in part from the invasion of the suspension-feeding mussel, *M. senhousia*, which has the ability to achieve high abundances in soft sediments.

Over the course of the sampling in Mission Bay, there have been major fluctuations in the densities of some of the dominants, especially among the suspension feeders (Fig's 3-3 and 3- 5). In contrast, the densities of the dominant deposit feeders fluctuate less (Fig's. 3-2 and 3-5). In support of the observation that populations of suspension feeders tend to fluctuate more than deposit feeders (Levinton 1972), suspension-feeders as a group tended to display considerably more temporal variability than deposit feeders (Fig. 3-5). There is also some seasonality evident in the bay, although the relationships between the stations are consistent in both summer and winter (Fig. 3-4). In addition, there appears to be a general trend for increased species richnesses over time at several stations in the bay (e.g., Stations A, C, and G; Fig. 3-6). The timing of this increase tends to correspond with the increase in *M. senhousia* population densities (Fig. 3-3), and may represent a response to some change in environmental conditions.

One striking feature of the faunal composition in the bay is this increased dominance by the mussel *M. senhousia*. The presence of this accidentally-introduced mussel was first noted in the intertidal salt marsh creeks of Mission Bay in the mid-1960's (MacDonald 1969). It was very rare within the Mission Bay sampling during 1970 through 1976; only 15 specimens among over 20,000 benthic invertebrates were collected (Dexter 1983). Since then, over 15,000 *M. senhousia* have been collected in our quantitative studies. *Musculista senhousia* appears to be well suited as an estuarine invader. It has anatomical adaptations to living in and processing fine sediments, broad temperature tolerances, and plastic habitat requirements (Morton 1974; Crooks 1992, 1996). *M. senhousia* also has life-history characteristics typical of the classic weedy, invasive species. The species is short-lived (maximum of 2 years) and fast-growing, attaining sizes of 25 mm within 1 year. The mussel also has flexible reproduction and recruitment periodicity (Crooks 1996 and references therein). These traits were observed in the current study.

The potential effects of this invader are varied and appear to be scale-dependent (Chapters 5 and 6). At small spatial scales, mussel mats have been reported to facilitate macrofauna. In the intertidal of Mission Bay, species richness, total macrofaunal densities, and densities of taxa such as crustaceans, small gastropods, and insect larvae are higher within mussel mats (Chapter 5). Similar increased densities or species richnesses of small macrofauna have also been reported in Hong Kong (Hutchings and Wells 1992) and New Zealand (Creese et al. 1997). These patterns appear related to the increased structural complexity and provision of biogenic habitat created by mussel mats (Chapters 5 and 6). In this study, the positive relationship between species richness and abundance of *M. senhousia* (Fig. 3-7B) could reflect a positive effect of the mussel. However, this also could be accounted for by similar responses of *M. senhousia* and other species to environmental conditions. Such an explanation might be favored by noting the resemblance of the species richness curve (Fig. 3-6) for Station A (where the mussel is rare and therefore would be unlikely to affect other species), and the curve of average *M. senhousia* densities over time (Fig. 3-3).

At larger spatial scales, *M. senhousia* appears to have negative effects on resident biota. Descriptive studies of bivalve abundances, as well as laboratory and field experiments, demonstrate negative effects of the mussel on abundance, growth, and survivorship of native clams (Sugawara et al. 1961; Anonymous 1965; Uchida

1965; Willan 1987; Crooks 1992; Creese et al. 1997; Chapter 2). Thick mats of *M. senhousia* can also inhibit vegetative propagation of the eelgrass *Zostera marina* (Reusch and Williams 1998). In this study, bivalves such as *Solen rosaceaus, Tagelus californianus*, or *Laevicardium substriatum* were not sufficiently abundant to document negative correlations, although there has been a substantial decrease in the *Solen rosaceus* in the same time frame as the increase of *Musculista senhousia.* Negative correlations were reported between *M. senhousia* and the polychaetes *Euchone limnicola* and *Diplocirrus* sp. One possible explanation for this is that both these species live in tubes which protrude above the sediment surface, and could thus be negatively impacted by the dense byssal mats of *M. senhousia.* Similarly, densities of the intertidal, tube-building polychaete *Pseudopolydora paucibranchiata* were lower in experimental plots containing artificial mussel mats (Chapter 5). However, this tube-builder was not found in lower abundances within natural mussel mats (Chapter 6). Experimental manipulations would be necessary to further evaluate the relative importance of competitive interactions and responses to environmental factors in shaping these benthic communities.

Within Mission Bay, the higher representation of *M. senhousia* in the back bay compared to the front bay (Table 3-2) appears to be a fairly general pattern that can be observed with other exotic species. For example, in San Francisco Bay, the percent of native molluscs is greater in the mouth of the bay and nearer the open ocean than towards the upper reaches (Hopkins 1986; Nichols and Pamatmat 1988). Such patterns appear to fit the general positive relationship between a decline in habitat quality and the abundance of exotic species (e.g., Elton 1958; Orians 1986; Hobbs 1989; Pysek 1993; Kowarik 1995). In addition, this pattern could be explained by the prevalence of bay-to-bay transport mechanisms for marine exotics, which would tend to move more bay species than species associated with the open ocean (Carlton 1979; Cohen and Carlton

1998). For *M. senhousia* in Mission Bay, however, the sedimentary parameters known for Station A (where the mussel is rare) are well within the reported range for the species (Crooks 1992). Although densities of *M. senhousia* increase towards the back of Mission Bay, densities decrease again as flushing decreases (even though percent representation remains high; Table 3-2). It is likely that degraded conditions limit this species. Although *M. senhousia* is known to tolerate some degree of organic enrichment, mussels disappear from the highly enriched areas beneath fish pens in Japan (Tsutsumi et al. 1991).

The long-term sampling of Mission Bay has revealed that the PRM, in general terms, appears to describe the benthic communities in relation to the gradient of flushing in the bay. The success of the invasive mussel, *M. senhousia*, at a point intermediate in the gradient of habitat degradation and corresponding to the peak of opportunists in the PRM, suggests that areas such as this may be particularly vulnerable to invasion by non-native species (see also Kowarik 1995 for terrestrial ecosystems). Further studies of the distribution of exotics in other bays and estuaries, evaluated in the context of the PRM, would help to demonstrate if this model can be used to predict the success of invasive species.

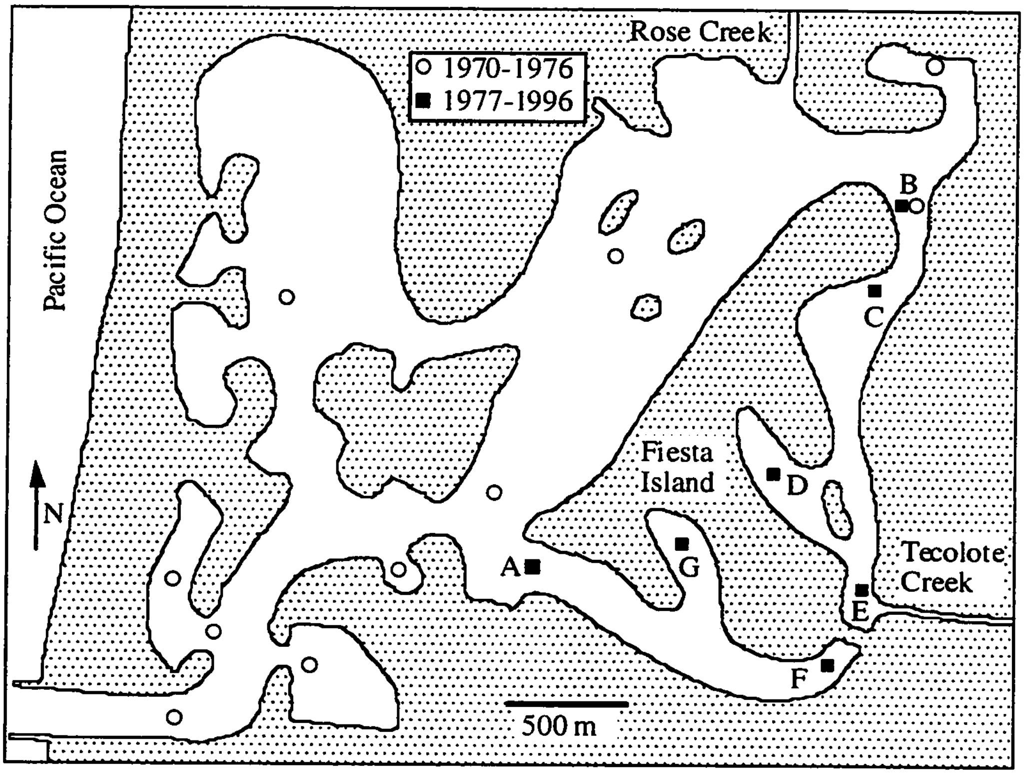


Figure 3-1. Mission Bay, San Diego, California, showing sample sites in this and a previous study (Dexter 1983).

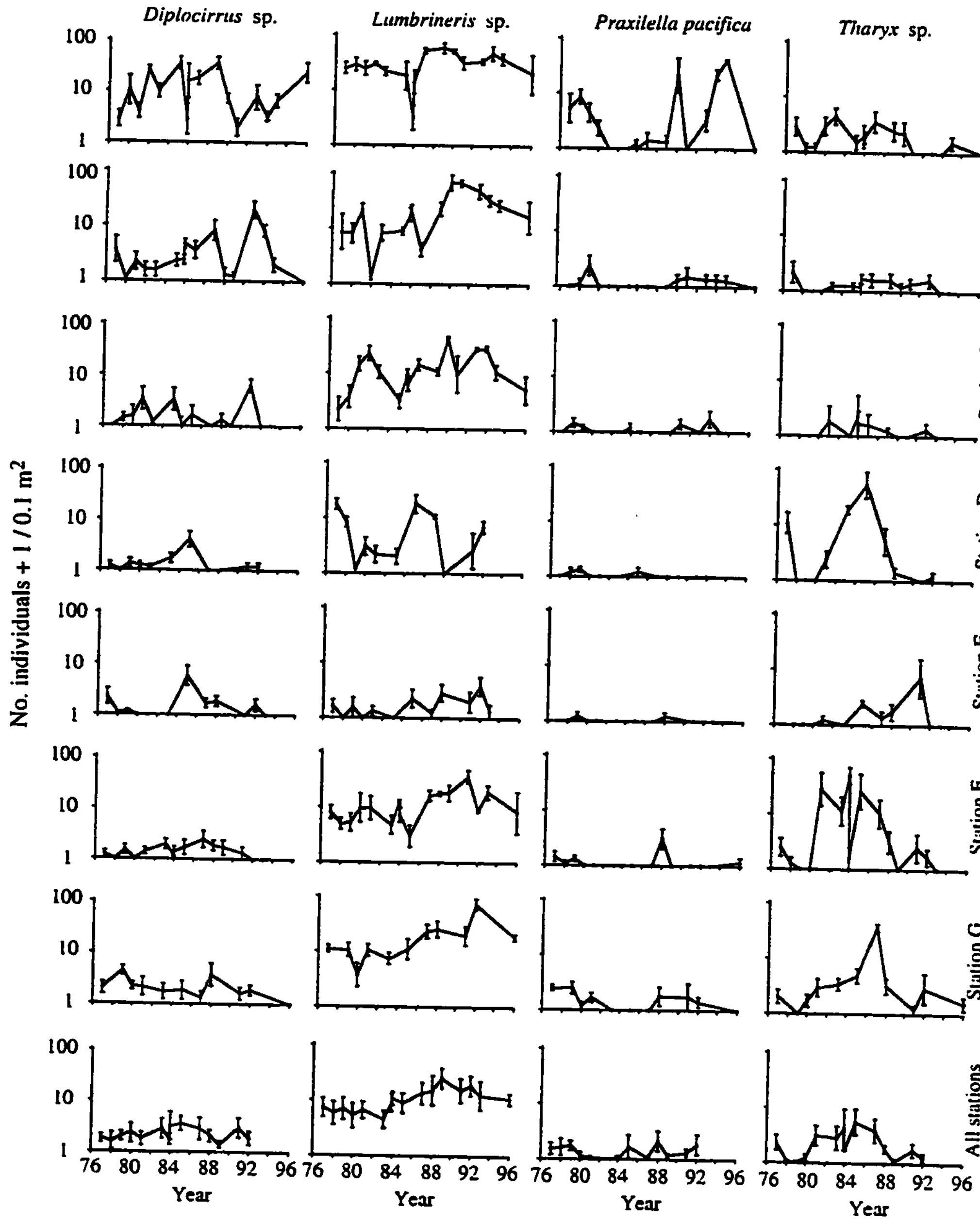


Figure 3-2. Mean abundances (± 1 s.e.) of the dominant deposit-feeding species.

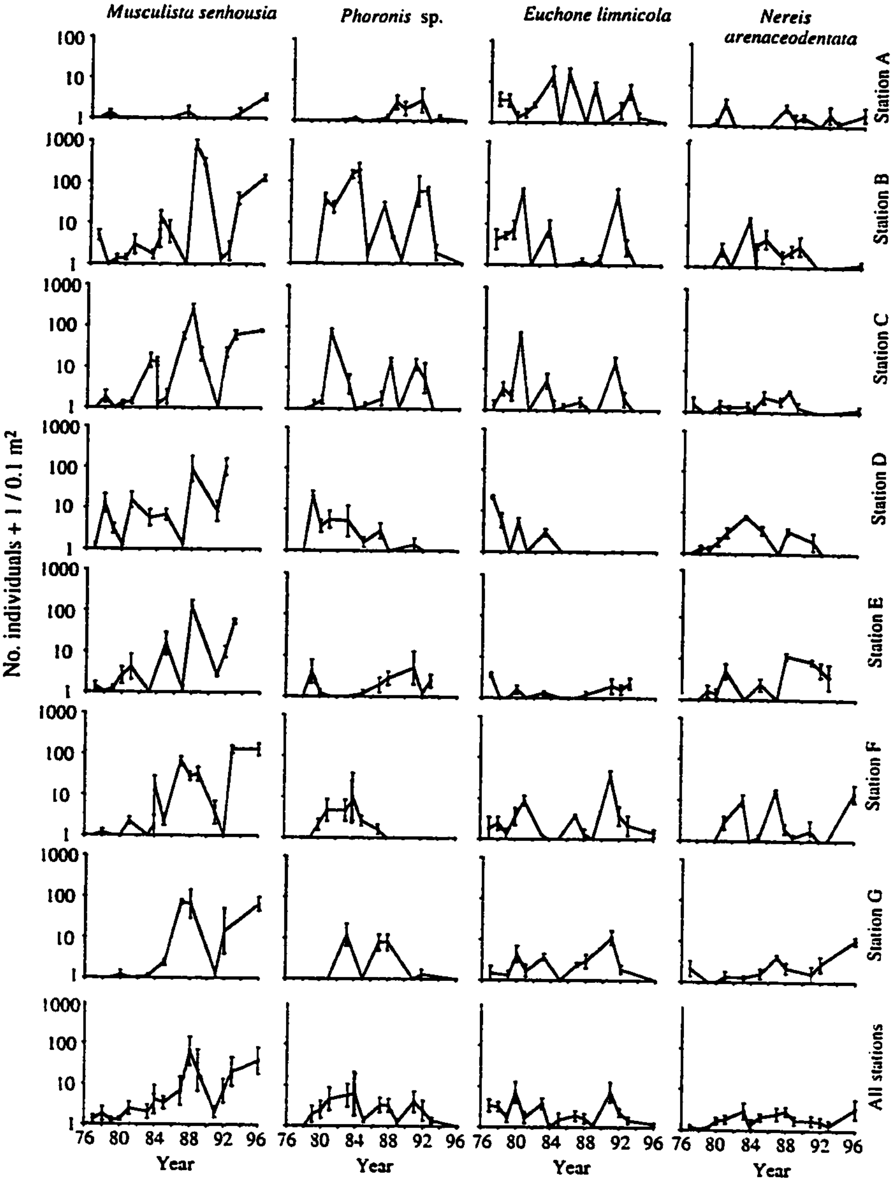


Figure 3-3. Mean abundances (± 1 s.e.) of the dominant suspension-feeding and carnivorous (*Nereis arenaceodentata*) species.

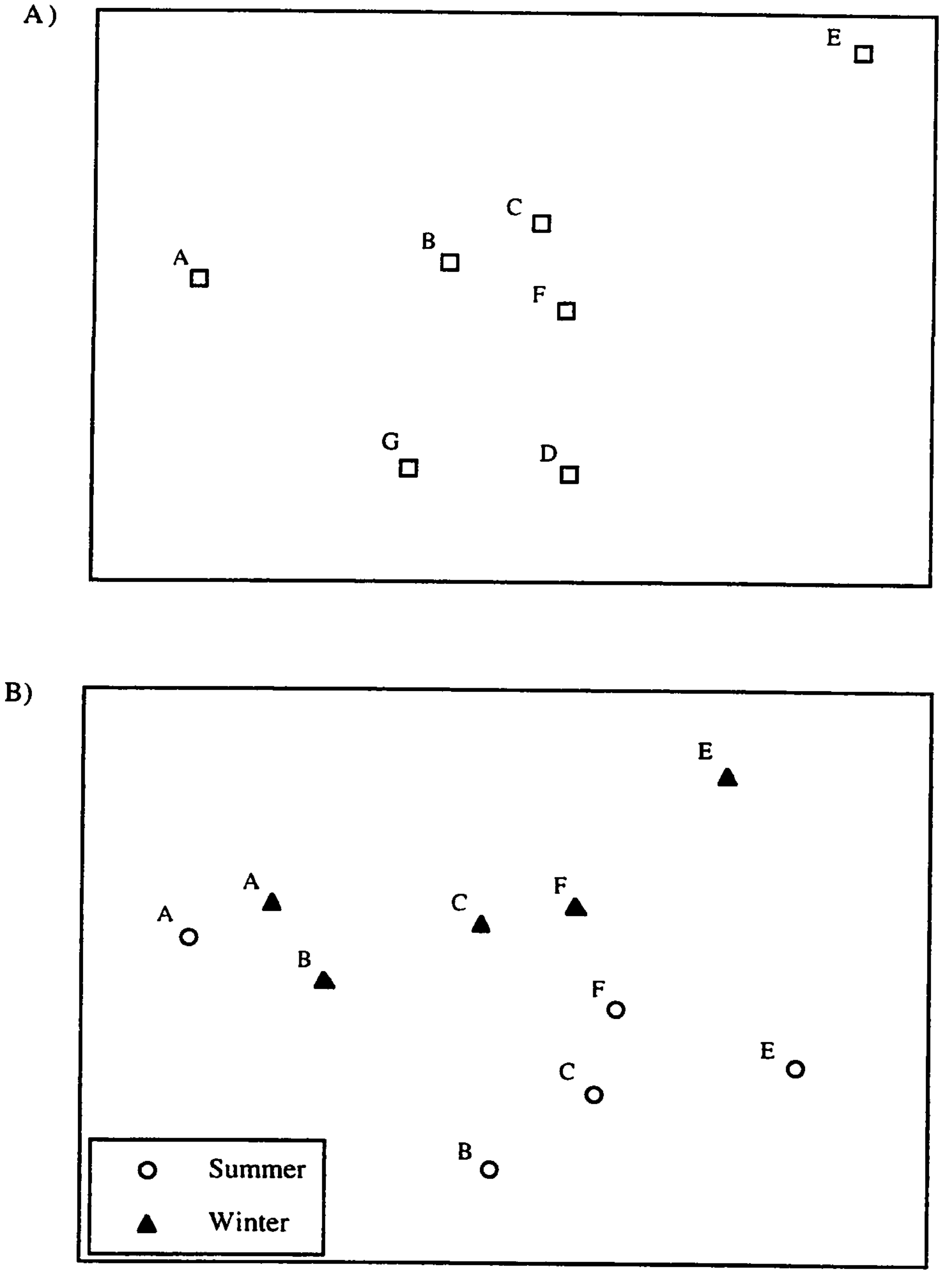


Figure 3-4 Results of non-metric multi-dimensional scaling (MDS) analyses for A) each station averaged across all dates (stress = 0.01), and B) stations A,B,C,E, and F for summer and winter samples (stress = 0.05).

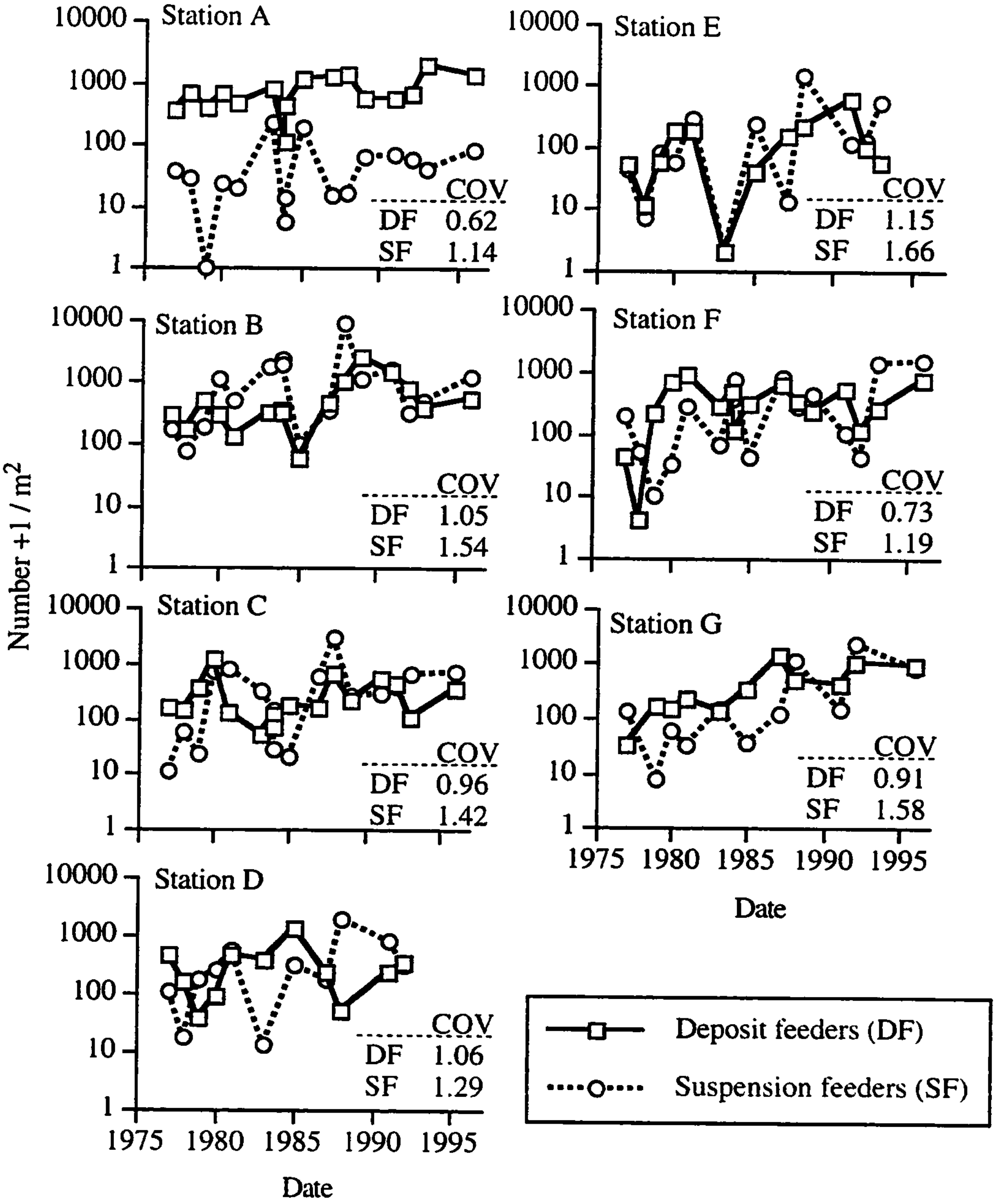


Figure 3-5. Average densities of suspension feeders and deposit feeders over time. Coefficients of variation (COV) are also provided.

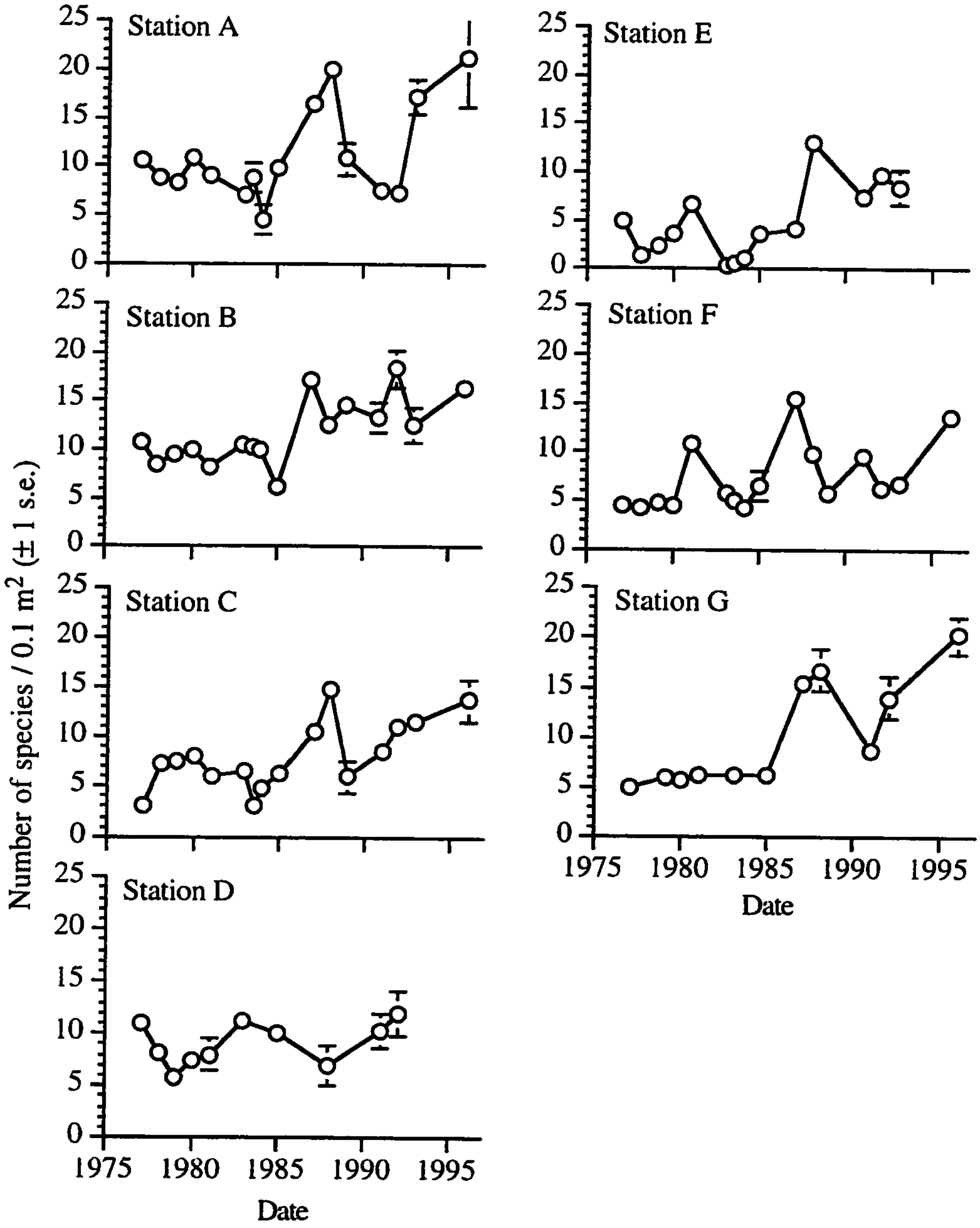


Figure 3-6. Species richnesses over time at the stations.

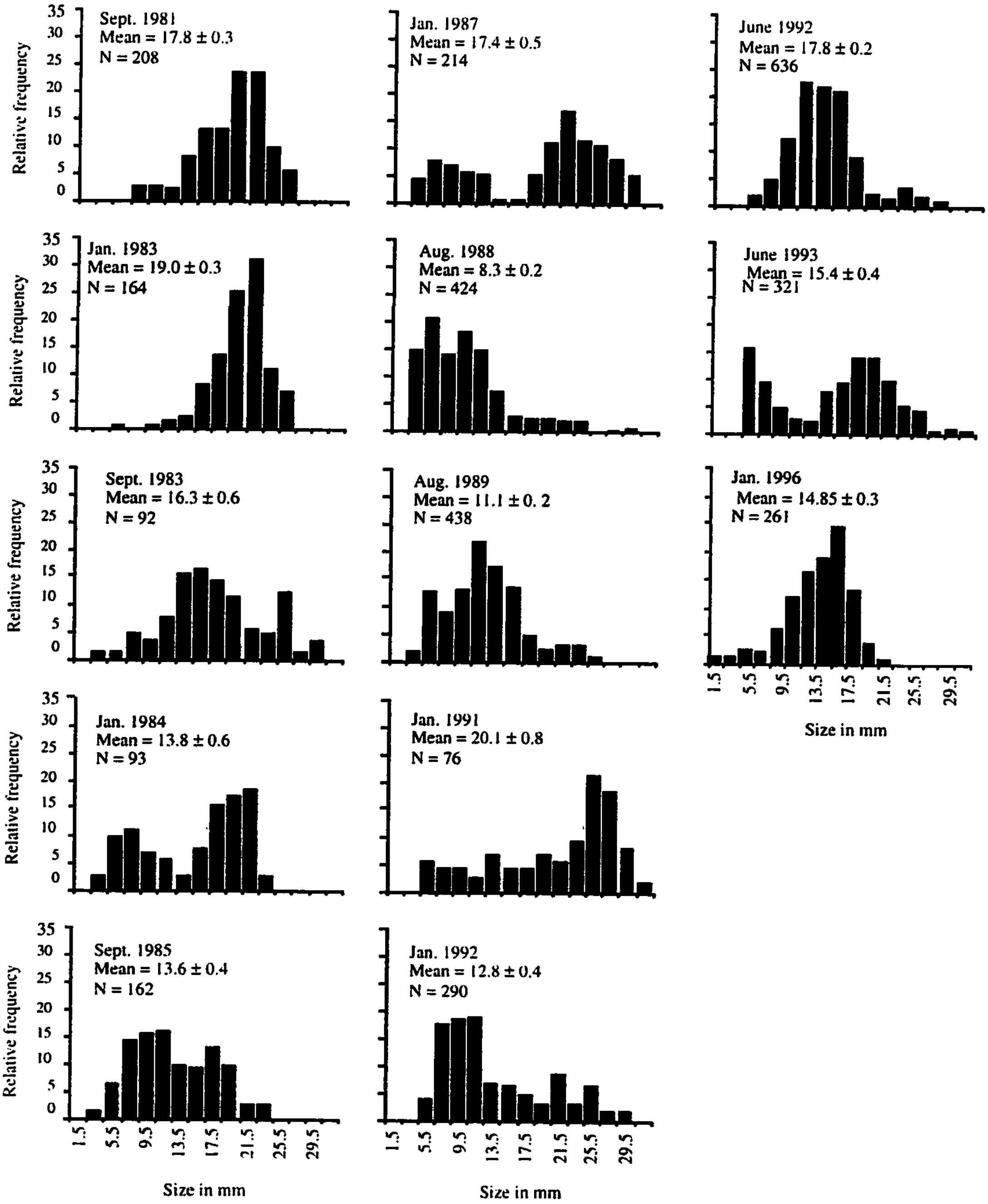


Figure 3-7. Length-frequency distribution of *Musculista senhousia*. N = number of mussels measured.

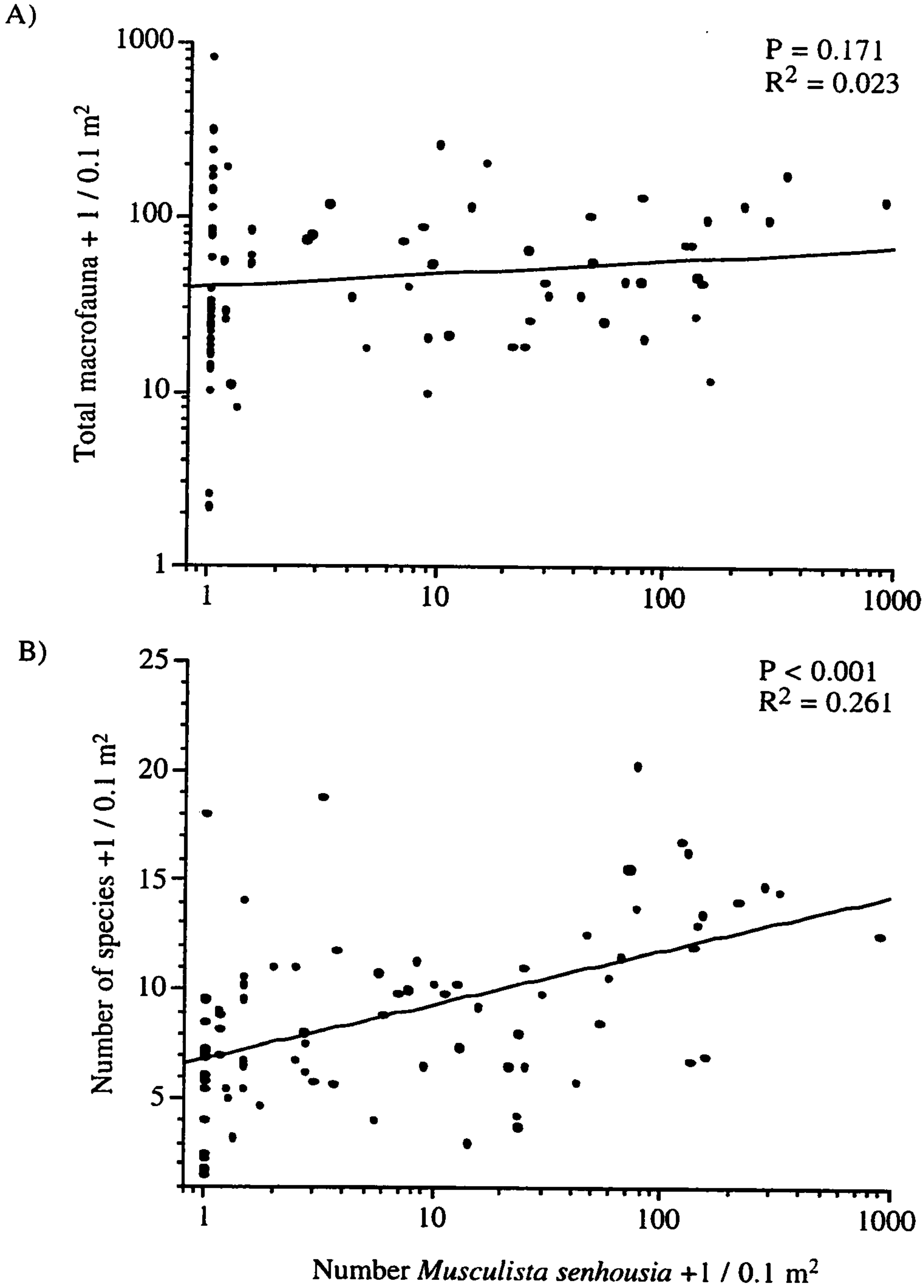


Figure 3-8. *Musculista senhousia* vs. A) total number of individuals and B) total number of species. Data points are station means (excluding Station A) and calculations of total macrofaunal densities and species richnesses exclude *Musculista senhousia*.

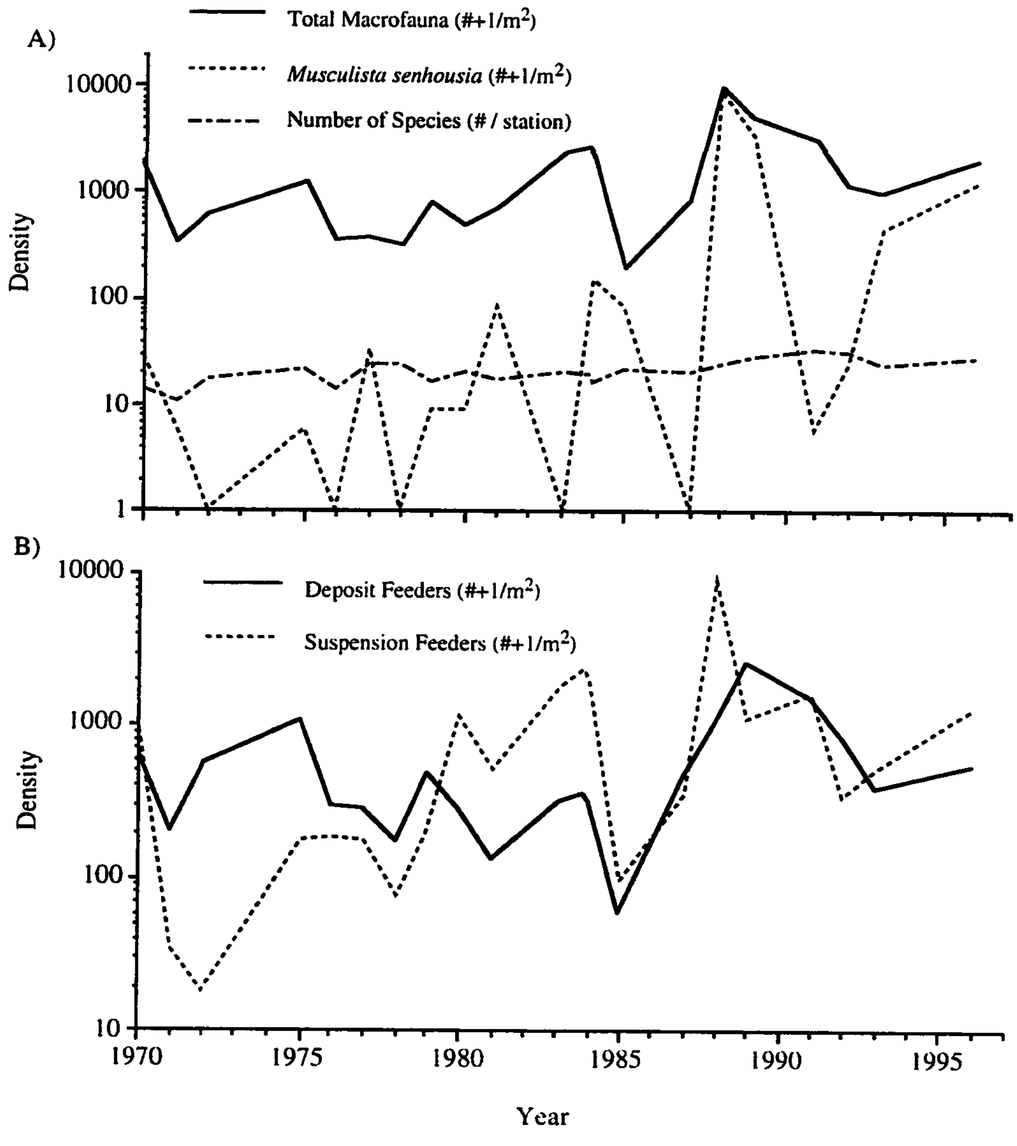
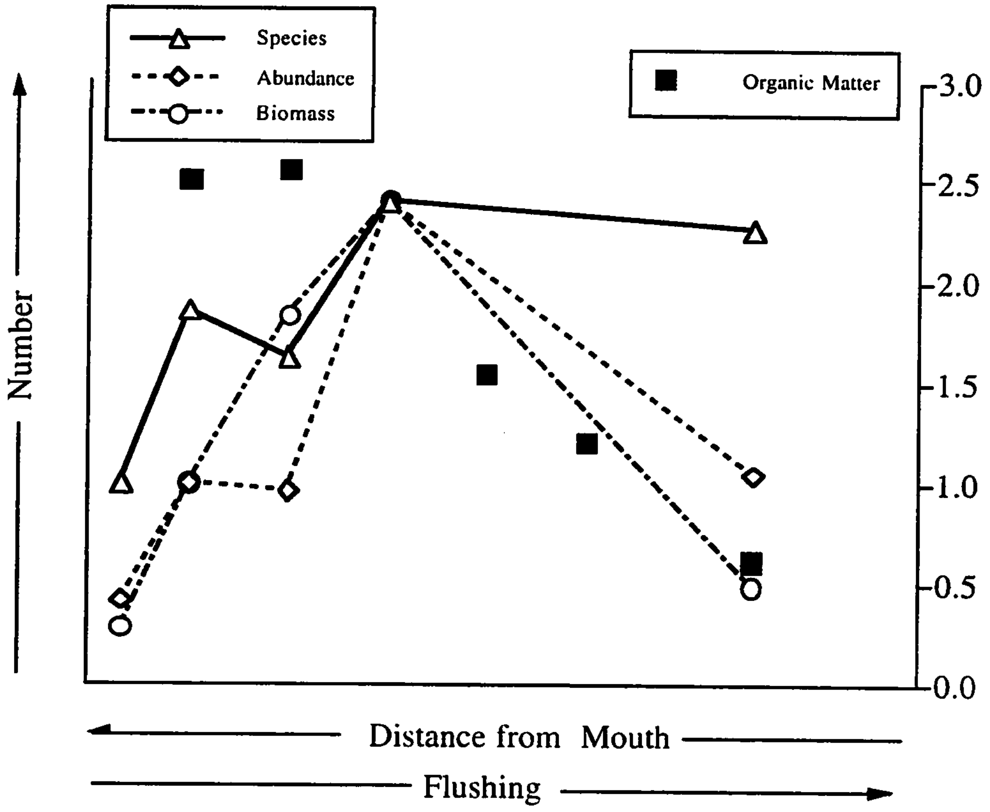


Figure 3-9. Station B from 1970-1996. A) Average total densities (number m^{-2}), total number of *Musculista senhousia* (number m^{-2}), and species richness (number per station). B) Average densities of suspension and deposit feeders.



Moderately polluted
Musculista senhousia
Nereis arenaceodentata
Tharyx sp.
Phoronis sp.

Transitory
Musculista senhousia
Phoronis sp.
Lumbrineris sp.
Euchone limnicola

"Normal"
Lumbrineris sp.
Diplocirrus sp.
Praxilella pacifica

Figure 3-10. Species-abundance-biomass curves and characteristic species for Mission Bay. Sediment data from Fairey et al. (1997).

Table 3-1. Percent representation of major taxonomic groups at the stations. Data are means across all times.

	Station						
Taxa	A	B	C	D	E	F	G
Mollusca	4.6	44.6	38.0	40.3	41.3	31.7	44.4
Polychaeta	84.0	30.2	46.2	39.2	47.3	54.7	46.9
Crustacea	9.1	2.4	3.3	9.0	6.4	2.3	4.7
Other	4.6	22.8	12.5	11.5	5.0	11.3	4.0

Table 3-2. Dominant species at the stations. Data are means across times.

Species	Station	% Contribution to Total Number of Individuals						
		A	B	C	D	E	F	G
Musculista senhousia		0.3	43.6	43.3	34.6	42.1	18.8	41.8
Phoronis sp.		0.7	25.9	10.7	8.6	4.9	21.4	2.3
Lumbrineris sp.		36.6	12.7	16.6	7.6	2.6	10.1	14.7
Euchone limnicola		4.5	5.9	9.0	2.3	1.3	1.7	3.3
Diplocirrus sp.		14.0	2.9	1.6	2.5	2.1	0.4	1.5
Tharyx sp.		3.3	0.2	0.4	11.7	5.7	10.5	2.2
Nereis arenaceodentata		0.8	1.1	0.6	2.3	8.0	2.5	2.0
Praxillella pacifica		9.2	0.1	0.2	0.0	0.0	0.2	0.8
% these species contribute to total		69.4	92.4	82.4	69.7	66.7	65.6	68.6

Table 3-3. Correlation coefficients for interactions among dominant species (P<0.001).

Species	Correlation
Musculista senhousia vs. *Euchone limnicola*	-0.36
Musculista senhousia vs. *Diplocirrus*. sp.	-0.29
Musculista senhousia vs. *Neanthes arenaceodentata*	+0.42
Lumbrineris spp. vs. *Praxilella pacifica*	+0.44
Phoronis sp. vs. *Praxilella pacifica*	-0.36

Table 3-4. Benthic community characteristics and within-station similarities. Data are means ± 1 s.e.

Characteristics	Stations A	B	C	D	E	F	G
A) Community Characteristics							
Density (no./m^2)	941 ± 140	2166 ± 623	869 ± 230	902 ± 189	379 ± 134	847 ± 161	996 ± 320
Biomass (wet weight (g)/m^2)	23 ± 5	114 ± 32	87 ± 31	47 ± 14	13 ± 5	109 ± 47	100 ± 45
Species richness (no./m^2)	11.1 ± 1.2	11.8 ± 0.8	8.0 ± 0.9	9.1 ± 0.7	4.9 ± 1.0	7.3 ± 0.9	10.1 ± 1.7
B) Within-station Similarities							
Within-year	0.56 ± 0.02	0.56 ± 0.03	0.55 ± 0.04	0.41 ± 0.03	0.30 ± 0.06	0.44 ± 0.03	0.46 ± 0.04
Between-year	0.51 ± 0.04	0.32 ± 0.01	0.33 ± 0.05	0.24 ± 0.05	0.21 ± 0.05	0.28 ± 0.05	0.34 ± 0.05

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CHAPTER IV

LAG TIMES IN POPULATION EXPLOSIONS OF EXOTIC SPECIES: CAUSES AND IMPLICATIONS

Abstract

Biodiversity losses caused by invasive species may soon surpass the damage done by habitat destruction and fragmentation. Some invaders explode quickly; others have a long "lag" period. Three categories of lags can be recognized: (1) inherent lags caused by the nature of population growth and range expansion; (2) environmental lags caused by changes (improvements) in ecological conditions that favor an alien; and (3) genetic lags caused by the relative lack of fitness of the alien in a novel environment. The likelihood of overcoming a genetic lag (fitness deficit) is proportional to the population size of the alien; there is a positive feedback between population size and the rates of genetic adaptation. Some principles regarding lags include: (1) determining whether a given lag is prolonged or not is often difficult because of lack of data, (2) past performance of an exotic is a poor predictor of potential population growth, range expansion, and ecological impact, (3) containment can end suddenly and disastrously for both ecological and genetic reasons, and (4) the larger the size of the alien colony, the more likely it will eventually become invasive. Policy makers should understand that good surveillance and monitoring are essential, and that extirpation should be early and vigorous.

Introduction

It may not be long before invasive species surpass habitat loss and fragmentation as the major engines of ecological disintegration. We make this prediction for two reasons: First, it may be soon when most of the habitat that is susceptible to destruction, modification, and fragmentation will have been so affected; there will be little more habitat to destroy for urbanization, farms, clear-cutting, and water projects, at least in the tropics and temperate zones. Second, damaged, denatured lands and waters are quite vulnerable to the growing avalanche of alien species, many of which prosper in disturbed, over-grazed, over-logged, over-hunted places. This is why the basic discipline of ecology may be replaced by a more applied science, such as mixo-ecology or recombination ecology, the study of recombined biotas (Soulé 1990; Townsend 1991). Therefore as scientists we are compelled to understand the dynamics of invasions and to discover and promote the needed countermeasures. In this paper, we examine the critical, early stage of an alien invasion.

During these early stages of biological invasions, the rates of population growth and range expansion of an alien species can vary markedly. Some invasive species (e.g., Africanized bees, muskrats, and zebra mussels) have had rapid rates of local population growth and range expansion. Many other species, however, (e.g., Collared Doves and the Oxford ragwort) appear to have long lag times between initial introduction and subsequent population explosions (Hengeveld 1988; Cousens and Mortimer 1995; Hobbs and Humphries 1995; Kowarik 1995). Despite these apparent differences in the colonizing history of invasive species, the relevant biological factors operating during the early stages of invasions are poorly understood. As such, the management and policy implications of lag times in the invasion of exotic species remain relatively unexplored (but see Hobbs and Humphries 1995).

In order to examine the lag effect and the processes involved in the early stages of invasion we will present case histories of species that apparently had long lag times between initial invasion and subsequent population explosions. These will be used to highlight three sets of mechanisms (inherent, environmental, and genetic causes of lags) that might affect invasion dynamics. Finally, we will speculate on the management and policy implications of lag effects.

Case Histories

We group invasions into three categories: 1) invasions by exotic species, 2) range expansions by native species, and 3) hybridization events between native and exotic species that are followed by explosive range expansion.

Invasions by Exotic Species

One of the most famous examples of a lag time in the population explosion of an invasive species is the Collared Dove (*Streptopelia decaocto*) in Europe. This South Asian species spread into China and the Middle East centuries ago (Hengeveld 1988). Probably beginning in the 16th century, the dove spread through Syria and Turkey, where it was protected by the Ottoman Turks (Hengeveld and van den Bosch 1991). For at least two hundred years, however, the Collared Dove did not spread beyond this area. But starting suddenly in the early 1900s, the dove rapidly colonized temperate Europe and north-west Africa, covering much of this area in around 50 years (Isenmann 1990). It has been suggested that the cause may be related to increasing urbanization in the region as well as climate change which allowed longer breeding seasons (Isenmann 1990). Similar patterns of delayed population expansions have also been displayed by other European birds such as the Penduline Tit (*Remiz pendulinus*) and Serin Finch (*Serinus serinus*) (Hengeveld 1989).

Several weeds in Britain have also displayed a "slow rate of spread followed by a rapid one" (Salisbury 1953). The "Oxford ragwort" (*Senecio squalidus*) is a southern European weed that accidentally escaped from a botanical garden in Oxford, England before 1794 (Baker 1965). For many decades the species was primarily confined to old walls in that city and Cork, Ireland (Perring 1974). This weed slowly began to spread, however, due to the building of a railway between Oxford and London. After World War II, the species rapidly spread throughout England and Ireland, along railways and in habitat created by bombings during the war (Baker 1965). Another weed, the gallant soldier, *Galinsoga parviflora*, from South America was purely a local resident in Kew (after its escape from the Royal Botanical Gardens) for many years before its dramatic spread during World War II. This delayed range expansion was partially attributed again to the bombings in England, which were thought to send the plant's propagules high in the air thus allowing dispersal by winds (perhaps lending new meaning to "explosive" spread). Wild lettuce plants, *Lactuca virosa* and *L. scariola*, first reported in Britain in 1570 and 1632, respectively, also displayed delayed range extensions. For example, in Surrey and Hertfordshire, both species were considered rare until the middle of the 1900's, when they became common in gravel pits (Salisbury 1953).

The cut-leaved teasel (*Dipsacus laciniatus*) is a weed that arrived to New York prior to 1900, and in 1913 it was reported only from Albany (Solecki 1993). However, in the last thirty years the plant, which is capable of forming monocultures that exclude most native vegetation, has spread quickly throughout much of the mid-west. This rapid spread has been attributed to dispersal via the interstate highway system, as the teasel is particularly common along highways and roads.

In Florida, two major plant invaders, the paper-bark tree or melaleuca (*Melaleuca quinquenervia*) and the Brazilian pepper (*Schinus terebinthofolius*), also were "present long before they were conspicuous elements of the landscape" (Ewel 1986). These evergreen trees were intentionally introduced and since have become major pests in the nearly treeless Everglades. Melaleuca was first introduced into Florida in the early parts of the 1900's, although it wasn't until decades later that the population began to expand. Likewise, the Brazilian pepper, although introduced over 100 years ago, did not "explode across the landscape until the 1950s" (Ewel 1986). The causes of these lags are unknown, although Ewel lists four possibilities: 1) Florida became more invasion-prone; 2) the species may have been undergoing rapid yet undetected expansion due to inherent lags; 3) it may have taken several decades to build up large enough populations to have significant reproductive potential ("infection pressure"); and 4) the new colonists were confined to restricted habitats until mutations favorable for further colonization became available. We will return to the issue of causation and its typology below.

In a thorough treatment of the population dynamics of introduced woody plants in Brandenburg, Germany, historical records were used to determine the length of time between the initial release for cultivation and first evidence of spontaneous spread of a large number of species (Kowarik 1995). For the 184 species considered, there was an average of 147 years between first planting and first appearance of seedlings in the wild. Moreover, only 2% of the species became established, and 1% invaded natural vegetation. Intrinsic population factors, climatic shifts, and habitat availability were cited as possible reasons for the long lag phases displayed by many of the plant species.

The Channel Islands off southern California have been heavily affected by introduced species. Historically, the islands were almost free of large grazers, the exception being the extinct dwarf mammoths (Laughrin et al. 1994). In the mid-1800's, thousands of cattle, horses, sheep, and pigs were brought to the islands. As part of a recent conservation effort on Santa Cruz Island, more than 36,000 feral sheep and 1,500 head of cattle were removed from the western 90% of the island (Brenton and Klinger

1994). Before removal of the grazers, the European weed, fennel (*Foeniculum vulgare*), which had been present on the island for over 100 years, was not considered a dominant species except in a few small areas (Beatty and Licari 1992). With the removal of the grazers, however, the fennel population expanded in range and density and now dominates ca. 10% of the island (Brenton and Klinger 1994). This explosion has in turn benefited other exotics, because alien weeds (e.g. European annual grasses) are the most abundant herbaceous plants typically encountered within dense stands of fennel (Brenton and Klinger 1994). Feral pigs (*Sus scrofa*), too, have rapidly increased due at least in part to the removal of the grazers (Crooks and Van Vuren 1994).

The Asian mitten crab, *Eriocheir sinensis*, was first found in Europe in 1912 (Barnes 1994). Until recently, however, it had met with considerably less success in Britain than it had in other European countries (Cohen 1995). These catadromous species spend the majority of their lives in rivers, but migrate to estuaries to reproduce. Their failure to establish in Britain has been at least partially explained by the presence of fast-flowing rivers which may inhibit the settlement and recruitment of these migratory crabs (Atrill and Thomas 1996). From 1989 to 1992, however, severe droughts in southeast England led to reduced river flow and hordes of crabs were found upriver, some even wandering into local homes.

One particularly successful exotic species in the heavily invaded estuarine ecosystems of the Pacific coast of North America is the small, soft-sediment dwelling bivalve *Musculista senhousia* (Crooks 1996). Although this mat forming species first appeared in San Diego in the mid-1960s, it was not until the early 1980s that the mussel could be commonly found in high density patches of around 10,000 m^{-2}. In the summer of 1995, after a spring characterized by unusually heavy rainfall and strong red tides offshore, extraordinarily dense populations of the mussel were found carpeting thousands of square meters of Mission Bay's intertidal and shallow subtidal (Chapter

2). Densities up to 160,000 m^{-2} were recorded, a far higher concentration than reported for this species anywhere else in the world and among the highest ever reported for a marine bivalve.

Another southern California invader is the wood-boring gribble (Isopoda), *Limnoria tripunctata*. This small crustacean was introduced into the Long Beach-Los Angeles Harbor area before the turn of the century, probably via the hulls of wooden ships (Carlton 1979). In portions of the harbor (such as the Dominguez Channel and East Basin), however, no isopods were found because excessive pollution from industrial, domestic, and storm wastes resulted in a nearly sterile zone. With the advent of a pollution abatement program in the late 1960s, the isopod moved into the area, underwent a population explosion, and caused the collapse of a local wharf through its extensive boring activities (Reish et al. 1980).

Hybridization of Native with Exotic Species

In the early 1800s the U.S. east coast marsh cordgrass, *Spartina alterniflora*, was accidentally introduced via ballast water into the United Kingdom (Thompson 1991). About seventy years later, it was noticed that *S. alterniflora* had hybridized with the native European cordgrass, *S. maritima*. This hybrid, *S. townsendii*, was infertile. In the 1890's, cordgrass began to spread out of Southampton Water and into adjacent estuaries. This spread has been attributed to the production of a new, fertile species, *S. anglica*, through chromosome doubling of *S. townsendii*. This new cordgrass species is very well adapted to the intertidal areas of estuaries, and through both natural dispersal and intentional planting for march reclamation, *S. anglica* is now a characteristic feature of British salt marshes.

Range Expansions of Native Species

Range expansion of a native species may also lend insight into the processes involved in the early stages of invasion. The butterfly, *Coenonympha tullia*, is a holarctic species widely distributed throughout western North America (Wiernasz 1989). Before the 1950's, the butterfly's distribution in eastern North America was largely restricted to Quebec and Ontario north of the Saint Lawrence and portions of the Maritime Provinces. Here, the populations were univoltine (one generation per year). In the early 1960's the species began to spread southward into much of New England and New York, following a warming trend in the region. This was associated with the development of bivoltinism (two generations per year) in the southern part of the range. Once the bivoltine populations were established, further colonization proceeded quickly, perhaps because of the rapid population growth thus afforded.

Lags in Detection of Exotics

In this consideration of the lag effect during invasions, it should be noted that many estimates of the time between initial invasion and subsequent population explosion may be conservative. This arises from yet another lag effect: our lag in determining the presence of a new invasive species. It is likely that many invaders are present in low numbers for some time before they are first recorded. Such "early stage subdetectability" was suggested to occur for the medfly (*Ceratitis capitata*) in California, which may have been present for more than 50 years prior to its discovery in 1975 (Carey 1996). Such lags in detection of exotics will be especially likely for small or cryptic species in undersampled habitats.

The Inherent Lag Effect

Fundamental to the examination of lag times is the definition of what in fact constitutes a lag. As can be seen from the case histories, two basic categories of lags can be recognized: lags in local population increases and lags in range expansion. In order to define lags in either case, it is first necessary to explore some of the dynamics of a biological invasion.

The first thing to point out is that lags are normal; some kind of lag is built into the growth of any founder population, whether or not it is adapted to the new environment. The classic model for the early stage of an invasion is the simple exponential formula,

$$N_t = N_0 e^{rt}, \tag{1}$$

where N is the number of individuals, t is time, and r is the population's intrinsic rate of increase. Inherent in this familiar model is the shallow portion early in the growth curve when the population is growing relatively slowly in absolute numbers (Fig. 4-1A). Even vigorous, perfectly adapted populations follow such a trajectory.

In assessing whether an observed lag in the population growth of an invasive species is prolonged, it is necessary to determine if the observed lag is longer than the inherent lag given the r determined for the population when it is growing rapidly. Such a difference may be visualized by plotting the logarithmic equivalent of the former equation, giving

$$\ln N_t = rt + \ln N_0. \tag{2}$$

If plotted graphically and r is constant, the result will be a straight line with a slope of r (Fig. 4-1A and 2A). If the slope is less steep in the early portion of the curve, however, this is evidence for a prolonged lag due to lower values of r during the early stages of the invasion (Fig. 4-2A).

Models of range expansion are more complex than that for local population growth, because they include both this local numerical increase as well as emigration of individuals. There has been considerable effort devoted to describing the spatial spread of organisms, although most theory has concentrated on asymptotic rates achieved after the early stages of an invasion. The simplest model of range expansion assumes reaction-diffusion dynamics with individuals acting as random particles moving on an uniform plane (Kendall 1948; Skellam 1951). This model thus depends on only two processes, exponential population growth (as described above) and random diffusion of individuals. Using these, it can be determined that C, the expansion velocity, asymptotically approaches the equation:

$$C \approx 2(rD)^{0.5}, \tag{3}$$

where D is a diffusion constant (Williamson 1996). Thus, the velocity of the rate of spread is proportional to the square root of population growth rate (r) and the diffusion constant (D), and changes in either of these values will cause changes in expansion velocity. In many cases this model provide a very good description of the movement of organisms (Kareiva 1983; Holmes 1993; but see Lonsdale 1993), although models that take into account life-history and dispersal parameters of species (e.g., Van den Bosch et al. 1992; Hengeveld 1993) may have greater predictive powers. It also should be noted that species having two different modes of dispersal, such as the cholla (*Opuntia imbricata*), which has passive dispersal by the falling of seeds or stems to the ground and active dispersal by attachment of stems to animals (Allen et al. 1991), may appear to spread faster than the asymptotic rate by establishing foci beyond the range attained by passive dispersal.

A variety of related methods for quantifying the rate of spread (C) of an invasive species also have been developed (Andow et al. 1993). In the simplest case the contours of equal population density are modeled as circles expanding at a constant velocity (Van den Bosch et al. 1992). This gives the equation:

$$A_t = \pi p_t^2 = \pi(\Omega + Ct)^2, \tag{4}$$

where t is time since detectable spread began, A_t is the area occupied at time t, p_t is the radius of the expanding front at time t, Ω is a correction factor representing the area beyond which range expansion can be detected or the initial area occupied by the population, and C is the expansion velocity (Fig. 4-3). Because area increases as the square of time, a graph of area occupied over time will be a curve with an early lag phase (Fig. 4-1B). If the velocity of range expansion is constant, then plotting the square root of area versus time gives a straight line (Fig. 4-1B). The expansion velocity can be easily calculated from this graph by dividing the slope by $\pi^{0.5}$. It is also possible to plot the radial equivalent of the area, $(A/\pi)^{0.5}$, versus time, in which case the slope is simply C.

Although relatively simple, this relationship explains the observation that the square root transformation typically linearizes the time course of spread of an invasive species (Williamson and Brown 1986). This result appears to be quite robust once the invasion has "taken" in terrestrial systems (Roughgarden 1986), although known rates of spread in marine systems tend to be lower than predicted by the diffusion model (Grosholz 1996). The linear relationship between the square root of area and time is exemplified by the rapid spread of the muskrat (*Odontra zibethicus*) in Europe after the release of 5 individuals near Prague in 1905 (Nowak 1971). If the slope of the line relating the square root of area to time during the early stages of invasion is shallower than the slope later in the invasion, then early rates of range expansion are slower than that during the asymptotic spread phase (Fig. 4-2B). Such early, slow spread has been witnessed for a wide variety of species (Williamson 1996), such as the Japanese beetle, *Popillia japonica* (Hengeveld 1989), the House Finch, *Carpodacus mexicanus* (Veit and Lewis 1996), and the Starling (Okubo 1988). Several factors, however, make the unambiguous interpretation of early, sub-asymptotic rates difficult.

The first complicating factor is related to the ability to detect small-scale spread. In the circular growth model, Ω is the scale at which expansion can be detected. Below this level, spread can be occurring but it may go unnoticed (Andow et al. 1993). This would lead to an apparent lag in range expansion even though the population was expanding at a constant rate. Second, equation 3, relating spreading velocity (C) to r and D, is for spread at an asymptotic velocity. The precise form of the equation is more complicated and actually predicts lower values of C early in the invasion before reaching an asymptote (Holmes et al. 1994). This suggests that even given constant rates of r and D, there may be an initial, intrinsic lag. This result has also been echoed by the results of a stochastic model of areal spread, where the only parameter is the probability that an unoccupied site remains unoccupied at the next time step (Hastings 1996). This model demonstrates that lags in areal expansion can occur early in an invasion. Like the deterministic models discussed above, however, this stochastic model also predicts that the square root of area will asymptotically increase as a linear function of time. These factors make it difficult to determine how long sub-asymptotic rates must occur before they should actually be considered prolonged. However, the length of time before an asymptotic rate of range expansion is reached would appear to provide a relative indication of the likelihood of a prolonged lag.

Even given theory like that presented above, it is possible that the examination of any given invasion will prove difficult because of lack of information to analyze critically whether prolonged lags exist. Nevertheless, it is possible to recognize two broad categories of mechanisms able to produce prolonged lags in population growth and/or range expansions beyond that of inherent lags discussed above. These categories, which may act singly or in concert, are: 1) an increase in r or D following a change in the biotic and/or abiotic environment, and 2) an increase in r or D following a change in the phenotype (and presumably, the genotype) of the invader.

Prolonged Lags – Environmental Factors

An environmental change that enhances the fitness of an exotic will, by definition, trigger an increase, or a "release" in its growth rate, r. Therefore, if such an environmental enhancement has occurred in the history of an exotic, a plot of the colonist's population history will indicate a lag in its growth that is more profound (longer) than would be expected for the inherent lags discussed above. Such prolonged lags of this kind might be caused by any natural or anthropogenic change in a factor that limits the distribution and abundance of an invasive species.

There are several major ecological mechanisms that may result in the release of an invasive species. These include changes in habitat and food resources, climate, dispersal vectors, interspecific interactions, and intraspecific interactions. Such changes may occur either in the local environment, affecting population growth, or in potentially habitable areas, affecting range expansion.

Habitat and Food Resources

If increased quantities of a limiting resource are made available to an invasive species, rapid population growth and range expansions may result. For invasive species that are human commensals, such increased resources may be provided by expanding urbanization and human-mediated modification of natural habitats, as exemplified by the Oxford ragwort and the introduced lettuce species in the U.K. described above. In addition, the spread of the Collared Dove in Europe, which typically lives in human settlements, is probably related at least in part to increasing urbanization. Also related to increased human activities is the provision of artificial food resources, which has been suggested to account for the increase in numbers of birds such as gulls and the fulmar in Europe, both of which may feed on offal and/or garbage (Isenmann 1990).

In addition to changing the quantity of habitat, an alteration (usually a deterioration) of habitat quality may also permit an invasive population to explode. This mechanism corresponds to Ewel's (1986) hypothesis that the delayed spread of the trees in the Everglades was caused by increasing anthropogenic disturbance which recently has allowed more sites to become invasible. Change in habitat quality has also been implicated in permitting the recent explosion of the mitten crab in the U.K. and possibly *M. senhousia* in California. In Los Angeles Harbor, the beginning of a pollution abatement program allowed the release of the wood-boring gribble populations. This is an interesting counter-example to the idea that increased, rather than decreased, disturbance would favor an invasive species.

Climate

The proximate mechanisms through which climate change may affect a species are numerous, but relationships to breeding and growing seasons may be important. For example, warming trends may have permitted longer breeding seasons for the Collared Dove in Europe and may have aided in the development of the bivoltinism and southern expansion in the butterfly, *C. tullia*. In species like mosquitoes with temperature-dependent reproductive thresholds, a slight increase in temperature can produce a large increase in r, facilitating both a population increase and an expansion in geographic range (Soulé 1992). Mosquitoes such as *Aedes albopictus* and *A. aegypti*, the former already established in the Southeastern United States, can spread as the climate warms. These mosquitoes can act as vectors for dengue fever, yellow fever, equine encephalitis, filariasis, and the viruses that cause hemorrhagic fevers. In the face of long-term and universal greenhouse warming, it is not unreasonable to expect concomitant changes in the ranges and densities of many invasive species, including vectors of human disease (Soulé 1992).

Dispersal Vectors

In some instances, the delayed spread in invasive species can be attributed to the provision of a new or more efficient means of dispersal. The teasel in the eastern U.S. was provided with a means of transport via the interstate highway system, the Oxford ragwort spread along the railway lines in the U.K., and the gallant soldier may have been spread via bombings in England. Roads, themselves, are probably the major avenue of transport of many terrestrial exotics, including many plant diseases. In Australia "dieback" caused by the fungus *Phytopthora cinnamoni* and related species affects many plant communities and is an agent of extinction; its spores are spread more rapidly along roads and where traffic and machinery disrupts the soil. Thus, the increasing volume and efficiency of local and global transportation will not only continue to introduce new exotic species from abroad, it will also serve to spread invasive species already present in a region.

Interspecific Interactions

In addition to responding to conditions such as habitat quality and climate, invasive species must interact with resident plants and animals. A variety of interspecific interactions, such as competition, predation, disease, grazing, as well as indirect effects including animal-caused habitat modification, may facilitate the release of an invasive species. Such was the case on the Channel Islands, where the removal of the exotic grazers allowed the release of fennel. Similarly, the elimination of feral goats in the Volcanoes National Park on the island of Hawaii was followed by an explosive spread of alien, fire-conducting grasses; the result has been the near-deforestation of some Hawaiian uplands (D'Antonio and Vitousek 1992).

Many other interspecific interactions are undoubtedly important, including the anthropogenic initiation of trophic cascades, including those triggered by the removal of predators. For instance, there is evidence (K. Crooks pers. comm.) that the elimination of coyotes (*Canis latrans*) from remnant patches of scrub vegetation and coastal estuaries in urban areas removes a check on the distribution and activity of alien red foxes (*Vulpes vulpes*) and domestic cats (*Felis catus*), both of which harm native wildlife, including endangered species (see also Soulé et al. 1988).

Intraspecific Interactions

A variety of intraspecific interactions may be affected during the early stages of an invasion, when population densities are low. For example, species may have difficulty finding mates or fully utilizing a resource because of low numbers of individuals or "undercrowding" (Williamson and Brown 1986). These "Allee effects" have been suggested to be important in causing observed lags in the spread of invasive species (Lewis and Kareiva 1993). Models incorporating Allee dynamics (i.e., disproportionately low fecundity below a certain critical level) have successfully recounted the spatial spread, including the early lag phase, of the House Finch (Veit and Lewis 1996).

Prolonged Lags – Genetic Factors

Even though the general subject of the genetics of colonizing species has received considerable attention, and fundamental concepts such as the founder effect, population bottlenecks, and genetic drift are intimately related with the problem of invasive species, genetics remains the great unknown in the biological basis of lag effects and the causation of sudden, explosive growth and expansion of exotics. The question is to what extent are lags, when they occur, caused by the lack of local genetic adaptation to the abiotic environment, the biotic environment, or both?

The possibility of the lack of genetic "fit" of a colonizing population to cause prolonged lags was widely speculated upon at a conference on the genetics of colonizing species (Baker and Stebbins 1965). Fraser (1965) discussed situations where "migrants move into an environment to which they are not specifically adapted" and "will have an initial phase during which the specific adaptations will have to evolve". Lewontin (in Mayr 1965) also discussed this issue of "break-out" colonizations, where "under continuous identical selection, there is a long period of stalling of increase of fitness followed by a rapid rise." Similarly, Mayr (1965) suggested that the sudden spreading of the Serin Finch and Collared Dove may have been caused by genetic mutation. Baker (in Mayr 1965; Baker 1965) commented that the "sudden explosive spread of animals after a period when nothing very much seems to be happening is paralleled by plants," and that "if a newly introduced plant does not have appropriate 'general purpose' genotypes available, it may be confined to a restricted area until these do become available through recombination or introgression." The possibility of lags has also been recognized in the introduction of biocontrol agents, where time might be needed for postcolonization adaptation to the new environment (DeBach 1965; Wilson 1965; Waddington, in Wilson, 1965).

Despite these general predictions that time might be needed for some invasive populations to adapt when they are introduced into marginal environments, little empirical support has been forthcoming (Williamson 1996). Similarly, although genetics has been suggested to play a role in the outbreak of insect species, there has been little documentation of this (Myers 1987; Mitter and Schneider 1987). Some experimental evidence for genetic change allowing population increases does exist, as inbred lines of *Drosophila* increased their population sizes after introduction of new genetic material (Carson 1961; Cannon 1963; Carson 1968). However, we know of only one case where invasiveness of an exotic species has a demonstrable genetic cause: the cordgrass, *Spartina anglica* mentioned above. Even this case is special, in that the "mutation" was doubling of the genome, not a point mutation in a single gene. Statistically, however, it is inevitable that natural selection is a factor in the survival and fitness of any population.

From a technical standpoint, it is unlikely that particular gene mutations contributing to the success of an introduced species will be detected. Most mutations that are likely to contribute to fitness are subtle, quantitative changes in the phenotype, rather than qualitative, "Mendelian," phenotypic alterations. But the chances of researchers stumbling on such beneficial new mutations by random search are virtually nil. For example, mutations in major genes, such as those detectable by routine surveys of enzymes, are extremely rare (ca. 10^{-7}). New ones have yet to be found in all introduced rabbits in Australia, which number in the millions (Richardson et al. 1980), and the expected time for such a new mutation in a major gene to be detectable is about one million years (Gorman et al. 1980). On the other hand, it is quite likely that slightly advantageous mutations in the thousands of genes affecting quantitative traits (such as vigor, metabolic rate, growth rate, resistance to toxins) will occur and be selectively incorporated into the genome quite frequently in relatively large populations. But finding them is like searching for a needle in a haystack. Thus, mutations that enhance invasiveness are unlikely to be detected.

Nevertheless, population-genetics theory provides some insight into the interplay between population size and genetic evolution. First, because of founder effects (Mayr 1963), very small populations (less than 50 individuals or so) are unlikely to be able to evolve improvements in fitness (Franklin 1980; Soulé 1980). Although some examples exist where very small populations have successfully recovered to large, healthy populations (Mayr 1963), populations having gone through very small bottlenecks are more likely to decline genetically due to inbreeding (Soulé 1980).

Calculations based on balancing total mutation rates with genetic drift suggest that until the population size increases to about one thousand, natural selection will not be a very effective force in counteracting the randomizing effects of genetic drift (chance changes in the frequencies of genes, including new mutations), and most beneficial mutations, even if they occur, will have a low probability of being incorporated into the population (Soulé 1980). Furthermore, recent evidence suggests that near-neutral, potentially adaptive mutations may in fact occur an order of magnitude less frequently than mutations with large phenotypic effects, which tend to be highly detrimental (Culotta 1995; Lande 1995). This suggests that calculations based on total mutation rates may represent underestimates, and that even larger populations are required to overcome the effects of population bottlenecks. Only when populations are quite large (at least ten thousand) are slightly beneficial mutations likely to increase in frequency because of natural selection and are slightly harmful mutations likely to be weeded out efficiently.

What this implies is a positive feedback between population size and the chances that the population will improve genetically. It also implies that the longer that a population exists, at least if it numbers in the thousands, the more likely is a genetic "discovery" that makes it more invasive. The larger the population, the greater the chance that favorable mutations will arise, which in turn allows for larger populations. Moreover, mathematical models also suggest that the faster a population grows after a population bottleneck, the less the effects on average heterozygosity in the population (Nei et al. 1975).

In addition to acquiring new genetic material by mutation, existing populations of invasives can overcome potential founder effects by repeated introductions over time. This could serve to quickly increase the amount of genetic variability and allow for rapid population explosions. For example, the success of the cladoceran invader, *Bosmina coregoni*, in the Great Lakes may be related to repeated ballast water-mediated introductions (Demelo and Herbert 1994).

Implications for Policy and Management

The most effective form of protection against invasive and destructive alien species is a diverse and healthy assemblage of native species (e.g., Elton 1958; Case 1990). Thus, alien species can often penetrate zones of disturbance, particularly agricultural areas or urbanized lakes or estuaries. Furthermore, once an introduction has taken hold, there is often little that can be done to stop it, so we can expect very large losses in native biodiversity and ecological integrity of many ecosystems.

The first line of defense against invasive aliens should be vector management (i.e., the control of the means by which exotics are spread), including inspection and quarantine at ports and transportation hubs. One of the obvious goals of such practices is to prevent the introduction of new exotic species. Recognition of the lag effect also suggests at least two additional benefits of vector management. It decreases the potential for further introductions of previously established exotics, thus preventing the addition of new genetic stock which may make existing populations more aggressive invaders. Also, regional vector management will serve to slow the spread of already established species.

The lag effect also has important implications for the evaluation of the potential extent and effects of an invasive species. Recognition of both inherent and prolonged lags suggest that the past performance of an invasive species may be a poor predictor of its future potential for numerical increase, range extension, and ecological effects. It is dangerous to assume that ecological containment (mal-adaptation) will last forever, especially if numbers of individuals pass the threshold that increase the likelihood of enhancements of local adaptation by natural selection. Also, the lag phase (containment) of an exotic species can end suddenly when some aspect of the biotic or abiotic environment is altered. Often, such changes may be caused by human activities. For example, when another species, particularly a browsing or grazing mammal, is removed from the system, explosive and disastrous growth of exotic weeds may result (e.g., fennel on the Channel Islands). Therefore, care in manipulations of systems where exotics are present, such as the removal of feral livestock, is recommended. Given the ever increasing human-mediated alteration of whole ecosystems and the global climate, however, it is likely that there will be corresponding changes in the dynamics of established invaders. A further consideration is the potential for lags in ecological effects of non-native species to occur even after lags in numerical increase or range expansion have ended (Moyle 1996), or that introductions that were initially considered beneficial may have unanticipated negative effects (resulting in the "Frankenstein Effect;" Moyle et al. 1986).

In the effort to control exotic species, the consideration of the lag effect also suggests a second line of defense: the extirpation of founder colonies before the explosive growth phase has begun (Hobbs and Humphries 1995). Experience shows that the elimination of an exotic once the lag phase is over can be virtually impossible. Therefore, careful monitoring programs that may lead to early detection and, if possible, elimination of incipient invaders should be instituted, particularly if the population can be prevented from achieving sizes in the thousands of individuals.

On a global scale, international travel and commerce will accelerate the current rates of introductions of exotic species. Assuming the impossibility of reversing globalization, only superior surveillance and the development of innovative control measures can counter the current growing momentum of ecological disintegration and cosmopolitanization of biodiversity. A better understanding of the biological processes at work during the early stages of invasion will contribute to effective policy development and enforcement.

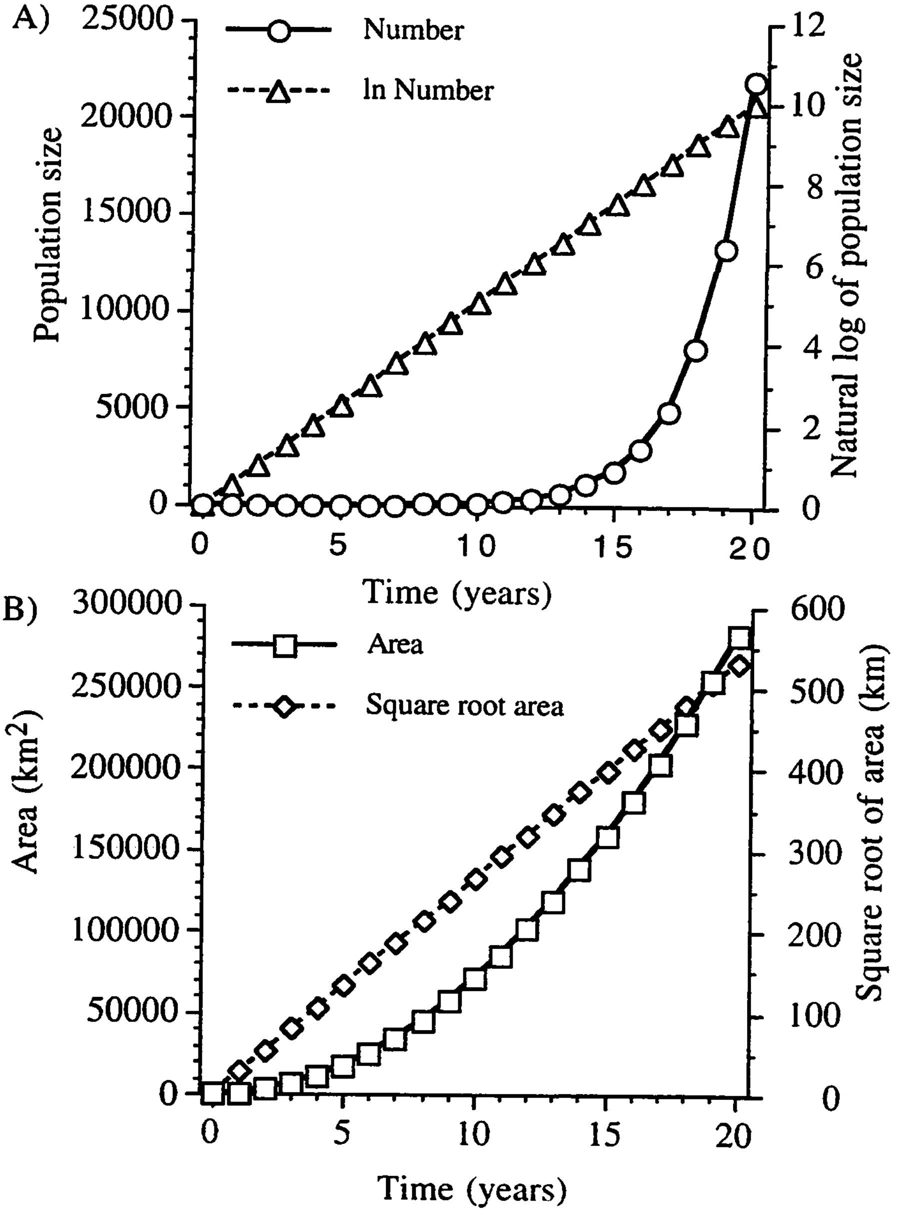

Figure 4-1. Local population growth (A) and areal expansion (B) of populations. For population growth, intrinsic increase r = 0.5 / yr. For areal expansion, velocity of range expansion (Ω) = 15 km / yr and the correction factor (C) = 0.

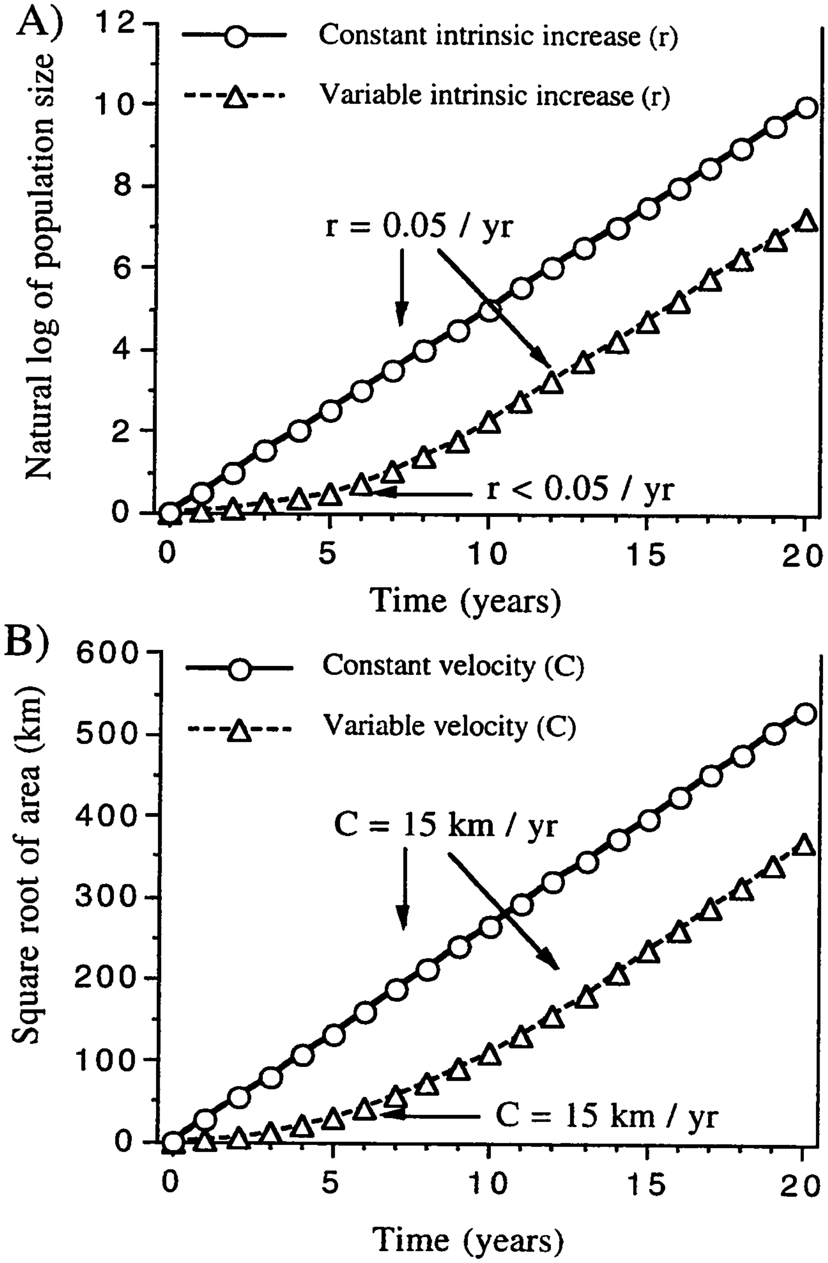

Figure 4-2. Comparisons of constant versus slow early rates of population growth (A) and range expansion (B).

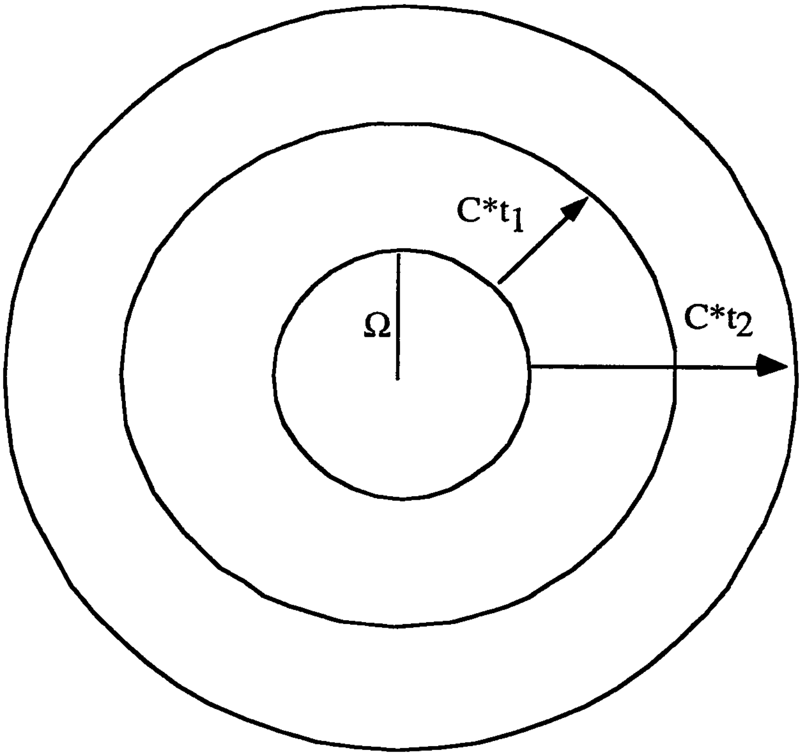

Figure 4-3. Circular areal expansion of a population, according to the equation, $A_t = \pi p_t^2 = \pi(\Omega + Ct)^2$, where t = time since detectable spread began, A_t is the area occupied at time t, p_t is the radius of the expanding front at time t, Ω is the correction factor representing the area beyond which range expansion can be detected or the initial area occupied by the population, and C is the expansion velocity. See text for more details.

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CHAPTER V

HABITAT ALTERATION AND COMMUNITY-LEVEL EFFECTS OF AN EXOTIC MUSSEL, *MUSCULISTA SENHOUSIA*

Abstract

The exotic mussel, *Musculista senhousia*, is capable of marked habitat alteration through the construction of byssal mats on the surface of soft sediments. Here I demonstrate the importance of this alteration on sedimentary properties and resident macrofaunal assemblages on a tidal flat in Mission Bay, San Diego, California. In well-developed mats, percent fine sediments, percent combustible organic matter, and sediment shear strengths were increased relative to adjacent areas without mats. Comparisons of naturally occurring areas with and without mats of *Musculista*, as well as comparisons of the same tidal flat when mussels were seasonally present and absent, revealed that assemblages within mussel mats differ from those in sediments without mats. The primary effect of the mussel and its mats was facilitation of other organisms. Total densities of all macrofaunal individuals as well as species richness were typically higher inside than outside mussel mats. Two species that exhibited large enhancements of densities within mussel mats were the tanaid *Leptochelia dubia*, and the gastropod *Barleeia subtenuis*. Oligochaetes, a numerically important component of the tidal flat, appear to be least facilitated by the presence of mats. A short-term, manipulative experiment that examined the effects of mussel-mat mimics on the colonization of macrofauna suggested that the presence of physical structure alone can produce several of the patterns observed in naturally occurring mussel mats. These results highlight that alteration of habitats is an

important effect of exotic species, and that these habitat alterations can have subsequent effects on resident biotic communities.

Introduction

Introduced species are known to influence invaded assemblages in many ways. Commonly considered mechanisms by which exotics affect other species include competition, predation, parasitism, and alterations of food webs or nutrient cycling (Vitousek 1990; Williamson 1996). Considered much less frequently are the effects of habitat-modifying species, or "ecosystem engineers," on resident biota (e.g., Vitousek 1990; D'Antonio and Dudley 1995; Williamson 1996, but see Simberloff 1981). This lack of recognition of exotic habitat modifiers reflects a general tendency to overlook the role of species in creating, destroying, or otherwise modifying habitats (Lawton 1994; Jones et al. 1994). In recent years, however, there has been an increased effort to better define the role of these species in ecosystems (Jones et al. 1997).

Estuarine ecosystems (including bays, lagoons, and true estuaries) provide ample opportunity to examine the effects of non-native organisms. They are among the most vulnerable of the world's ecosystems in terms of anthropogenic introductions (Carlton 1989), but relatively little is known about the effects of these non-native species. Previous research on estuarine exotics has concentrated on identifying invaders and transport mechanisms (e.g., Carlton and Geller 1993), autecology of invaders (e.g., Crooks 1996; Furota 1996a, 1996b), and interspecific interactions such as competition (e.g., Race 1982; Brenchley and Carlton 1983) and predation (e.g., Grosholz and Ruiz 1995). Fewer studies have examined if and how estuarine exotics can alter the physical nature of ecosystems. However, there is limited evidence that resident assemblages can be changed by invasive ecosystem engineers, for example, through the construction of habitat by autotrophs (Posey 1988) or the destruction of habitat by herbivores (Bertness 1984).

Among the most successful invaders in marine and freshwater systems are bivalves in the families Mytilidae (sea mussels) and Dreissenidae (false mussels). Mussels have the potential to dramatically affect communities and ecosystems, as they are often dominant space occupiers, can alter habitats through construction of dense beds, and can link benthic and pelagic systems through filtration of the water column and deposition in the benthos (Suchanek 1985; Seed and Suchanek 1992, and references therein). Most of the research on the effects of mussels, however, has concentrated on native species. One notable exception to this is the zebra mussel, *Dreissena polymorpha*, in freshwaters (e.g., Nalepa and Schloesser 1993). Other mussel invasions throughout the world include the blue mussel, *Mytilus galloprovincialis* in Australia, South Africa, Japan, and California (Seed 1992), *Perna perna* in Texas (Hicks 1993), *P. viridis* and *Limnoperna fortunei kikuchii* in Japan (Asakura 1992), and *Brachidontes variabilis* and *Xenostrobus* sp. in the Mediterranean (Safriel and Sasson-Frostig 1988; Lazzari 1994). Some soft-sediment dwelling, exotic mussels include the ribbed mussel, *Arcuatula demissa* (or *Geukensia demissa*), a salt marsh species that has been introduced from the east coast of the United States to California (Carlton 1979), and the Asian mussel, *Musculista senhousia*, which has been introduced into Australia (Willan 1987), the Mediterranean (Hoenselaar and Hoenselaar 1989), and the Pacific coast of North America (Kincaid 1947). This small mytilid typically weaves a byssal cocoon, and when it occurs in high densities these cocoons form a mat or carpet on the surface of the sediment (Morton 1974).

The objectives of this research were to document the effects of the exotic mussel, *Musculista senhousia* (hereafter referred to as *Musculista*), on the soft-sediment intertidal habitat of Mission Bay, San Diego, California, and to determine the response of the resident macrofaunal community to these habitat changes. Faunal responses to the invasion of *Musculista* can be viewed on several spatial and temporal scales. In a broad context, *Musculista* is a relatively new invader in the system (approximately 30 years, Crooks 1996), so observed interactions represent recent relationships that have not developed in a co-evolved community. On smaller scales, *Musculista* is patchy both in space and time; the mussel typically exists in patches of decimeters to meters and is only seasonally abundant on the tidal flat (Crooks 1996). This small-scale spatio-temporal variability permitted the testing of the hypotheses that abiotic and biotic properties inside and outside naturally occurring mussel mats are indistinguishable. Potential causal factors giving rise to observed differences between natural mussel-mat and no-mat communities were then explored with a manipulative experiment that tested the effects of addition of physical structure (i.e., mussel mat mimics) on macrofaunal communities.

Methods

Study Area

The research was carried out in the Northern Wildlife Preserve in the northeast corner of Mission Bay, San Diego, where remnant salt marsh (*Spartina foliosa* and *Salicornia* spp.), sand/mud flat, and eelgrass (*Zostera marina*) habitats are present. Mission Bay is a shallow, highly-modified system (through filling and dredging), and its salinity is usually near full seawater. The temperature of the bay generally ranges between 12 and 26°C (Levin 1983). The mats created by adult *Musculista* are often conspicuous elements of the sandy-mud intertidal landscape (Fig. 5-1), and it is possible to visually identify areas with and without high densities of adult mussels.

Musculista senhousia

Musculista was first found on the Pacific coast in Puget Sound in the 1920's, where it was accidentally introduced with the Japanese oyster *Crassostrea gigas* (Kincaid 1947). In the 1940's, the mussel appeared in San Francisco Bay (Carlton 1979), and in the mid-1960's it was first found in Mission Bay in southern California (MacDonald 1969), where it was probably introduced via ballast water or ship fouling (Cohen and Carlton 1995). By the mid-1980's, the mussel was one of the most common members of intertidal and subtidal soft-bottom communities of both San Diego Bay and Mission Bay (Crooks 1992). *Musculista* possesses many opportunistic characteristics: it is small (maximum length of about 3.5 cm), short-lived (most are annuals but some live up to two years), experiences high mortality, attains very high densities, grows quickly, and has high fecundity (Tanaka and Kikuchi 1978; Crooks 1996).

Field Sampling and Laboratory Procedures

Sediments and associated organisms (including *Musculista*) were collected quarterly from July 1993 to October 1996 from a site (20 m x 5 m) established on a sandy-mud tidal flat at approximately 0.33 m above MLLW (Mean Lower Low Water). On each sampling date, six stations were chosen at the site. Different stations were sampled on each date. Within each station, paired samples were collected approximately 0.5 m apart. The nature of the sampling varied according to the conditions present on the tidal flat. If mussel mats were visually present (July 1993, October 1993, July 1994, October 1995, and July 1996), the stations were chosen so that each contained patches with and without mussels mats. Within each station, a sample was taken from the mat area (sample a) and another sample was taken ca. 0.5 m away in a no-mat area (sample b). In general, it was relatively easy to accurately determine areas with and without mussels. On two occasions (July 1994 and October 1995), however, one of the no-mat samples in fact contained a relatively large number of mussels (over 8 times that of the average of the other no-mat samples) that were not observed during sampling but that were evident during processing of samples. These samples and their corresponding pair from the mat area in the station were eliminated from further analyses.

On sampling dates without obvious mussel mats (April 1994, January 1995, April 1996, and October 1996), the six stations at the site were randomly selected and each of the paired sets of samples within the station came from areas approximately 0.5 m apart, with samples arbitrarily designated a and b. One sample in April 1996 was lost, so both samples from that station were not considered in the analysis. Samples from other quarterly sampling dates are not considered here because conditions on the tidal flat (e.g., macroalgal blooms) did not permit either sampling of mat / no-mat or no-mat / no-mat sediments.

For characterization of macrofaunal communities, cores with a surface area of 0.001 m^2 were taken to a depth of 2 cm (preliminary studies demonstrated that over 90% of the animals on the tidal flat occurred within the top 2 cm). These cores were preserved unsieved in 10% buffered formalin, and later sieved through 300-μm mesh in the laboratory. All material retained on the sieve was sorted under a dissecting microscope and all macrofauna were counted and identified to the lowest taxonomic level possible (usually species) and then transferred to 70% alcohol. Mussel lengths were measured by ocular micrometer or digital caliper, and these were used to calculate dry flesh weight of the mussels according to the length-weight relationships defined for Mission Bay *Musculista* (Crooks 1996).

Information for each species regarding feeding strategy and larval development mode was obtained from the literature (Fauchald and Jumars 1979; Morris et al. 1980;

Wilson 1991). Animals with known larval development modes were categorized as having either planktonic (both planktotrophic and lecithotrophic) larvae or direct development. The animals also were categorized by feeding modes as surface feeders (including surface-deposit feeders, suspension feeders, and macrophages) or subsurface feeders (see Appendix 5-1).

Sedimentary analyses were performed on 3 dates (October 1993, July 1994, and October 1995) with mat / no-mat comparisons. Cores ($0.001 m^2$) were taken to a depth of 6 cm, and on two dates (July 1994 and October 1995) these were split into 0-2 and 2-6 cm fractions. The sediment was then frozen for later analysis. Sediment particle size (% weight of sand vs. % weight of silts and clays) was determined by wet-sieving thawed sediment through a 63-µm screen, drying the < 63-µm and > 63-µm fractions overnight at 60 °C, and then weighing them. Percent organic matter was determined by combusting pre-weighed sediment (< 1 mm) in a muffle furnace at 550°C for 24 h. The sediments used for both analyses were initially sieved through a 1-mm mesh to remove large material, primarily shells and large eelgrass and algal fragments. Shear strengths of sediments (to a depth of approx. 1 cm) within well-developed mussels mats and adjacent no-mat areas was measured *in situ* (August 1996) with a Torvane shear device.

Experimental Test of Effects of Physical Structure

In order to examine the hypothesis that mussel effects on macrofaunal colonization derive primarily from the physical structure of the mussel mats, an experiment was conducted in April, 1997. Ten blocks on the tidal flat were established, and within each block two circular areas ($0.0625 m^2$) were cleared of sediment to a depth of approximately 4 cm. Each excavated plot was then filled to the level of the surrounding sediment with high intertidal beach sand (containing no macrofauna), and one of two treatments was then randomly assigned to each plot. The two treatments consisted of (1) a mussel mat mimic (furnace filter material consisting of plastic-covered plant matter) held in place with buried plastic stakes , and (2) no mat mimic (a control). After two weeks, cores (0.001 m^2 and 4-cm deep) were taken from each plot to examine recruiting and migrating macrofauna. Only six of the blocks were sampled, because mats at the other plots had been disturbed and / or removed (probably by gulls). The samples were preserved in formalin, later sieved through 300-µm mesh, and all macrofauna were identified to the lowest taxonomic level possible.

Analyses

Statistical differences in means within each date in the mensurative and manipulative experiments were tested using paired t-tests (5 df for all dates except July 1994, October 1995, and April 1996, with 4 df each). Differences in means between mat samples and adjacent no-mat samples averaged across dates were tested using Randomized Complete Block ANOVA's, with date as a blocking factor. In this analysis, the average of values from July 1993 and October 1993 were used, because these represent the only two consecutive sampling dates when mats were present. On all other sampling dates mat presence and absence alternated. Comparisons of fauna at times when mats were present to times when mats were absent were made using ANOVA. All non-percentage data were log(x+1) transformed prior to analysis in order to aid in homogenizing variances and to evaluate relative rather than absolute differences in paired samples (Mead 1988). All percentage data were arcsine square-root transformed prior to analyses. Unless otherwise stated, all data are back-transformed means and standard errors (resulting in errors that are asymmetric about the mean). No attempt has been made to control experiment-wise error rates (Mead

1988; Stewart-Oaten 1995), and P values below 0.05 were considered significant. *Musculista* counts were removed from total densities for all calculations and statistics involving macrofauna.

For comparisons of macrofaunal assemblages both within and among stations on each sampling date, percentage similarities (Krebs 1989) were calculated using the formula:

$$\text{P.S.} = \sum_{i=1}^{n} \text{minimum}\,(p_{ai},\ p_{bi}) \qquad (1)$$

where P.S. = percentage similarity between the two samples, p_{ai} = percentage of species i in sample a, p_{bi} = percentage of species i in sample b, and n is the number of species in samples a and/or b. Three sets of percentage similarities were calculated for each sampling date. First, each within-station pair of samples (a vs. b) was compared. In addition, two among-site comparisons were made: (1) each sample a with other sample a's, and (2) each sample b with other sample b's.

For analyses of species diversity patterns, expected species richness as a function of number of individuals was determined using the rarefaction method (Hurlbert 1971).

Results

Musculista senhousia

Musculista was seasonally abundant on the tidal flat (Fig. 5-2), with highest abundances and the presence of recognizable mats typically occurring in the summer and fall. There was, however, variation in the timing and intensity of recruitment, as is indicated by the size structure, densities, and biomass of *Musculista* (Fig. 5-2). For example, in July 1994, the mussels were smaller and the biomass less than in other months with mats, suggesting that these mats were younger than those observed at other times. Following the 1993 and 1994 recruitment events, mussel mats persisted throughout the fall, but were not evident in either January 1994 (Crooks pers. obs.) or 1995 (Fig. 5-2). In January 1996, however, well-developed mats were present on the tidal flat, remaining from a very heavy recruitment of mussels the previous spring (Crooks pers. obs). A few large mussels also persisted into April 1996, although these did not form obvious mats (Fig. 5-2). The recruitment event of 1996 appeared to be relatively weak, and the mats that were present in July had disappeared by October (Fig. 5-2).

Alteration of the Benthic Habitat by *Musculista*

Through its construction of byssal mats, *Musculista* is capable of changing the physical nature of the sediment (Fig. 5-1). Generally, mats consisted of relatively large amounts of mussels, living and dead macroalgae, eelgrass and shell fragments, byssal threads, sediments, and associated biota. Living mussels were usually the largest structures within the mats. Mats were typically raised several centimeters relative to areas without mats, and this mat construction can stabilize the sediment surface. Shear strength measurements (August 1996) were 70 % greater in mats (0.48 kg/m^2 ± 0.026, n=12) than in mat-free sediments (0.28 kg/m^2 ± 0.016, n=12; t_{11}, P<0.001). However, the mussel mats are transient features on the tidal flat. Shells of the dead mussels (which tend to break apart quickly) or remains of uninhabited byssal cocoons were rare on the tidal flat (Crooks pers. obs.).

Sedimentary properties within well-developed mussel mats, present in October 1993 and October 1995 (Fig. 5-2), differed from those in areas without mats (Table 5-1). In October 1995, sediment within mats had significantly higher percentages of silts / clays (for both the 0-2 and 0-6 cm fractions) and percent organic matter (for the 0-2 cm fraction) than mat-free sediments. In October 1993, the amount of fine sediments and organic matter in the 0-6 cm fraction was greater than in adjacent no-mat areas. In July 1994, when mats contained smaller mussels and less biomass (Fig. 5-2), there were no significant differences in percent fines or combustible organic matter between mat and no-mat areas. In October 1995, potential effects of the mussels on grain sizes and organic matter were limited to the surface of the sediment. When significant differences existed in the 0-2 cm fractions for grain size and organic matter and in the 0-6 cm fraction for grain size (Table 5-1), no significant differences were found for the 2-6 fractions (not shown) for either organic matter ($t_5 = 0.47$, $P=0.663$) or grain size ($t_5 = 0.30$, $P=0.777$).

Macrofaunal Density

Total macrofaunal densities (excluding *Musculista*; Fig. 3A, B) ranged from a low of 30 ind. 0.001 m^{-2} (outside mussel mats in July 1993) to 277 ind. 0.001 m^{-2} (inside mussel mats in October 1993). Averaged across all dates with mat / no-mat comparisons, 2.7 times more individuals were found within mats than in adjacent sediments without mats ($F_{1,3}=17.7$, $P=0.025$). Macrofaunal densities were significantly higher in mats during four of the five months with mat / no-mat comparisons (Fig 3A). In months without mats, no significant differences in macrofaunal densities between a and b samples existed (Fig. 5-3B).

Most major taxonomic groups exhibited increased densities within mussel mats relative to mat-free sediments (Fig. 5-4). On all five dates, crustaceans (primarily tanaids and amphipods) were significantly more abundant within mats. Insect (midge) larvae were significantly more abundant on three dates. Molluscs (primarily *Barleeia subtenuis*) and polychaetes (including *Exogene* cf. *lourei*, *Capitella* sp., and *Schistomeringos rudolphi*) were significantly more abundant within mats on one date each. Oligochaete densities appeared to be more comparable in mat and no-mat areas, as they only experienced significantly increased densities within mats on one date, and this difference was relatively small (Fig. 5-4). In terms of percent representation (averaged across dates), oligochaetes were the only taxa that showed a significant difference, comprising 15% of the individuals within mats and 34% of the individuals in no mat areas (t_3= 4.78, P = 0.017).

In months with no mussel mats, there was only one significant difference (oligochaetes in April 1994) in the 24 comparisons of abundances between the a and b samples (Fig. 5-4). This is in accord with the prediction that the means of the samples should be equal given random sampling and that approximately one in every twenty comparisons will be significant at $\alpha = 0.05$.

The increase in density of major taxonomic groups (Fig. 5-4) reflects a general increase in abundance of many species (and higher taxa) within mats (Table 5-2). On all five dates with mat / no-mat comparisons, more species had higher abundances inside than outside mats, and this difference was significant on three dates. Averaged across months, 4.1 times as many species were more abundant inside than outside mats ($F_{1,3}$=19.7, P=0.016).

Mats of *Musculista* appeared to enhance densities of several species, while no single species had increased densities in no-mat areas (Appendix 5-1). Mats appeared to benefit two species in particular. The tanaid *Leptochelia dubia* was significantly more abundant within mats on four of five dates (Fig. 5-5A, B). In October of 1993, the species achieved the highest density of any species observed during the course of the study, with a density in mats of 190 ind. 0.001 m^{-2}. The small gastropod, *Barleeia subtenuis* was significantly more abundant within mats on three dates (Fig. 5-5C, D). The largest difference was in July 1994, when the snail's density was thirty times greater within mats.

Species Richness

The number of species (i.e., species richness) per core (Fig. 5-3C, D) was greater inside mussel mats than in adjacent, mat-free sediments, with an average of 1.6 times as many species within mats ($F_{1,3}$=277.3, P<0.001). Species richness was significantly higher within mats on three dates (July 1993, July 1994, and July 1996; Fig. 5-3C). No significant differences existed in months without mats (Fig. 5-3D).

Species richness per number of individuals (from rarefaction estimates) also differed between mat and no-mat areas (Fig. 5-6). Mat / no-mat rarefaction curves during months with mussel mats were consistently less similar than the no-mat / no-mat curves during months without mats. On four of the five dates with mat / no-mat comparisons, within-mat rarefaction curves were higher than no-mat curves (Fig. 5-6). On the one date (October 1993) where the mat curve fell below the no-mat curve, the average number of species per core also was not significantly higher within mats (Fig. 5-3C). However, this was the date with the greatest differences in total macrofaunal densities (Fig. 5-3A), due largely to the abundance of the tanaid, *Leptochelia dubia* (Fig. 5-5A).

Macrofaunal Community Similarities

Mussel mats increased the small-scale spatial heterogeneity of macrofaunal community composition on the tidal flat (Table 5-3). The similarities of assemblages in within-station, paired cores (a vs. b) from months with mats (i.e., mat / no-mat comparisons) were significantly lower than the similarities of within-station, paired cores (a vs. b) from months with no mats (i.e., no-mat / no-mat comparisons; t_6= 4.2, P=0.006). When mussel mats were present, the similarity of mat / no-mat pairs from within a station were lower than the comparisons of mat samples to other mat samples and the comparisons of no-mat samples to other no-mat samples ($F_{2,6}$=12.0, P=0.008).

When mats were absent, however, the similarities of paired cores were not significantly different than the similarities of cores taken from different stations ($F_{2,6}$=3.26, P=0.110). Thus, mats appear to alter the spatial structure of the tidal flat on approximately one-half meter scales. When no mats were present, randomly selected areas 0.5 m away tended to be the most similar to each other, whereas when mats were present, mat and no-mat areas 0.5 m away tended to be the least similar.

Life Habits

The representation of macrofaunal feeding modes within mats differed from that in no-mat areas (Fig. 5-7A, B). Surface feeders were significantly more abundant in mat than in no-mat samples (Fig. 5-7A). No significant difference existed between density of subsurface feeders in mat and no-mat areas. In terms of percent composition, subsurface feeders were relatively more abundant in no-mat samples while surface feeders were more abundant in mat samples (Fig. 5-7B).

Direct developers had significantly higher densities inside than outside mats (Fig. 5-7C). No significant differences existed for the densities or percent representation of planktonic developers or for the percent representation of direct developers (Fig. 5-7C, D).

Experimental Test of Mat-Mimic Effects

Results of the 2-wk mat mimic experiment support the hypothesis that the presence of physical structure associated with mussel mats may facilitate some macrofauna. A number of the patterns characteristic of the natural mats were observed in the mat mimics (Table 5-4). Crustaceans (primarily gammarid amphipods), which as a group always had higher densities in the natural mussel mats than in mat-free sediments (Fig. 5-4), were also significantly more abundant within the mat-mimic treatment. The small gastropod *B. subtenuis*, which was significantly more abundant within natural mats on three dates (Fig. 5-5C), was significantly more abundant within mat-mimic treatments, even though abundances were relatively low. Nemerteans were also found in significantly higher abundances within the mat-mimic treatment. Although differences were not significant, densities of macrofauna (per core) were almost twice as high in the presence of mat mimics than in control areas, and species richness was approximately 1.5 times greater. The tanaid (*L. dubia*) which was very abundant in natural mats (Fig. 5-5A), was no more abundant in the mat mimics than in the controls. However, tanaid densities were relatively low in the experimental treatments, and April may be a time of low abundance for the species (Fig. 5-5B).

Differences in the feeding modes of macrofauna found in plots with and without mat mimics (Table 5-4) resembled differences found in natural mat and no-mat areas (Fig. 5-7A, B). The percent representation of surface feeders, as well as their absolute densities, were significantly higher within the mat-mimic treatments. Conversely, subsurface feeders were proportionately more abundant within the control treatment. No significant differences were found for densities or percent representation of larval development modes in mat-mimic and control treatments, although 2.5 times more direct developers were found in mat-mimic than in control treatments (Table 5-4). In natural mat / no-mat comparisons, averaged across dates (Fig. 5-7C, D), the only significant difference was for densities of direct developers

Discussion

Patterns of Abundance and Species Richness within Mussel Beds

In a remnant natural wetland of Mission Bay, mats created by *Musculista* are often distinctive features that alter the physical environment and composition of biotic communities. Typically, decimeter to meter-sized patches of mats appear to facilitate other organisms, as species richness (Figs. 5-3 and 5-6) and density of individuals (Figs. 5-3, 5-4, and 5-5) are typically higher within mussel mats compared to adjacent no-mat patches. Some of the taxa that appear able to exploit the new habitat provided by *Musculista* include tanaids, gastropods, amphipods, insect larvae, and polychaetes. Surface-feeding, direct-developing species appear to benefit most from the presence of mussel mats (Fig. 5-7).

As in Mission Bay, *Musculista* in other locations has been reported to facilitate organisms (Table 5-5). The small bivalve *Nucula hartvigiana* in New Zealand (Willan 1987) and polychaetes in Hong Kong (Hutchings and Wells 1992) were found in higher abundances within mats than in areas without mussels. The epifaunal mussel, *Mytilus edulis*, when forming beds in soft sediments, can also facilitate infauna such as oligochaetes (Commito 1987), crabs (Thiel and Dernedde 1994), and other macrofaunal taxa (Dittmann 1990; Table 5-5). Negative effects of mussel beds have also been reported. Larger bivalves and eelgrass have been reported to be inhibited by *Musculista* mats (Sugawara et al . 1961; Uchida 1965; Willan 1987, Reusch and Williams 1998). Polychaetes and other small infauna (Commito 1987; Ditmann 1990; Jaramillo et al. 1992) have been reported in lower densities within beds of other mussel species (Table 5-5).

The positive effects of mussel mats in soft-sediment habitats resemble the effects of mussel beds on rocky substrates. Despite the ability of hard-substrate dwelling mussels to outcompete larger organisms for space (e.g., Paine 1974), mussel beds can provide unique habitat for other, typically smaller, organisms (Suchanek 1985; Seed 1996). Increased abundances and/or diversities within mussel beds have been reported for a variety of mussel species, including *Mytilus californianus* (Kanter 1980), *M. edulis* and *M. galloprovincialis* (Tsuchiya and Nishihara 1986; Tsuchiya and Bellan-Santini 1989; Matsumasa and Nishihara 1994), *Semimytilus algosus*

(Tokeshi and Romero 1995), *Modiolus modiolus* (Brown and Seed 1977; Witman 1985), *Septifer virgatus* (Ong Che and Morton 1992; Seed and Brotohadikusumo 1994), *S. bilocularis* (Jackson 1976), and *Brachidontes rostratus* (Stephenson and Stephenson 1972; Peake and Quinn 1993). It has also been found that species outcompeted for primary space by mussels can live epizoically on the mussel shells (Lohse 1993; Tokeshi and Romero 1995). Even beds created by zebra mussels, *Dreissena polymorpha*, benefit populations of a wide variety of small invertebrates (Dermott 1992; Stewart and Haynes 1994).

Habitat Alteration by Mussels

The above cases of facilitation by mussels are the effects of habitat alteration caused by mussel-induced, architectural changes. Mussel beds provide structurally complex habitats that may alter water flow, ameliorate environmental conditions such as temperature and humidity, accumulate sediments on hard substrates (Suchanek 1985; Seed and Suchanek 1992), and stabilize sediments on soft substrates (this study). These effects result from the presence of mussel shells themselves ("autogenic engineering"), as well as from binding of sediments and other material by byssal threads ("allogenic engineering;" Jones et al. 1994). In addition, mussels may filter the water column (Kautsky and Evans 1987; Wilkinson et al. 1996). This activity by zebra mussels in fresh waters of the eastern U.S. has led to increased light penetration and growth of aquatic macrophytes at depth (Lowe and Pillsbury 1995).

For *Musculista* in Mission Bay, habitat alteration produces a variety of inter-related effects. At the broadest level, *Musculista* is creating physical structure on the tidal flat. The results of the manipulative experiment suggest that simply the presence of structure can facilitate resident biota (Table 5-4). This may relate to any of a variety of mechanisms, including the alteration of environmental parameters (discussed above), active habitat selection or thigmotactic responses of motile macrofauna such as crustaceans (e.g., Olyslager and Williams 1993), or refuge from predation afforded by the presence of structure (Witman 1985; Medeiros-Bergen and Miles 1997). Similar patterns of increased faunal abundances or diversities have been seen with a variety of other species that provide structural complexity, including other mussels (as discussed above), tube-building worms (Haines and Maurer 1980) and seagrasses (Homziak et al. 1982).

In addition to creating structure, mats of *Musculista* incorporate a variety of organic and inorganic material (e.g., algal and eelgrass fragments and fine sediments) to which other species may respond. For example, the tanaid *Leptochelia dubia* is a small crustacean which constructs tubes out of sediment and organic debris. The three-dimensional matrix created by the mussel mats may offer *L. dubia* both a supply of materials with which to construct their tubes and a structure in which the tubes can be built. In other bays, *L. dubia* is often found associated with physical structures such as green algae on mudflats and fouling growth on pier pilings (Morris et al. 1980).

Because of the binding of sediments and organic matter, trapping of feces and pseudofeces, and passive deposition of low-density material, *Musculista* mats also alter sedimentary properties (Morton 1974). In this study, well-developed mats contained more fine sediments and combustible organic matter than nearby areas without mats (Table 5-1). In Hong Kong, *Musculista* was observed to convert a sand flat into a mud flat (Morton 1974), and the sediment under dense beds of *Musculista* can appear black and anoxic (Anonymous 1965; Crooks pers. obs). Similar patterns have also been observed in New Zealand (Creese and Hooker 1996). Other mussels (e.g., *Mytilus edulis*) can also increase fine sediment and organic matter through biodeposition (Kautsky and Evans 1987; ten Brinke et al. 1995). On rocky shores, passive deposition and trapping of fine sediments within mussel beds can occur to an extent that an "infaunal" component of the fauna has been recognized (Suchanek 1985; Ong Che and Morton 1992; Tokeshi 1995).

The alteration of organic matter within sediments may serve to increase food resources which may favor surface feeders, as was seen in natural *Musculista* mats (Fig. 5-7A, B). However, sedimentary properties alone can not fully explain observed differences within *Musculista* mats, because even when no differences in sediment properties were evident (July 1994), some differences in the macrofaunal communities existed (e.g., species richness, Fig. 5-3C). Although increased organic matter within mussel mats might be expected to benefit subsurface as well as surface feeders, there was no increase in density of the latter group (Fig. 5-7A, B).

One predicted effect of the mussels, related to suspension feeding by *Musculista*, was the inhibition of organisms with planktonic larvae (Woodin 1976). In this study, however, this inhibition was not observed; densities of species with planktonic larvae were comparable inside and outside mats (Fig. 5-7C,D). Possible explanations for this result include the lack of actual inhibition of larval settlement or post-settlement migration from no-mat to mat areas. Although densities of species with planktonic larval forms were not inhibited, neither were they greatly facilitated. Direct-developers were typically much more abundant in mats than in adjacent mat-free sediments (Fig. 5-7C). Commito (1987) and Commito and Boncavage (1989) also reported increased abundances of a direct-developer (the oligochaete *Tubificoides benedeni*) within soft-sediment beds of the mussel *Mytilus edulis*.

Habitat Alteration by Exotics

Examination of invasive habitat modifiers permits us to evaluate the mechanisms and time-scales of response of resident species to biogenically altered environmental conditions. For example, in this study, *Musculista* mats facilitated many small infauna, largely through the construction of physical structure that provided habitat for these species. Resident species appeared to rapidly and repeatedly take advantage of the seasonal appearance and disappearance of the mats on the tidal flat, and significant faunal responses were also seen after just two weeks in the manipulative experiment. In a broader sense, the resident biota have also responded rapidly to the presence of *Musculista* in that this species has only been abundant in the intertidal of Mission Bay for less than three decades (Crooks 1992).

Although there are relatively few studies on invasive aquatic species capable of ecosystem alteration, those that exist provide insights into invasion biology. In New England, the introduced periwinkle, *Littorina littorea*, is able to alter habitats by bulldozing algae on hard shores and inhibiting the growth and spread of cordgrass (*Spartina alterniflora*) on soft substrates (Bertness 1984). Organisms that are able to create structure have facilitory effects similar to those of *Musculista*. In the U.S. Pacific Northwest, intertidal beds of the exotic eelgrass, *Zostera japonica*, have more fine-grained sediments, combustible organic matter, and species than unvegetated sediments (Posey 1988). Within beds of the exotic vascular plant, *Hydrilla verticilatta*, in Chesapeake Bay, eight taxa experienced increased abundances (Posey et al. 1993). It is important to remember, however, that this facilitation may be scale-dependent (as is the case for *Musculista*) and that these exotics may have different effects on other organisms (Chapter 7). This is exemplified by the zebra mussel which, despite its ability to facilitate some small macrofauna, adversely affects other species through smothering and filtration of the water column (Nalepa and Schloesser 1993; Stewart and Haynes 1994; Lowe and Pillsbury 1995). Nonetheless, positive interactions between exotics and resident biota is rarely recognized as a general consequence of a biological invasion.

Habitat modification by exotic species, such as that seen for *Musculista*, *Littorina littorea*, and *Zostera japonica*, is by no means limited to marine systems. Non-native species capable of altering the physical environment are found in many of the world's invaded ecosystems (Chapter 7). Given the potential consequences of these invasions, habitat alteration should be considered a major effect of exotic organisms. Although the continued introduction of habitat-modifying exotics into ecosystems poses serious management and conservation concerns, the further study of the role of these organisms will provide a better understanding of the relationships between individual species, biotic communities, and habitats.

Fig. 5-1 Patchy mats (raised areas) of *Musculista senhousia* in the Northern Wildlife Preserve, Mission Bay, San Diego, CA.

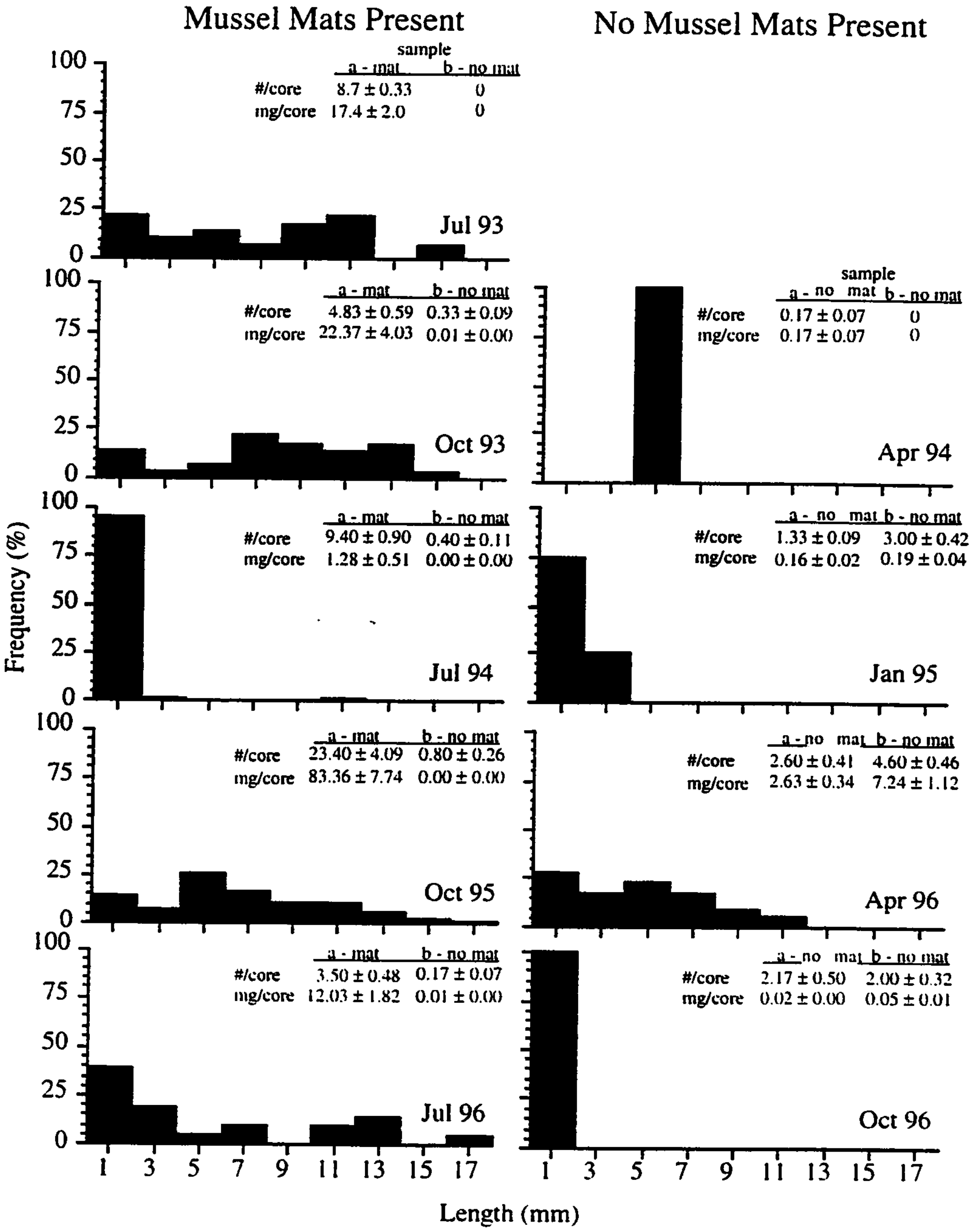


Fig. 5-2. Size - relative frequency (%) distributions of *Musculista senhousia* (for samples a and b combined). Also provided are untransformed mean numbers of individuals (± 1 s.e.) and mean biomasses (mg dry flesh weight ± 1 s.e.) per core (0.001 m^2).

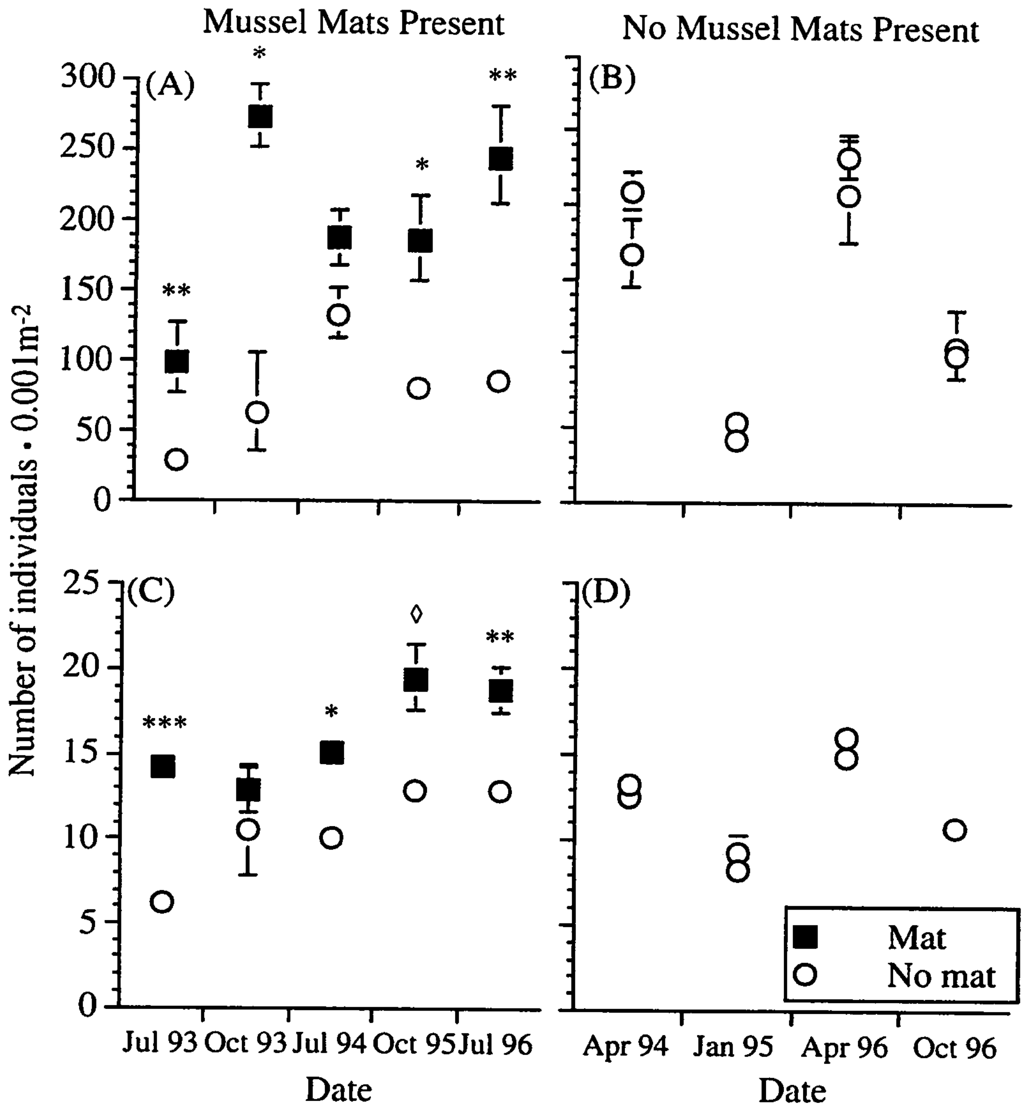


Fig. 5-3. Total macrofaunal densities and species richness on the tidal flat. Data are mean numbers $0.001\text{m}^{-2} \pm 1$ s.e. (n=6 except in July 94, Oct 95, and Apr 96, when n=5). Panels are total densities of macrofauna (excluding *Musculista*) when mats were present (A) and absent (B), and numbers of species when mats were present (C) and absent (D). Data for each date are from sets of paired samples taken approximately 0.5 m apart (see text for more details). *** = $P < 0.001$, ** = $P < 0.01$,* = $P < 0.05$, ◊ = $P < 0.1$, no symbol = $P > 0.1$.

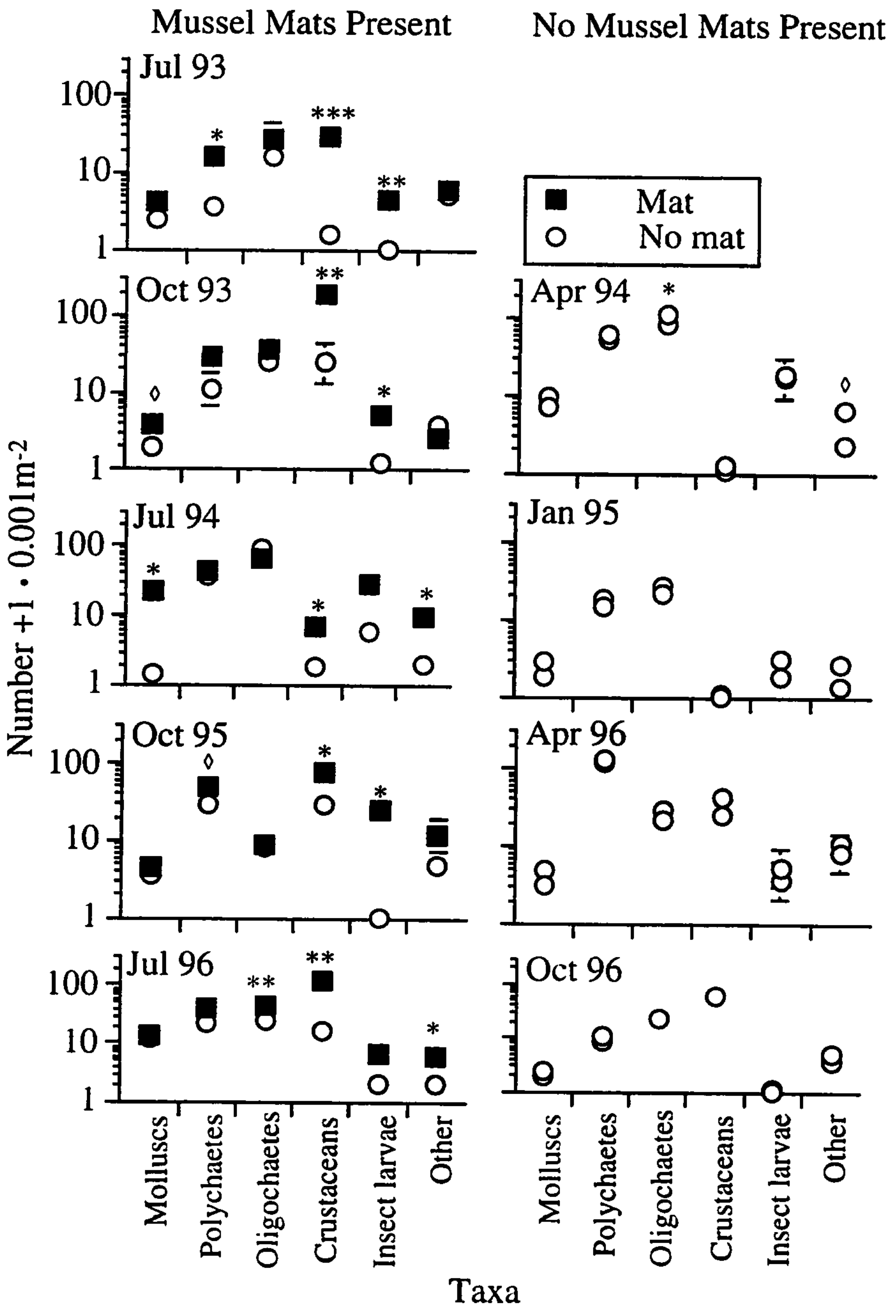


Fig. 5-4. Densities of major macrofaunal taxa. Data are mean numbers $0.001\text{m}^{-2} \pm 1$ s.e. (n=6 except in July 94, Oct 95, and Apr 96, when n=5). The category "other" includes cnidarians, turbellarians, nemerteans, and holothurians. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, ◊ = $P < 0.1$, no symbol = $P > 0.1$.

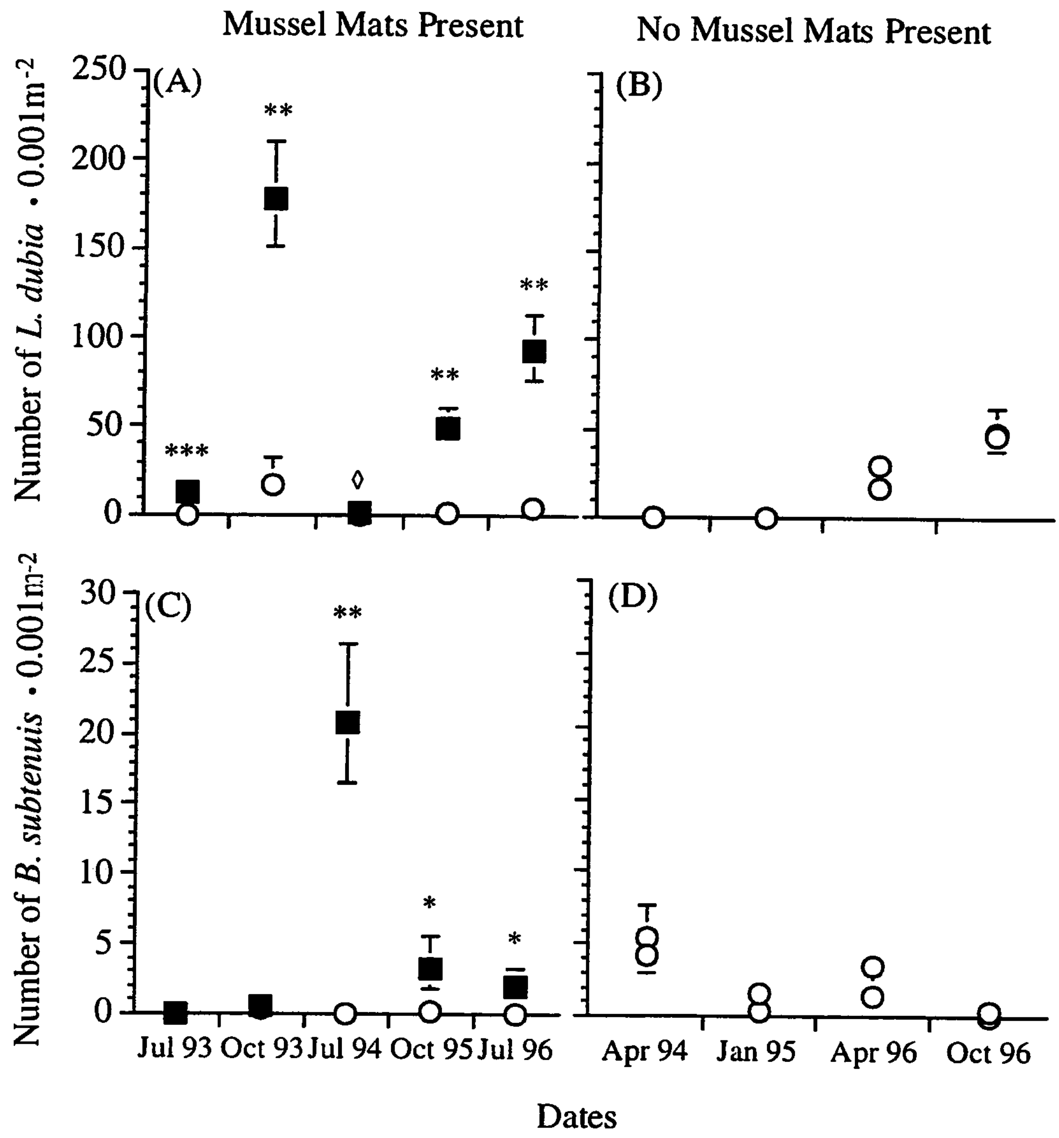


Fig. 5-5. Densities of two macrofaunal species. Data are mean numbers $0.001\text{m}^{-2} \pm 1$ s.e. (n=6 except in July 94, Oct 95, and Apr 96, when n=5). Panels are densities of the tanaid *Leptochelia dubia* when mats were present (A) and absent (B) on the tidal flat, and densities of the gastropod *Barleeia subtenuis* per core when mats were present (C) and absent (D). *** = $P < 0.001$, ** = $P < 0.01$,* = $P < 0.05$, ◊ = $P < 0.1$, no symbol = $P > 0.1$.

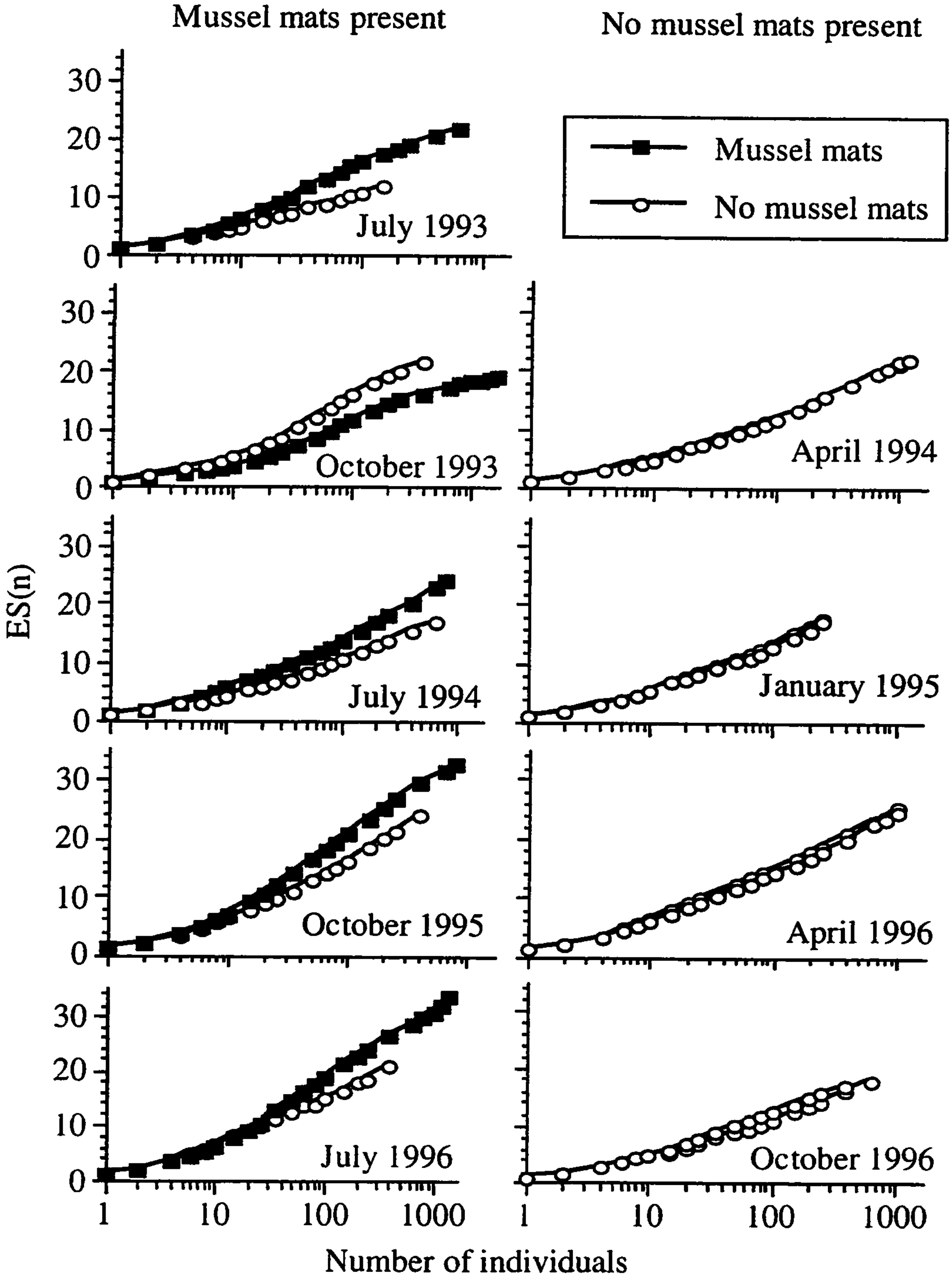
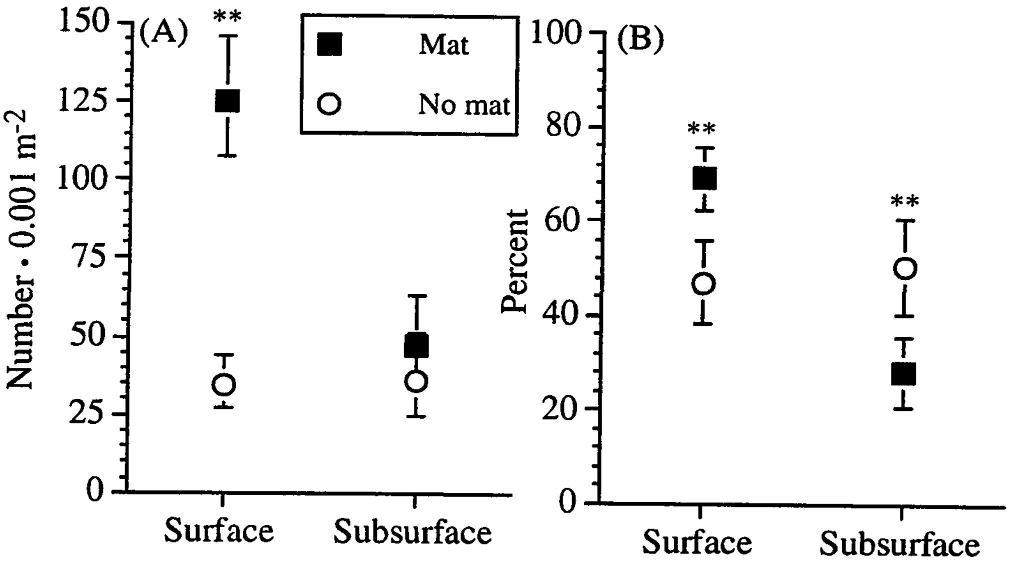


Fig. 5-6. Rarefaction curves plotting expected number of species as a function of number of individuals [$E(S_n)$] for each sampling date. Note log scale on X - axis.

Feeding Modes



Larval Development Modes

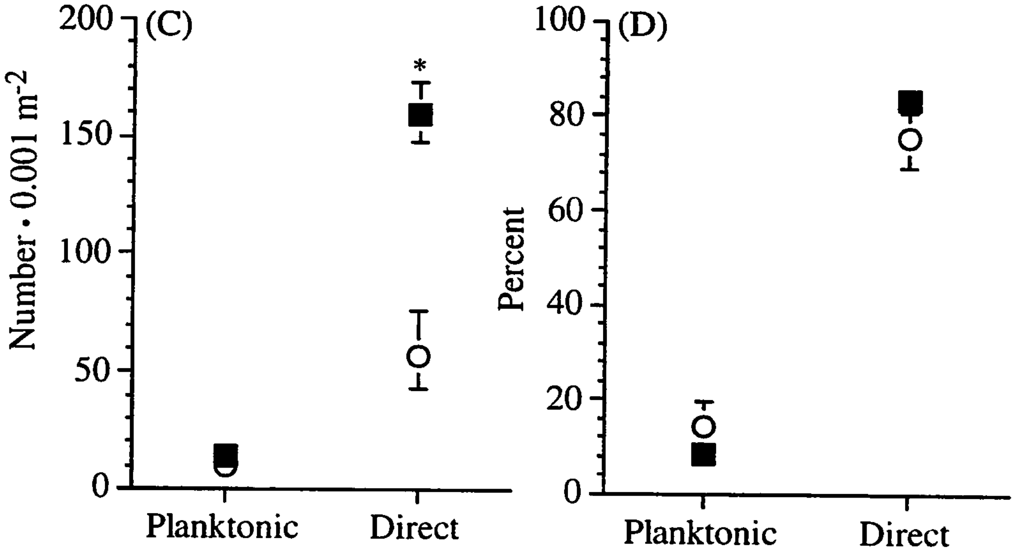


Fig. 5-7. Abundance and proportion of macrofauna exhibiting different feeding and development modes in mat and no-mat areas, averaged across months when mats were present. Panels are comparisons of (A) densities (mean number $0.001\text{m}^{-2} \pm 1$ s.e., n=4) and (B) proportions (mean percentage ± 1 s.e., n=4) of different feeding modes, and comparisons of (C) densities (mean number $0.001\text{m}^{-2} \pm 1$ s.e., n=4) and (D) proportions (mean percentage ± 1 s.e., n=4) of different larval development modes. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, ◊ = $P < 0.1$, no symbol = $P > 0.1$.

Table 5-1. Sediment properties (percent silts / clays and percent combustible organic matter) on three dates with mat / no - mat comparisons. P - values are from paired t-tests (df=4, except in Oct 93 when df=5). na = not analyzed; $^{+}$ = poorly-developed mat; $^{++}$ = well-developed mat.

	0-2 cm		0-6 cm	
	Silts/Clays (%)	Organic Matter (%)	Silts/Clays (%)	Organic Matter (%)
October 1993^{++}				
mat	na	na	15.6 ± 1.6	1.72 ± 0.12
no mat	na	na	9.7 ± 1.1	1.13 ± 0.08
P-value			0.018	0.005
July 1994^{+}				
mat	9.5 ± 0.9	0.98 ± 0.13	10.4 ± 0.4	1.17 ± 0.09
no mat	10.6 ± 1.7	1.39 ± 0.34	16.8 ± 4.7	1.12 ± 0.06
P-value	0.422	0.279	0.344	0.709
October 1995^{++}				
mat	20.1 ± 3.5	0.70 ± 0.10	12.9 ± 1.2	0.70 ± 0.06
no mat	8.4 ± 1.8	0.37 ± 0.11	8.1 ±0.4	0.55 ± 0.06
P-value	0.035	0.007	0.036	0.062

Table 5-2. Comparisons of the number of species (and higher taxa) with higher densities inside mussel mats vs. outside mats (mat>no mat), the number of species with lower densities inside vs. outside mats (mat<no mat), and the number of species with equal densities in each (mat = no mat). Departure from an expectation of equal proportions in the mat < no mat and mat > no mat categories was tested using $\chi^2_{1\,df}$. Bold-faced values equal $P < 0.05$.

	mat > no mat	mat < no mat	mat = no mat	P - value
July 1993	21	2	0	**< 0.001**
October 1993	15	8	1	0.145
July 1994	16	9	1	0.322
October 1995	24	8	2	**0.005**
July 1996	28	5	1	**< 0.001**

Table 5-3. Similarities (eq. 1) of macrofaunal communities (excluding *Musculista*) for months with mat / no-mat comparisons and months with no-mat / no-mat comparisons. Similarities were calculated for the paired samples within a station (a vs. b) as well as for samples between stations (a vs. a and b vs. b) Values are averages (± 1 s.e., n=4) across dates.

	Within – station pairs	Between stations	
	a vs. b	a vs. a	b vs. b
Mats present (a = mat; b= no mat)	43.4 (±6.2)	61.6 (±5.7)	59.9 (±4.2)
Mats absent (a = no mat; b = no mat)	71.2 (±3.1)	64.4 (±3.9)	63.4 (±6.4)

Table 5-4. Results of 2-week mat-mimic experiment. Values are back-transformed means per core ($0.001m^2$), and numbers in parentheses represent the range for the mean ± 1 s.e. P - values are from paired t-tests (5 df), and bold-faced values represent $P < 0.05$. The number of dates with significant differences between natural mat and no-mat areas (out of 5 total) are also given.

	Experimental treatments			
	Mat mimic	Control	P-value	Number of dates w/ differences between natural mat / no-mat areas
Total number of individuals	52.3 (43.2-63.2)	27.4 (17.3-42.9)	0.060	4
Number of species	12.3 (11.7-12.9)	7.6 (5.9-9.7)	0.094	4
Number of crustaceans	26.4 (20.1-34.6)	5.4 (2.6-10.5)	**0.010**	5
Number of *B. subtenuis*	0.8 (0.4-1.2)	0.0	**0.042**	3
Number of nemerteans	3.2 (2.3-4.3)	0.5 (0.2-1.0)	**< 0.001**	1
Number of *L. dubia*	5.2 (3.5-7.4)	4.3 (2.2-7.9)	0.549	4
Percent surface feeders	70.6 (67.0-74.0)	27.5 (16.3-40.2)	**0.010**	4
Percent subsurface feeders	29.8 (26.3-33.4)	72.7 (60.0-83.7)	**0.010**	4
Number of surface feeders	36.6 (29.3-45.6)	8.5 (4.2-16.3)	**0.018**	5
Number of subsurface feeders	15.2 (12.7-18.2)	17.4 (12.6-24.0)	0.603	1
Percent direct developers	64.9 (61.9-67.9)	44.7 (29.9-60.0)	0.218	3
Percent planktonic developers	5.0 (3.1-7.3)	3.8 (1.6-6.9)	0.733	2
Number of direct developers	33.7 (27.1-42.0)	13.08 (6.6-25.2)	0.086	4
Number of planktonic developers	2.3 (1.6-3.3)	1.6 (0.8-2.7)	0.625	0

Table 5-5. Reported interactions of soft-sediment dwelling mussels with benthic fauna. b = bivalve; c = crab; g = gastropod; p = polychaete; t = tanaid; sf = suspension feeder; df = deposit feeder

Species	Inhibit	Facilitate	Comments	Reference
Musculista senhousia	*Meretrix lusoria* (b), *Mactra chinensis* (b), *M. veneriformes* (b)		Japan	Sugawara et al. 1961
Musculista senhousia	*Tapes phillipinarum* (b)		Japan	Uchida 1965
Musculista senhousia	*Protothaca staminea* (b), *Chione undatella* (b)		San Diego	Crooks 1992
Musculista senhousia	scallops, *Xenostrobus pulex* (b)	*Nucula hartvigiana* (b)	New Zealand	Willan 1987
Musculista senhousia		polychaetes	diversity & density higher in bed; Hong Kong	Hutchings & Wells 1992
Musculista senhousia		*Leptochelia dubia* (t), *Barleeia subtenuis* (g), and other taxa; not oligochaetes	density typically higher in bed; San Diego	this study
Mytilus edulis		*Carcinus maenas* (c)	Europe	Thiel and Dernedde 1994
Mytilus edulis	sf polychaetes, ostracods, nematoda, predatory platyhelminthes	df polychaetes, oligochaetes, epibenthic & epiphytic spp., grazing platyhelminthes	#spp. higher in bed; density lower in bed; North Sea	Dittmann 1990
Mytilus edulis	*Nepthys incisa* (p), "non-oligochaetes"	oligochaetes	density higher in bed; New England	Commito 1987, Commito & Boncavage 1989
Mytilus chilensis, *Choromytilus chorus*	Capitellidae (p), *Polydora* sp. (p)		density, #spp., diversity (H') comparable or lower in bed; Chile	Jaramillo et al. 1992, Quijón et al. 1996

Appendix 5-1. List of fauna found during the study. Occurrence is the abundance of the species in the samples, averaged across dates: uncommon is < 1 / core ($0.001m^2$), common is < 10 / core, and abundant is > 10 / core. Mat < no mat represents number of dates (out of 5) where the average number in the mat samples was significantly greater than the number in the adjacent no-mat samples (approximately 0.5 m away). In no instance was the number in the no-mat samples significantly greater than the number in the mat samples. Also provided are assigned feeding and larval development modes of the species: surface = surface-deposit feeders, suspension feeders, and macrophages; subsurface = subsurface-deposit feeders; planktonic = planktotrophic and lecithotrophic developers; direct = direct benthic developers. * = exotic (Cohen and Carlton 1995); ** these taxa were not identified to species and therefore contributed only one species to tallied species counts.

Taxa	Occurrence	Mat > no mat	Feeding mode	Larval mode
Cnidarians **	Uncommon		Surface	Unknown
Platyhelminthes **	Common	1	Unknown	Direct
Nemerteans **	Uncommon	1	Surface	Unknown
Molluscs				
Bivalves				
Musculista senhousia *	Common		Surface	Planktonic
Mytilus galloprovincialis *	Uncommon		Surface	Planktonic
Gastropods				
Acteocina sp.	Common		Subsurface	Planktonic
Barleeia subtenuis	Common	3	Surface	Direct
Caecum californicum	Uncommon		Surface	Unknown
Annelids				
Polychaetes				
Armandia brevis	Uncommon		Subsurface	Planktonic
Capitella sp.	Abundant	3	Subsurface	Unknown
Eteone californica	Common		Surface	Planktonic
Eteone pacifica	Uncommon		Surface	Planktonic
Exogene cf. *lourei*	Abundant	1	Surface	Direct
Fabricinuda limnicola	Common		Surface	Direct
Haploscoloplos elongatus	Uncommon		Subsurface	Unknown
Polydora ligni *	Uncommon		Surface	Planktonic
Prionospio (Minuspio) sp. A	Uncommon		Surface	Unknown
Prionospio heterobranchia	Uncommon		Surface	Planktonic
Pseudopolydora paucibranchiata *	Abundant		Surface	Planktonic
Sabellid sp. B	Uncommon		Surface	Direct
Schistomeringos rudolphi	Common	1	Surface	Planktonic
Streblospio benedicti *	Uncommon		Surface	Planktonic
Ampharetid sp A	Uncommon		Surface	Unknown
Opheliid sp A	Uncommon		Unknown	Unknown
Syllid sp A	Uncommon		Surface	Unknown
Lumbrinerid sp A	Uncommon		Surface	Unknown
Nereid sp A	Uncommon		Surface	Unknown

Appendix 5-1 (cont.)

Maldanid sp A	Uncommon		Subsurface	Unknown
unidentified **	Uncommon		Unknown	Unknown
Oligochaetes				
Limnodriloides barnardi	Abundant		Subsurface	Direct
Paranais littoralis	Uncommon		Subsurface	Direct
Tubificoides brownea	Abundant		Subsurface	Direct
unidentified **	Uncommon		Surface	Direct
Arthropods				
Amphipods				
Ampithoe pollex	Uncommon		Surface	Direct
Corophium acherusicum *	Common		Surface	Direct
Elasmopus bampo	Uncommon		Surface	Direct
Grandidierella japonica *	Common	1	Surface	Direct
Hyale sp. A	Common	2	Surface	Direct
Mayerella banksia	Uncommon	1	Surface	Direct
Podocerus cristatus	Uncommon		Surface	Direct
Pontogenia rostrata	Uncommon		Surface	Direct
Protomedeia sp.	Uncommon		Surface	Direct
unidentified gammarids **	Uncommon		Surface	Direct
Tanaids				
Leptochelia dubia	Abundant	4	Surface	Direct
Cumaceans				
Cumacean sp A	Uncommon		Surface	Direct
Isopods				
Haliophasma geminatum	Uncommon		Surface	Direct
unidentified **	Uncommon		Surface	Direct
Insects				
Chironomid larvae	Common	3	Surface	Direct
unidentified Coleoptera A	Uncommon		Unknown	Unknown
Phoronids				
Phoronis architecta	Uncommon		Surface	Planktonic
Echinoderms				
Holothuroids				
Leptosynapta albicans	Uncommon		Surface	Direct

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CHAPTER VI

ARCHITECTURAL VS. BIOLOGICAL EFFECTS OF A HABITAT-ALTERING, EXOTIC MUSSEL, *MUSCULISTA SENHOUSIA*

Abstract

Musculista senhousia is a small mytilid mussel that has been introduced from Asia onto three continents, including the Pacific coast of North America. The mussel often forms dense mats that can increase infaunal density and species richness. This research experimentally examines the relationship between the physical structure of the mussel mat habitat and the biological activities of the mussel as it relates to the macrofaunal assemblages in Mission Bay, San Diego, California. The results of this experiment demonstrate that the effects of physical structure typically outweigh the effects of living mussels. Total macrofaunal densities, species richness, and densities of a variety of taxa (e.g., the snail *Barleeia subtenuis*, the polychaete *Haploscoloplos elongatus*, nemerteans, and amphipods) were enhanced by the presence of the artificial mats. The tube-building, planktonically-developing polychaete, *Pseudopolydora paucibranchiata*, however, was apparently inhibited by mats, as were planktonic developers as a group. The effects of structure provided by mussel shells themselves appeared to be weaker than the mat effects, although some taxa, such as the gastropod *B. subtenuis*, responded to shells alone. The influences of living mussels were also less pronounced than that of artificial mats, although non-planktonic developers,

including midge larvae and the tanaid *Leptochelia dubia*, showed positive responses to live mussels. In general, these results are consistent with observed effects of other habitat-creating exotics, and suggest that facilitation of biota by non-native species capable of creating physical complexity in ecosystems may be a major and predictable consequence of biological invasions.

Introduction

The invasion of non-indigenous species is altering the composition of biotic communities worldwide (Soulé 1990; Williamson 1996). Exotic species also can alter the functioning of communities through interspecific interactions such as competition and predation as well as alterations of the physical environment (Vitousek 1990; Williamson 1996; Simberloff et al. 1997). Although there are relatively many descriptions of direct, interspecific interactions between exotics and natives (e.g., Race 1982; Diamond and Case 1986; Okubo et al. 1989; Petren and Case 1996; Shigesada and Kawasaki 1997), there has been less general attention to the role of exotics as habitat modifiers (but see Bertness 1984; Posey 1988; Richardson et al. 1995; Ricciardi et al. 1997; Schmitz et al. 1997; Chapter 5).

One exotic species capable of both direct, interspecific effects as well as effects mediated by habitat-alteration is the mytilid mussel, *Musculista senhousia* (hereafter referred to as *Musculista*). This Asian species has been introduced to Australasia, the Mediterranean, and the Pacific coast of North America, where it typically lives on the surface of intertidal and shallow subtidal soft sediments in bays and estuaries (Carlton 1979; Crooks 1996). *Musculista* uses byssal threads to create byssal bags or cocoons, and when the mussel occurs in high densities (typically up to 5,000 to 10,000 m^{-2}) a mat or carpet is formed on the sediment surface (Morton 1974; Crooks 1996; Creese et al. 1997). *Musculista* is small, short-lived, grows rapidly, and experiences dramatic population fluctuations (Crooks 1996).

The habitat alteration caused by *Musculista* mat formation can have a variety of effects on resident flora and fauna. Dense mats may inhibit vegetative spread of eelgrass (*Zostera marina*), although lower densities of mussels may actually enhance growth of the plant through biodeposition (Reusch and Williams 1998). In Mission Bay, several macrofaunal taxa, such as amphipods, tanaids, small gastropods, and polychaetes, are found in higher densities within mussel mats than in adjacent sediments without mats (Chapter 5). Similar patterns can also be found for mussel mats on soft sediments in Hong Kong and New Zealand (Hutchings and Wells 1992; Creese et al. 1997). Also, sedimentary properties inside and outside naturally occurring mussel beds may be different, with beds having higher amounts of fine sediments and organic matter (Anonymous 1965; Morton 1974; Creese et al. 1997; Reusch and Williams 1998; Chapter 5).

Two different mechanisms may influence macrofaunal patterns within mussel mats: effects caused by the biological processes of living mussels (such as filter feeding and biodeposition) and those caused by the structural change in the benthic habitat resulting from the presence of shells and the creation of mats. As *Musculista* is a densely-living suspension feeder, it may have negative effects on organisms with planktonic larvae by ingesting young animals attempting to settle upon the bottom (Woodin 1976; Williams 1980; Andre and Rosenberg 1991). In addition, increased biodeposition coupled with binding of sediments by byssal threads and creation of structure might serve to inhibit some motile taxa (Brencheley 1982). Still further, other benthic species may be facilitated by increased structural complexity such as that caused by tube-building worms (Haines and Maurer 1980), seagrasses (Homziak et al. 1982; Posey 1988), and blue mussels (Commito 1987; Dittmann 1990). Studies on the zebra mussel (*Dreissena polymorpha*) have shown that both the physical structure provided by shells as well as biodeposition by living mussels are important for shaping invertebrate communities (Slepnev et al. 1994; Ricciardi et al. 1997). Experimental studies on *Musculista* in Mission Bay suggest that the presence of physical structure (in the form of artificial mats) may produce many of the patterns observed in natural mats (Chapter 5), although the relative effects of living mussels in relation to the effects of physical structure have not been investigated.

The goal of this study was to evaluate the relative importance of architectural versus biological effects of *Musculista* and its mats in creating patterns of macrofauna associated with *Musculista* beds. This was accomplished by creating experimental plots containing living mussels, mussel mimics, and artificial mats in various combinations and examining subsequent patterns of faunal recruitment and colonization. The development of macrofaunal communities under these experimental conditions was then compared with the macrofaunal communities found in naturally occurring mussel mats, as well as with an experiment in which responses to physical structure alone (i.e., artificial mats) were examined (Chapter 5).

Methods

Study Site

The experiment was carried out on the sandy-mud intertidal mudflat of the Northern Wildlife Preserve of Mission Bay, San Diego. *Musculista* can typically be found year-round, although summer and fall are times of highest abundances of adult mussels. When mussel densities are high, the thick mats that form are easily visible. The experimental site was approximately 0.33 m above MLLW and was adjacent to the study area described in Chapter 5. The experiment ran for six weeks, starting in May 1997.

Experimental Procedures

The experiment was conducted as a Randomized Complete Block Design with 8 blocks. The experimental units were circular plots of defaunated sediment 20-cm in diameter and 6-cm deep. Each plot received one of 4 experimental treatments: 1) artificial mussel mats and mussel mimics, 2) artificial mussel mats and live mussels, 3) mussel mimics and no mats, 4) live mussels and no mats (since no natural mats were involved in the study, the term mats will be used in the remainder of the paper to refer to the artificial mussel mats). Also in each block was a plot of bare, defaunated sediment as a control.

To generate experimental material, twenty gallons of sediment from the study area were removed and frozen at -20°C for 24 hours. Approximately 640 mussel mimics were manufactured using Aquamend epoxy-putty to fill the shells of *Musculista* that had been boiled and had the flesh removed. Approximately 640 live mussels were harvested from nearby, naturally-occurring mats. Mat-mimics were created by cutting sheets of furnace filter material (Frost-King brand), made of dried plant material coated with plastic, into 20-cm diameter by 1-cm thick disks. To exclude avian predators which had demonically intruded (*sensu* Hurlbert 1984) in previous experiments, four 2-m by 1.5-m cages made from PVC pipe and 2.5 cm plastic mesh were placed over experimental plots. The placement of treatment within blocks was randomized and recorded, and a small plastic marker stake was placed in the center of each treatment.

For the no mat / live mussel treatment, 40 live mussels (= 2,500 mussels / m^2) were haphazardly pushed into the sediment with approximately 10% of the overall length of each mussel left exposed above ground. Care was taken to place the mussels in the natural position so as not to hinder siphoning ability. Forty mussel mimics were planted in the no mat / mussel mimic treatment in the same manner. For mat / live mussel and mat / mussel mimic treatments, the artificial mats were attached to 10-ml plastic pipettes and staked down as anchors with the pipette completely buried. Each mat was placed so that it rested on top of the sediment in order to most accurately simulate real mussel mats. Exactly 40 mussels or mimics were then pushed into the artificial mat accordingly. An additional plot in each block served as a control. After all of the treatments were set up, the bird-exclusion cages were set in place.

Sampling and Laboratory Analyses

Sediment samples for biological analyses were taken three and six weeks after establishment of the experimental treatments. On each sampling date, one core (5-cm in diameter and 4-cm deep) was taken from each plot. Samples were preserved unsieved in formalin and then stained with rose bengal. In the laboratory, samples were sieved through a 300-µm mesh. The material retained on the mesh was sorted under a dissecting microscope. All macrofauna were removed, identified to the lowest taxonomic level possible, counted, and stored in alcohol. Identifications and larval development modes of species were determined as described in Chapter 5.

Samples for sedimentary analyses were taken after 6 weeks. One core was taken from each experimental plot and frozen for later analyses. All sediments were initially sieved through 1 mm mesh to remove large material such as mussel, mimics, and mat material. Sediment grain sizes were determined by wet sieving sediment through 63-µm mesh to calculate percent sand (>63µm) and percent silts and clays (<63µm). Sediments from each fraction were dried overnight in an oven set at 60°C and then weighed. Percent organic matter was determined by combusting dried, pre-weighed sediments in a muffle furnace (set at 550°C) for 24 hours.

Statistical Analyses

For all data on abundance and representation of taxa, two sets of comparisons were conducted. First, each experimental treatment was compared to the control by paired t-tests. These data are graphically presented as the relative difference between the treatment and the control ± one 95% confidence interval. Thus, non-overlap of the confidence interval with zero can be considered as a significance test at $\alpha = 0.05$. Second, the experimental treatments (excluding controls) were treated as two factors in a factorial ANOVA. The treatments, with two levels each were: mats, either present or absent, and mussels, either live or mimics. This was analyzed by a randomized complete block ANOVA with two factors. All count data were log-transformed prior to analysis to homogenize variances and investigate relative rather than absolute differences (Mead 1988), and all percentage data were arcsine-square root transformed. *Musculista* experimentally placed in the plots were excluded from the analyses, but naturally recruiting individuals (determined based on size) were included. Comparison-wise P-values below 0.05 were considered significant.

Species richness was examined by calculating expected species richnesses for 100 individuals, using rarefaction methodology on all replicate samples combined (Hurlbert 1971). Also, the total number of species collected in all replicate samples of each treatment and the control are presented.

Results

The experimental manipulations persisted well over the 6-week course of the experiment. At the conclusion of the experiment, all but one of the mats were relatively intact (the exception had about 1/3 missing). Also, mussels and mimics tended to remain in the experimental plots. After 6 weeks, the average densities of mimics (± 1 s.e.) were 1.4 ± 0.5 and 2.5 ± 0.5 (per 0.001 m^2 core) in the mat / mussel mimic and no mat / mussel mimic treatments, respectively. Densities of large, experimentally-placed mussels (i.e., not new recruits) were 2.4 ± 0.5 and 2.1 ± 0.5 (per core) in the mat / live mussel and no mat / live mussel treatments respectively. None of these values is significantly different from a density of 2.5 per core, which would be expected if there were no change from the original value of 40 per plot.

In consideration of the macrofaunal responses in the experiment, each individual treatment will first be analyzed versus the control plots. Then, in order to examine the mat effects, live mussel effects, and any interaction between the two, the experimental treatments will be compared among themselves.

Mat / Mussel Mimic Treatment

The presence of mats and mussel mimics in experimental plots tended to create relatively large differences in community structure compared to controls, especially at the conclusion of the experiment. Species richness (measured as the average number of species per core) was significantly higher in this treatment than in controls at both 3 and 6 weeks (Fig. 6-1a). In addition, the expected number of species per 100 individuals in the mat / mussel mimic treatment was approximately 20% higher than for the control treatment at both 3 and 6 weeks, and was the highest of all experimental treatments (Table 6-1). The total number of species found in all replicates combined was highest at 3 weeks and tied for highest at 6 weeks (Table 6-1).

Total macrofaunal densities were significantly different than controls at both 3 and 6 weeks (Fig. 6-1b). However, the direction of the difference changed over the course of the experiment. At 3 weeks, total density within the mat / mussel mimic treatment was significantly lower than controls. Among the major taxa at 3 weeks, polychaetes were the only group that showed significant differences, with reduced densities (Fig. 6-1c). Some individual species that exhibited lowered densities at this time were the tube-building polychaete *Pseudopolydora paucibranchiata* and the small gastropod *Acteocina* sp. (Table 6-2). The gastropod *Barleeia subtenuis*, as well as the amphipods *Pontogenia rostrata* and *Grandidierella japonica*, all showed elevated densities (Table 6-2). Total density within the mat / mussel mimic treatment was significantly higher at the conclusion of the experiment (6 weeks), with over 50% more individuals than controls (Fig. 6-1b). Much of this difference could be accounted for by large differences in insect (midge) larvae and molluscs (primarily *B. subtenuis*) (Fig. 6-1c). Juvenile *Musculista* were also present in higher abundances in this treatment than in the control. Other taxa with significantly increased densities included the amphipod *Hyale* sp., a sphaeromatid isopod, and unidentified nemerteans (Table 6-3). The polychaete *P. paucibranchiata* still exhibited reduced densities at 6 weeks. Another polychaete, the syllid *Exogene* cf. *lourei*, also was in significantly lower abundances at the conclusion of the experiment (Table 6-3).

The density of individuals with planktonic development modes (such as *P. paucibranchiata* and *Acteocina* sp.) was significantly lower in the mat / mussel mimic treatment than in controls at 3 weeks (Fig. 6-2). Non-planktonic developers showed no significant difference at 3 weeks but were significantly more abundant at 6 weeks.

Mat / Live Mussel Treatment

The mat / live mussel treatment again exhibited some relatively large differences compared to controls, and macrofaunal patterns within this treatment were similar to those observed for the mat / mussel mimic treatment. Species richness per core was marginally significantly higher at 3 weeks and significantly higher at 6 weeks (Fig. 6-1a), and ES(100) was higher than controls at both 3 and 6 weeks (although not as high as in the mat / mussel mimic treatment; Table 6-1).

No significant differences were observed at 3 weeks in total density (Fig. 6-1b), and no major taxa had significantly different abundances in the treatment and control (Fig. 6-1c). As in the mat / mussel mimic treatment, the densities of *P. paucibranchiata* and *Acteocina* sp. were lower than controls while the density of *Pontogenia rostrata* was higher (Table 6-2).

At 6 weeks, total macrofaunal density was significantly higher in the mat / live mussel treatment (Fig. 6-1b). Like the other mat treatment, this was primarily due to increased densities of molluscs (*B. subtenuis*), insect larvae, *Hyale* sp., and nemerteans

(Table 6-3). Also, like the mat / mussel mimic treatment, *Pseudopolydora paucibranchiata* was less abundant in mat / live mussel treatment. Other species showing differences were the tanaid *Leptochelia dubia*, the oligochaete *Limnodriloides benedicti*, and the polychaete *Haploscoloplos elongatus* (all with elevated densities), and the amphipod *Grandidierella japonica* (with decreased densities). *Musculista* showed no significant differences (Table 6-2).

The developmental modes of fauna in the mat / live mussel treatment were again similar to those in the mat / mussel mimic treatment (Fig. 6-2). Planktonic developers were significantly less abundant at three weeks. Non-planktonic developers showed no differences at 3 weeks but were significantly more abundant at 6 weeks.

No Mat / Mussel Mimic Treatment

In the no mat / mussel mimic treatment, species richnesses (per core) and expected species richnesses were lower than those in the mat treatments, and tended to be more comparable to the control (Fig. 6-1a, Table 6-1). There were also no significant differences in total density at both 3 and 6 weeks (Fig. 6-1b). The only major taxa showing significant difference were the molluscs at 6 weeks (primarily *B. subtenuis*; Fig. 6-1c). Another taxon that showed significantly increased densities in this treatment was *H. elongatus*, while juvenile *Musculista* exhibited significantly reduced densities (Table 6-3). No differences were found in representation of larval development types (Fig. 6-2).

No Mat / Live Mussel Treatment

Faunal responses in this treatment tended to be intermediate between the no mat / mussel mimic treatment and the two mat treatments. Species richness per core was significantly higher than controls at 3 weeks, although no difference was found at 6 weeks (Fig. 6-1a). Expected species richness, however, was the lowest of all experimental treatments (Table 6-1). At six weeks, total macrofaunal densities were significantly higher than controls, with molluscs (primarily *B. subtenuis*) the only major group to show significant differences (Fig. 6-1b,c). Nemerteans and non-planktonic developers were also significantly more abundant within this treatment at six weeks (Table 6-3, Fig. 6-2). Juvenile *Musculista* showed no differences.

Mat and Mussel Effects

The comparisons of the relative effects of experimental treatments (using ANOVA's on 6 week data) demonstrated that mat effects tended to be much stronger than the effects of living mussels (Table 6-4). Also, positive effects were more common and strong than negative effects of mats. Species richness (per core), total macrofaunal density, as well as the densities of insect larvae showed significantly positive mat effects. Molluscs also had a positive mat effect, although the interaction term was also significant. Polychaetes were negatively affected by mats. *Barleeia subtenuis*, *L. dubia*, and juvenile *Musculista* also showed significant and positive mat effects, although there was also a significant interaction term for *Musculista*.

Representation of larval modes was affected by mats, with fewer planktonic developers and more non-planktonic developers.

Living mussel effects were smaller in magnitude than mat effects and only two significant differences were found (Table 6-5). *Leptochelia dubia* and benthic developers as a group were positively influenced by living mussels. Insect larvae showed the largest relative difference, although this difference was not significant at $\alpha = 0.05$.

Sediment Properties

Like macrofaunal properties, sediment properties (taken at 6 weeks) were also altered by the experimental treatments (Table 6-5). Again, the mat treatments had the largest effects, although more of a live mussel effect was evident than for macrofaunal properties. The mat / live mussel treatments had the highest values of both % combustible organic matter and % silts and clays, and the mat / mussel mimic treatments had the next highest values for both of these sedimentary properties. The no mat / live mussel treatment also had significantly higher organic matter than the controls. For organic matter, both the mat and live mussel effects were significant. For grain size, the mat effect was significant.

In order to investigate the relationship between macrofaunal and sedimentary properties, both species richness (per core) and total density were regressed against % organic matter and % silts and clays for all samples combined (Fig. 6-3). For both organic matter vs. total density and grain size vs. total density, there were highly significant positive relationships. Neither relationship was significant for species richness.

Discussion

These results indicate that the abundances of a variety of taxa are increased by the presence of physical structure in the form of artificial mussel mats. Such patterns are in general agreement with the results of an earlier, 2-week experiment in which artificial mats were compared to controls (Table 6-6), but the effects of live mussels or mussel mimics were not assessed (Chapter 5). Both experiments suggest that many of the differences in macrofaunal communities existing between locations with and without naturally occurring mats can be explained by the physical structure that mats provide and can develop on the timescales of weeks (Table 6-6).

Increased densities within naturally forming mats were typically a function of increased densities of most major taxonomic groups (Table 6-6). For example, in the 25 comparisons of the densities of major taxa inside and outside natural mats (i.e., 5 taxa on 5 dates), on only one occasion was the average density of a taxon lower inside mats (Chapter 5). This one taxon, the oligochaetes, was also least influenced by mats in the two experiments. The two species identified as particularly benefiting from the presence of natural mussel mats, the small gastropod *B. subtenuis* and the tanaid *L. dubia* (Chapter 5), also showed responses in one or both of the experiments (Table 6-6). *Barleeia subtenuis* responded strongly to the presence of physical structure, while *L. dubia* responded to both structure and living mussels (Table 6-4).

Although the creation of biogenic structure appears to be the ultimate cause of alteration of these intertidal benthic communities, there are in fact a variety of proximate mechanisms that may produce observed patterns within mats. Natural mussel mats, which are typically raised several centimeters relative to ambient sediments (especially on sandy substrates) and incorporate a range of materials (e.g., byssus, shells, sediments, and algae), may cause complicated alterations of hydrodynamic, sedimentary, and microtopographic features on the tidal flat. The activities of living mussels appear to have a further influence. Thus, mussel mats can elicit both active and passive responses of larvae, juveniles, and adults, which could involve either increased immigration into plots and / or differential survivorship within plots. Another possibility, increased reproductive output within mats, would seem to be not as important on the short-time scales examined in these studies.

The physical structure of mussel mats is likely to have complicated effects on the local flow of water, which could influence the recruitment of macrofauna including the settlement of planktonic larvae as well as redistribution of settled individuals (reviewed in Snelgrove and Butman 1994). However, specific mechanisms which may be at work (such as passive deposition of larvae versus active habitat selection for microenvironments) remain unclear. It has been found that biogenic structures (e.g., worm tubes or eelgrass blades) or their mimics can result in increased recruitment of planktonic and non-planktonic developers (Eckman 1979; Reise 1981; Bell and Coen 1982; Gallagher et al. 1983; Stoner and Lewis 1985; Kern and Taghon 1986). In this study, increased densities associated with structure were generally seen for benthic developers, but not planktonic developers (Table 6-6). Because effect sizes were comparable in the live mussel and mussel mimic treatments (Fig. 6-2), the inhibition of planktonic developers cannot be attributed to the effects of living mussels, such as the ingestion of larvae (Woodin 1976). Other possible causes for this negative relationship between the presence of mats and the abundance of organisms with planktonic larvae include correlation with some other characteristics of the species (discussed below for *P. paucibranchiata*), differential post-recruitment mortality inside and outside mats, and emigration from or avoidance of mats. Also, in natural mussel mats, reduced densities of these species were not observed (Chapter 5), again suggesting that other factors are operating.

In addition to flow itself, it is possible that animals are actively responding to some physical property correlated with flow (Snelgrove and Butman 1994). For example, mats appear to be depositional environments, and in both mat treatments fine sediments and organic matter were greater than controls (Table 6-5). In addition, live *Musculista* can alter sedimentary properties through biodeposition and binding of sediments (Morton 1974; Reusch and Williams 1998), as has been seen for other mussel species (e.g., Stanczykowska and Planter 1985; ten Brinke et al. 1995). It is thus possible that there is active habitat selection based on these sedimentary properties, as has been demonstrated experimentally for a variety of species (Meadows 1964; Jones 1970; Zimmerman et al. 1988). Further support for this may come from the observed positive relationship between sediment properties and macrofaunal densities (Fig. 6-3), although it is important to recognize that both sediment and macrofauna could be responding similarly to the same extrinsic factor (such as flow).

In addition to altering sedimentary parameters, physical structure may also trap materials that can be used by other species. Within mussel mats, there may be an increased supply of materials for tube-builders as well as a stable matrix in which the tubes can be built (Chapter 5). This may explain the abundance of *L. dubia* within mats, as this species typically constructed tubes from sediment and algal detritus and attached tubes to other structures. In other bays, this species also is often associated with physical structure, although it can live on relatively bare tidal flats (Morris et al. 1980). Also, tanaids as a group have responded favorably to the addition of structure in a number of other experiments, which has been suggested to be related to the increased food supply (Woodin 1974; Eckman 1979; Gallagher et al. 1983; Miller 1993). Other tube-builders, however, may be inhibited by mats. For example, the exotic polychaete *P. paucibranchiata*, a planktonically-developing species that constructs sediment tubes and maintains discrete territories (Levin 1984), was significantly less abundant within experimental mats (Tables 6-2 and 6-3). In natural mats, however, this species did not exhibit decreased densities, suggesting that there may be some feature of older or natural mats which counteracts possible structural inhibition of tube-building.

The presence of structure may provide several benefits to benthic organisms, such as amelioration of environmental conditions or provision of refuge from predation (Keough and Downs 1982; Dewitt and Levinton 1985; Witman 1985; Heck and Hambrook 1991; Sebens 1991; Gosselin and Chia 1995). In this study, however, large predatory nemerteans were actually found in higher densities within mats, although density of these organisms does not necessarily correlate with predation efficiency. Also, refuge from predators such as birds and large fish does not appear to account for observed differences, because these predators were excluded from all treatment and control plots in the current experiment. Another important behavioral response of the macrofaunal organisms may be to the presence of physical structure itself. It is known that some benthic species display thigmotactic responses to physical structure (Dubois et al. 1980; Uryu et al. 1996; Olyslager and Williams 1993), and it is likely that motile species, such as *B. subtenuis*, are actively choosing sites with structure. For *B. subtenuis*, even the presence of mussel mimics alone, which produced little difference in sedimentary properties compared to controls, elicited a positive numerical response (Tables 6-2 and 6-3). In the field, *B. subtenuis* is often found associated with other structures such as macroalgae and discarded plastic bags (Crooks pers. obs).

Whatever factor or factors actually produce the observed facilitation of resident biota by mussel mats, increased abundances of small macrofauna associated with benthic biogenic structures appears to be a general response in aquatic systems. In the soft-sediment benthos, mussel beds (Valentine and Heck 1993; Chapter 5), eelgrass beds (Orth 1973; Homziak et al. 1982; Virnstein et al. 1983; Stoner and Lewis 1985), worm tubes or reefs (Bailey-Brock 1979; Haines and Maurer 1980; Gherardi and Cassidy 1994), salt-marsh plants (da Cunha Lana and Guiss 1991), and macroalgae (Everett 1984; Sogard and Able 1991) have typically been found to facilitate suites of resident organisms. Increased architectural complexity produced by other aquatic flora and fauna has also been shown to result of facilitation of organisms in fouling communities (Dean 1981; Bros 1987), on rocky shores (Suchanek 1985; Tsuchiya and Nishihara 1986; Seed 1996), and in the water column (Krecker 1939; Dvorak and Best 1982). In terrestrial systems, structurally complex species of grasses and trees may support increased diversities of insects (Murdoch et al. 1972; Dixon 1985; Denno and Roderick 1991), and, at larger spatial scales, foliage height diversity is positively correlated with bird species diversity (MacArthur and MacArthur 1961; Recher 1969). Although responses of species will vary depending on the nature of the structure and the requirements of individual species, including body size and ambit (Morse et al. 1985; Hanson 1990; Gee and Warwick 1995), production of physical structure and increase in habitat complexity appears to generate the sorts of positive interactions that have been shown to be important in ecological systems (Gallagher et al. 1983; Schaffner 1990; Thrush et al. 1992; Bertness and Callaway 1994; Bertness and Leonard 1997).

Given that *Musculista* is an exotic species and has only been present in Mission Bay for several decades (Crooks 1996), it suggests that facilitation may be a general response of species to the creation of physical structure by habitat modifiers, or ecosystem engineers (*sensu* Jones et al. 1994; Jones et al. 1997). Indeed, a number of other exotic species that increase structural complexity are also known to facilitate other organisms. In terrestrial systems, plantation tree species can support more species of birds than structurally simple row crops (but less than stands of native forest), and it has been suggested that bird diversity can be maximized in plantations by increasing structural diversity (Hanowski et al. 1997). Exotic tank bromeliads in Florida create small pond habitats that attract the exotic *Anopheles* spp. mosquitoes (O'Meara et al. 1995). In lakes, parrot's feather (*Myriophyllum aquaticum*) also creates *Anopheles* microhabitats (Orr and Resh 1992), and water hyacinth can create snail habitat and provide predation refuges for small fish (Ogutu-Ohwayo 1996). Abundances and / or diversities of macrobenthos can also be increased within meadows of rooted vascular plants (Posey 1988; Posey et al. 1993). Within beds of the zebra mussel, *Dreissena polymorpha*, conditions are enhanced for small macroinvertebrates (Dermott 1992; Stewart and Haynes 1994), which appears to be related to both the presence of mussel shells as well as the effects of living mussels (Ricciardi et al. 1997). It thus appears that both exotic and native species capable of increasing habitat complexity may predictably benefit resident biota.

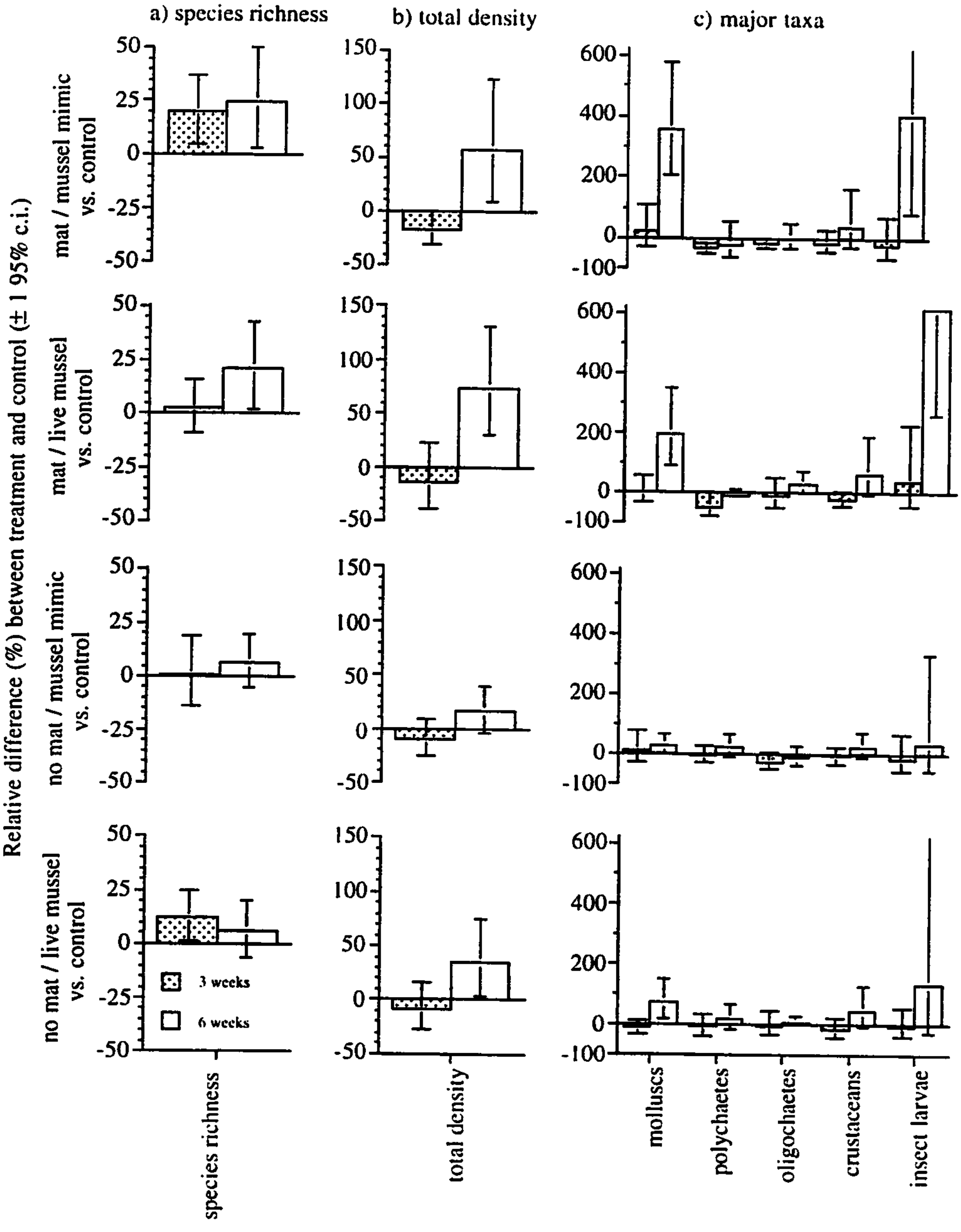

Figure 6-1. Relative differences in macrofaunal densities (per core) between each of the four experimental treatments and the control for a) species richness, b) total density, and c) density of major taxa. Plotted are back-transformed mean differences expressed in terms of percentages ± one 95% confidence interval. Non-overlap of the confidence intervals with 0 indicates that the difference between the treatment and control was statistically significant at $\alpha = 0.05$.

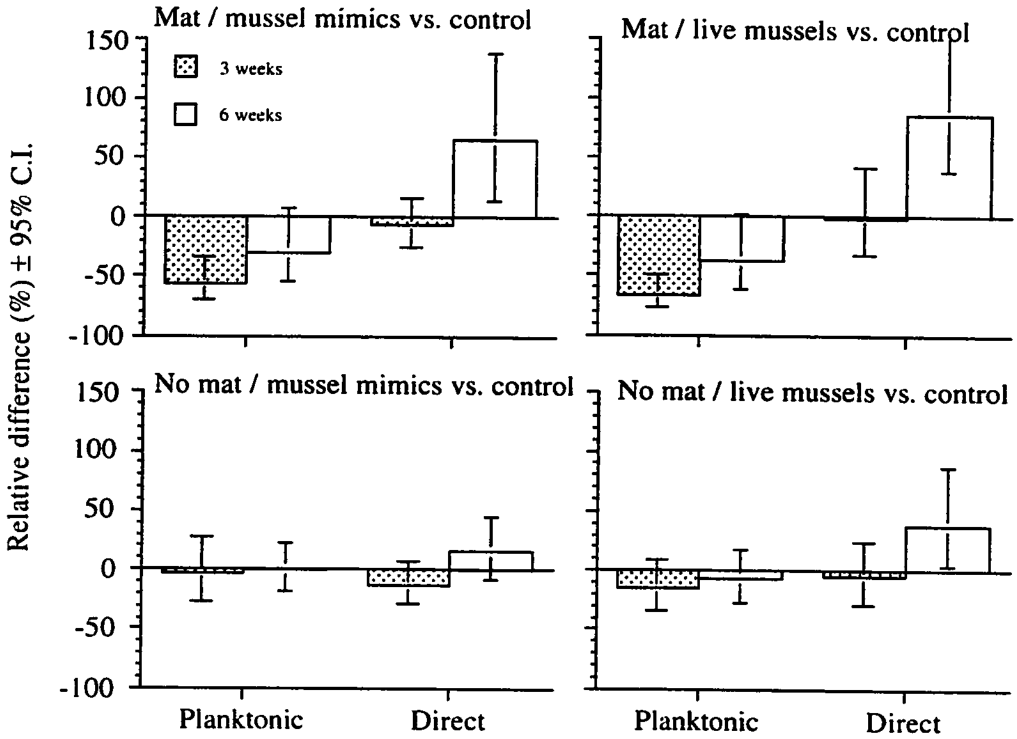

Figure 6-2. Relative differences in densities of planktonic and benthic developers between each of the four experimental treatments and the control. See Fig. 6-1 for more details.

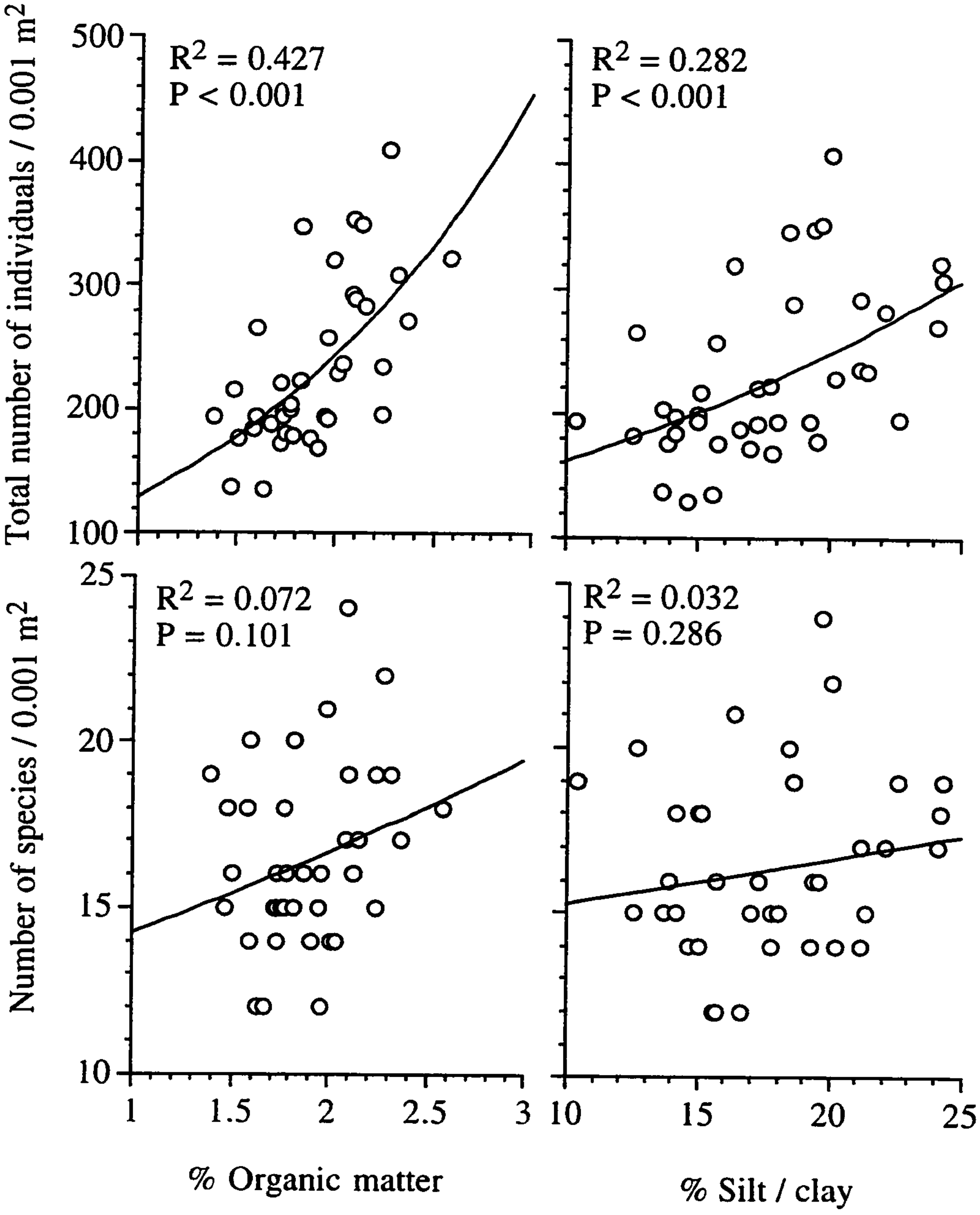

Figure 6-3. Relationships between sedimentary properties and total macrofaunal density and species richness (per core). Data are for all treatment and control plots pooled.

Table 6-1. Expected species richnesses for 100 individuals ($ES_{(100)}$) and the total number of species (S) found for each treatment and the control (from all replicates combined).

	3 Weeks		6 Weeks	
	$ES_{(100)}$	Total S	$ES_{(100)}$	Total S
Mat / mussel mimics	16.8	26	16.1	30
Mat / living mussels	15.4	22	14.3	28
No mat / mussel mimics	15.0	25	12.3	27
No mat / living mussels	14.8	25	12.3	30
Control	13.8	22	13.5	25

Table 6-2. Densities of taxa (per 0.001 m^2) in experimental treatments and controls at 3 weeks. Values are back-transformed means, and numbers in parentheses represent the range for the mean ± 1 s.e. * these taxa were not identified to species and therefore contributed only 1 species to tallied species counts.

	Mat / mussel mimic	Mat / live mussel	No mat / mussel mimic	No mat / live mussel	Control
Cnidarians *	0.1 (0.0 - 0.2)	0.1 (0.0 -0.2)	0.0	0.1 (0.0 - 0.2)	0.0
Platyhelminthes *	1.6 (1.2 - 2.1)	1.4 (1.1 - 1.7)	1.7 (1.3 - 2.3)	3.1 (2.7 - 3.7)	2.6 (1.8 - 3.5)
Nemerteans *	0.3 (0.0 - 0.6)	1.1 (0.6 - 1.9)	0.2 (0.1 - 0.3)	0.2 (0.1 - 0.3)	0.3 (0.1 - 0.5)
Molluscs					
Bivalves					
Musculista senhousia	0.0	0.0	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)	0.0
Unidentified juvenile	0.0	0.0	0.1 (0.0 - 0.2)	0.0	0.0
Gatropods					
Acteocina sp.	6.8 (5.5 - 8.3)	6.1 (4.9 - 7.7)	13.7 12.1 - 15.4)	10.8 (9.1 - 12.8)	13.6 (11.6 - 15.9)
Barleeia subtenuis	10.0 (8.4 - 11.8)	7.5 (6.0 - 9.4)	2.0 (1.1 - 3.1)	1.3 (1.1 - 1.5)	0.6 (0.2 - 1.1)
Annelids					
Polychaetes					
Armandia brevis	0.0	0.0	0.0	0.0	0.0
Capitella sp.	6.1 (5.1 - 7.3)	5.3 (3.1 - 8.9)	11.7 (10.1 - 13.6)	9.7 (8.0 - 11.7)	9.1 (8.6 - 9.7)
Eteone californica	0.0	0.0	0.0	0.0	0.0
Exogene cf. *lourei*	1.4 (1.0 - 1.8)	0.5 (0.2 - 0.8)	0.7 (0.4 - 1.0)	1.6 (1.2 - 2.1)	0.7 (0.4 - 1.0)
Fabricinuda limnicola	0.0	0.1 (0.0 - 0.2)	0.0	0.2 (0.1 - 0.3)	0.1 (0.0 - 0.2)
Haploscoloplos elongatus	7.4 (6.6 - 8.2)	4.2 (2.8 - 6.2)	5.9 (5.1 - 6.8)	4.6 (3.6 - 5.8)	7.1 (5.5 - 9.2)
Polydora sp.	0.0	0.0	0.0	0.0	0.0
Pseudopolydora paucibranchiata	2.9 (2.3 - 3.7)	1.5 (1.0 - 2.2)	8.9 (7.8 - 10.2)	8.4 (6.8 - 10.3)	9.2 (7.7 - 10.9)
Nereid sp. A	0.8 (0.5 - 1.1)	0.4 (0.2 - 0.7)	0.4 (0.2 - 0.6)	1.3 (1.0 - 1.7)	1.0 (0.6 - 1.6)
Serpulidae sp. A	0.0	0.0	0.0	0.0	0.0
Unidentified *	0.1 (0.0 - 0.2)	0.0	0.2 (0.1 - 0.3)	0.2 (0.1 - 0.3)	0.0
Oligochaetes					
Limnodriloides barnardi	25.7 (22.4 - 29.4)	27.9 (23.8 - 32.7)	18.9 (15.1 - 23.7)	27.4 (22.4 - 33.6)	28.3 (23.2 - 34.5)
Paranais littoralis	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.3)	0.1 (0.0 - 0.3)	0.1 (0.0 - 0.2)
Tubificoides brownea	14.9 (12.6 - 17.6)	15.7 (13.2 - 18.6)	19.4 (15.3 - 24.5)	20.0 (17.2 - 23.2)	23.3 (19.5 - 27.9)
Arthropods					
Amphipods					
Ampithoe sp.	1.1 (0.7 - 1.7)	0.6 (0.2 - 1.0)	0.1 (0.0 - 0.2)	0.2 (0.1 - 0.3)	0.0
Corophium sp.	3.3 (2.0 - 5.2)	0.8 (0.5 - 1.3)	2.8 (1.4 - 5.0)	3.0 (1.8 - 4.6)	4.1 (2.7 - 6.1)
Grandidierella japonica	9.3 (7.6 - 11.4)	6.6 (5.2 - 8.4)	3.8 (2.9 - 5.0)	7.6 (5.4 - 10.5)	4.7 (3.0 - 7.1)
Hyale sp.	3.2 (2.1 - 4.6)	0.8 (0.3 - 1.3)	2.1 (0.9 - 4.1)	1.3 (0.7 - 2.1)	1.2 (0.9 - 1.7)
Mayerella banksia	0.0	0.0	0.0	0.0	0.0
Pontogenia rostrata	1.5 (1.0 - 2.2)	3.5 (2.1 - 5.6)	0.0	0.1 (0.0 - 0.2)	0.0
Gammarid sp. A	0.0	0.0	0.0	0.0	0.0
Gammarid sp. B	0.1 (0.0 - 0.2)	0.0	0.0	0.0	0.0
Unidentified *	0.1 (0.0 - 0.2)	0.0	0.7 (0.2 - 1.4)	0.0	0.0
Isopods					
Haliophasma geminatum	0.0	0.0	0.1 (0.0 - 0.2)	0.0	0.1 (0.0 - 0.2)
Sphaeromatid sp. A	0.5 (0.3 - 0.7)	0.0	0.0	0.0	0.0
Tanaids					
Leptochelia dubia	11.8 (9.1 - 15.1)	14.7 (12.3 - 17.5)	16.1 (11.7 - 22.1)	18.8 (15.5 - 22.6)	24.8 (22.1 - 27.9)
Insects					
Chironomid larvae	12.6 (9.9 - 16.0)	22.3 (17.1 - 29.1)	14.4 (12.3 - 17.0)	16.4 (13.5 - 20.0)	17.0 (14.5 - 19.8)
Unidentified *	0.0	0.0	0.0	0.0	0.1 (0.0 - 0.3)
Phoronids					
Phoronis architecta	0.1 (0.0 - 0.2)	0.0	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)	0.3 (0.1 - 0.5)
Holothuroids					
Leptosynapta albicans	0.0	0.4 (0.1 - 0.9)	0.1 (0.0 -0.2)	0.1 (0.0 - 0.3)	0.1 (0.0 - 0.2)

Table 6-3. Densities of taxa (per 0.001 m^2) in experimental treatments and controls at 6 weeks. Values are back-transformed means, and numbers in parentheses represent the range for the mean ± 1 s.e. * these taxa were not identified to species and therefore contributed only 1 species to tallied species counts.

	Mat / mussel mimic	Mat / live mussel	No mat / mussel mimic	No mat / live mussel	Control
Cnidarians *	0.3 (0.1 - 0.5)	0.2 (0.0 - 0.5)	0.0	0.0	0.0
Platyhelminthes *	0.5 (0.3 - 0.9)	0.6 (0.3 - 0.9)	0.9 (0.6 - 1.3)	0.4 (0.2 - 0.6)	1.2 (0.9 - 1.6)
Nemerteans *	1.6 (1.0 - 2.4)	1.9 (1.2 - 2.8)	0.4 (0.2 - 0.7)	0.6 (0.4 - 0.9)	0.0
Molluscs					
Bivalves					
Musculista senhousia	4.4 (3.1 - 6.2)	2.3 (1.6 - 3.2)	0.2 (0.1 - 0.3)	0.8 (0.5 - 1.1)	0.9 (0.6 - 1.3)
Unidentified juvenile	0.0	0.1 (0.0 - 0.2)	0.0	0.1 (0.0 - 0.2)	0.0
Gastropods					
Acteocina sp.	5.3 (4.2 - 6.6)	7.6 (6.1 - 9.4)	9.7 (8.5 - 11.2)	7.7 (6.5 - 9.1)	9.7 (8.9 - 10.7)
Burleeia subtenuis	44.8 (39.2 - 51.2)	23.7 (19 - 29.4)	5.2 (4.4 - 6.3)	7.6 (4.7 - 12.0)	0.6 (0.3 - 0.9)
Annelids					
Polychaetes					
Armandia brevis	0.3 (0.1 - 0.5)	0.1 (0.0 - 0.2)	0.0	0.1 (0.0 - 0.2)	0.0
Capitella sp.	2.4 (1.6-3.5)	5.2 (4.5 - 6.0)	3.6 (3.1 - 4.2)	6.7 (5.7 - 7.8)	3.3 (2.3 - 4.8)
Eteone californica	0.1 (0.0 - 0.2)	0.0	0.3 (0.1 - 0.5)	0.0	0.3 (0.1 - 0.5)
Exogene cf. *lourei*	0.6 (0.4 - 0.9)	1.7 (1.3 - 2.3)	2.7 (1.8 - 4.0)	1.4 (0.8 - 2.2)	2.4 (1.7 - 3.2)
Fabricinuda limnicola	0.2 (0.0 - 0.5)	0.5 (0.3 - 0.7)	0.3 (0.1 - 0.5)	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)
Haploscoloplos elongatus	2.6 (1.6 - 4.0)	2.6 (1.8 - 3.7)	4.2 (3.4 - 5.2)	2.5 (1.8 - 3.4)	0.9 (0.5 - 1.4)
Polydora sp.	0.0	0.0	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.3)	0.1 (0.0 - 0.2)
Pseudopolydora paucibranchiata	1.0 (0.6 - 1.6)	1.1 (0.7 - 1.5)	7.8 (6.7 - 9.0)	7.8 (6.6 - 9.1)	7.1 (5.9 - 8.5)
Nereid sp. A	0.3 (0.1 - 0.5)	0.4 (0.2 - 0.6)	0.2 (0.1 - 0.3)	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)
Serpulidae sp. A	2.1 (1.1 - 3.7)	1.4 (0.9 - 2.0)	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)	0.0
Unidentified *	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)	0.0	0.2 (0.1 - 0.3)
Oligochaetes					
Limnodriloides barnardi	37.3 (31.4 - 44.3)	50.2 (42.8 - 58.7)	31.4 (25.1 - 39.1)	42.2 (37.9 - 47.1)	34.8 (30.5 - 39.8)
Paranais littoralis	0.0	0.0	0.0	0.0	0.0
Tubificoides brownea	13.2 (10.9 - 15.0)	19.5 (17.6 - 21.5)	18.2 (16.1 - 20.6)	15.3 (13.8 - 16.9)	18.5 (16.6 - 20.6)
Arthropods					
Amphipods					
Ampithoe sp.	0.3 (0.1 - 0.5)	0.1 (0.0 - 0.2)	0.0	0.0	0.0
Corophium sp.	5.2 (3.8 - 6.9)	3.5 (2.4 - 4.9)	9.6 (8.2 - 11.2)	10.7 (8.2 - 14.0)	7.7 (6.0 -9.9)
Grandidierella japonica	17.5 (15.4 - 19.8)	9.2 (7.1 - 11.7)	27.1 (25.3 - 29.0)	22.5 (19.5 - 25.9)	23.9 (21.2 - 26.9)
Hyale sp.	6.1 (3.8 - 9.6)	3.0 (1.5 - 5.4)	0.2 (0.1 - 0.3)	0.5 (0.2 - 0.9)	0.4 (0.2 - 0.6)
Mayerella banksia	0.1 (0.0 - 0.3)	0.0	0.2 (0.0 - 0.5)	0.1 (0.0 - 0.3)	0.0
Pontogenia rostrata	1.6 (0.7 - 2.9)	0.3 (0.1 - 0.6)	0.0	0.5 (0.1 - 1.0)	0.2 (0.1 - 0.3)
Gammarid sp. A	0.0	0.0	0.0	0.4 (0.0 - 1.1)	0.0
Gammarid sp. B	0.0	0.0	0.0	0.5 (0.0 -1.2)	0.0
Unidentified *	0.3 (0.1 - 0.5)	0.1 (0.0 - 0.2)	0.6 (0.2 - 1.2)	0.5 (0.1 - 0.9)	0.5 (0.1 - 1.0)
Isopods					
Haliophasma geminatum	0.5 (0.2 - 0.8)	0.0	0.1 (0.0 - 0.2)	0.0	0.0
Sphaeromatid sp. A	0.9 (0.6 - 1.4)	0.3 (0.1 - 0.6)	0.0	0.1 (0.0 - 0.2)	0.0
Tanaids					
Leptochelia dubia	61.8 (50.5 - 75.6)	93.4 (77.1 - 113.2)	49.1 (46.2 - 52.2)	61.4 (56.1 - 67.2)	36.6 (30.3 - 44.2)
Insects					
Chironomid larvae	22.6 (18.8 - 27.1)	32.6 (27.9 - 38.2)	5.3 (3.4 - 8.0)	9.9 (6.5 - 14.9)	3.6 (2.5 - 5.1)
Unidentified *	0.0	0.0	0.1 (0.0 - 0.2)	0.0	0.1 (0.0 - 0.2)
Phoronids					
Phoronis architecta	0.0	0.0	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)
Holothuroids					
Leptosynapta albicans	0.2 (0.1 - 0.3)	0.6 (0.3 - 0.9)	0.0	0.1 (0.0 - 0.2)	0.1 (0.0 - 0.2)

Table 6-4. Relative effects of artificial mats, living mussels, and the interaction between the two, expressed in terms of average percent differences. Data are from 2-factor Randomized Complete Block ANOVA's. The block effects were not significant except for *Leptochelia dubia* (P=0.035) and insect larvae (P=0.031). No block interaction terms were significant.

	Mat Effect (1 df)		Mussel effect (1 df)		Interaction (1 df)
	Difference (%)	P	Difference (%)	P	P
Species richness	+ 20	0.005	0	0.723	0.737
Total density	+ 35	0.003	+ 5	0.073	0.693
Crustaceans	+ 19	0.258	- 4	0.119	0.976
Molluscs	+ 64	<0.001	+ 9	0.585	0.042
Polychaetes	- 21	0.014	- 17	0.707	0.555
Oligochaetes	+ 47	0.341	+ 15	0.097	0.513
Insect larvae	+ 532	<0.001	+ 248	0.054	0.649
Barleeia subtenuis	+ 368	<0.001	- 12	0.400	0.128
Leptochelia dubia	+ 39	0.010	+ 16	0.011	0.339
Musculista senhousia	+ 350	0.001	+ 50	0.642	0.039
Planktonic developers	- 17	0.048	- 4	0.562	0.910
Benthic developers	+ 14	0.001	+ 6	0.044	0.637

Table 6-5. A) Sedimentary properties in the experimental treatments and control (mean ± 1 s.e.). B) Relative effects of mats and living mussels (% difference) on sedimentary properties. $^{0}P<0.1$, $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

		% Silts / Clays	% Organic Matter
A)	Mat / mussel mimics	18.1 ± 0.72 **	1.96 ± 0.05 ***
	Mat / living mussels	22.2 ± 0.72 ***	2.28 ± 0.05 ***
	No mat / mussel mimics	15.6 ± 0.85	1.69 ± 0.05
	No mat / living mussels	15.7 ± 1.50	1.81 ± 0.10 *
	Control	15.7 ± 0.70	1.64 ± 0.05
B)	Mat effect	+ 29 % **	+ 21 % ***
	Living mussel effect	+ 12 % ^{0}	+ 12 % *

Table 6-6. Responses of fauna in the mat treatments of the current experiment compared with a previous experiment (mat alone) and natural mats (from Chapter 5). 0 = no difference, ↑ = 1 – 100% increase, ↑↑ = 101 – 1000% increase, ↑↑↑ = > 1001% increase, ↓ = 1 - 100% decrease. $^{\lozenge}P<0.1$, $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

	Mat / live mussel		Mat / mussel mimic		Mat	Natural
	3 week	6 week	3 week	6 week	2 week	mats
Species richness	$\uparrow^{\lozenge}$	$\uparrow^{*}$	$\uparrow^{*}$	$\uparrow^{*}$	$\uparrow^{\lozenge}$	$\uparrow^{***}$
Total macrofauna	$\downarrow$	$\uparrow^{*}$	$\downarrow^{*}$	$\uparrow^{*}$	$\uparrow^{\lozenge}$	$\uparrow\uparrow^{*}$
Molluscs	0	$\uparrow\uparrow^{***}$	$\uparrow$	$\uparrow\uparrow^{***}$	$\uparrow$	$\uparrow\uparrow$
Polychaetes	$\downarrow^{\lozenge}$	$\downarrow$	$\downarrow^{*}$	$\downarrow$	$\uparrow$	$\uparrow\uparrow^{*}$
Oligochaetes	$\downarrow$	$\uparrow^{\lozenge}$	$\downarrow^{\lozenge}$	0	$\downarrow$	$\uparrow$
Crustaceans	$\downarrow^{\lozenge}$	$\uparrow$	$\downarrow$	$\uparrow$	$\uparrow\uparrow^{**}$	$\uparrow\uparrow^{*}$
Insect larvae	$\uparrow$	$\uparrow\uparrow^{***}$	$\downarrow$	$\uparrow\uparrow^{**}$	$\uparrow$	$\uparrow\uparrow^{**}$
Barleeia subtenuis	$\uparrow\uparrow^{***}$	$\uparrow\uparrow^{***}$	$\uparrow\uparrow^{***}$	$\uparrow\uparrow^{***}$	$\uparrow^{*}$	$\uparrow\uparrow^{\lozenge}$
Leptochelia dubia	$\downarrow^{*}$	$\uparrow\uparrow^{*}$	$\downarrow^{*}$	$\uparrow$	$\uparrow$	$\uparrow\uparrow\uparrow^{*}$
Planktonic developers	$\downarrow^{**}$	$\downarrow^{\lozenge}$	$\downarrow^{***}$	$\downarrow^{\lozenge}$	$\uparrow$	$\uparrow$
Direct developers	$\downarrow$	$\uparrow^{**}$	$\downarrow$	$\uparrow^{*}$	$\uparrow\uparrow^{\lozenge}$	$\uparrow\uparrow^{*}$

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CHAPTER VII

CONCLUSIONS

This research contributes to ecological understanding and practice in three ways: (1) through descriptions of general relationships between organisms and various aspects of the physical environment within Mission Bay, (2) through consideration of invasive species both as consequence and cause of ecological change, and (3) by suggesting implications for conservation and management of ecosystems.

Organism – Habitat Relationships

On relatively large spatial and temporal scales, human-derived habitat destruction and degradation in Mission Bay have been important forces of change for bivalve communities and benthic macrofauna in general (Chapters 2 and 3). The bay in its present state bears little physical resemblance to the system that existed there 150 years ago. This, coupled with other inter-related effects such as pollution, over-fishing, and invasion of exotic species, has resulted in qualitative and quantitative changes in the bivalve fauna of the bay (Chapter 2). The gradient of flushing in the bay, derived from the physical layout of the system as well as input of organic-rich urban runoff, affects benthic macrofauna in a manner which in general terms corresponds with patterns described in other systems (Chapter 3). There are relatively depauperate communities in the back bay, peaks of abundance and diversity mid-bay, and relatively high diversity nearer the mouth of the bay. *Musculista* is most successful in the mid-bay region, at a point often occupied by high densities of opportunistic species. Such areas, representing a point between excessive and relatively low levels of habitat degradation or disturbance (in this case poor flushing and organic enrichment), may be particularly vulnerable to invasions by exotic species (Kowarik 1995).

On smaller spatial and temporal scales, the dense byssal mats created by *Musculista senhousia* increase habitat complexity, which can facilitate a suite of small macrofauna able to live within this biogenic habitat (Chapters 5 and 6). Most macrofaunal organisms found in higher abundances within mussel beds respond to the physical structure of the mat, although the biological activities of the mussel do affect some taxa (Chapter 6). It is important to consider that effects of mats may be scale-dependent. Larger organisms, such as surface-dwelling, suspension-feeding clams (*Chione* spp.) can be inhibited either by competition for space and / or food (Chapter 2). A similar inhibition was not observed for a deeper-dwelling, deposit-feeding bivalve (*Macoma nasuta*).

Invaders as Consequence and Cause of Ecological Change

In addition to assessing some of the relationships between habitats and species, this research also highlights that biological invaders may be viewed as both a result and a cause of ecological change. Characterizing the invasibility of a system is more difficult than determining effects of invaders. It appears that there is positive relationship between disturbance and the success of exotic species (Elton 1958; Orians 1986; Hobbs 1989). Within Mission Bay, it is clear that the rate of invasion has increased markedly in recent years (Chapter 1). This is related to increased inoculation of foreign species, from sources such as ballast water transport, movement of fouling organisms, and secondary spread of invaders away from original sources of invasion (such as San Francisco Bay or Los Angeles / Long Beach Harbor). In addition, it is probable that Mission Bay is becoming more vulnerable to invasion due to factors such as increased pollution, fragmentation of habitat, and decrease in the diversity of native species (Chapters 2 and 3). The ability of exotics such as *Musculista senhousia* to rapidly exploit novel, low-diversity areas was exhibited in the restored Crown Point Mitigation

Site (Chapter 2). The pattern of *Musculista senhousia* abundance in the subtidal of Mission Bay, with increased representation away from the mouth of the bay, is also suggestive of the relationship between degraded environmental conditions and the presence of exotics (Chapter 3).

Exotic species can have a wide range of effects in invaded systems; a complete list of these effects would resemble a list of the roles of any species in an ecosystem. Nonetheless, it is useful to categorize known effects of invasive species, and a survey of the burgeoning literature on exotics reveals several often considered mechanisms by which exotics can affect native species and the ecosystem (Fig. 7-1) . They may alter the genetic make-up of native populations through hybridization of exotics with natives. They may also transmit pathogens or be pathogens themselves. Interspecific interactions between exotics and natives are typically considered in negative terms, which may involve predation, herbivory, and competition. Less frequently considered are positive interactions such as mutualism or facilitation (or commensalism). Introduced species may also benefit resident species by serving as trophic resources. These interspecific effects may translate into alterations of community structure, such as local increases or decreases in species diversity. The three primary ecosystem-level properties typically considered to be affected by exotics are alterations of food webs (or productivity), nutrient cycling, or disturbance regimes (Vitousek 1990; Cushman 1995; Williamson 1996). An assortment of other isolated ecosystem-level effects are also mentioned in the literature.

In the case of *Musculista senhousia*, several of the effects identified above either have been documented or implied (Table 7-1). This thesis has shown that *M. senhousia* fundamentally alters the nature of the benthic habitat through the construction of byssal mats and associated changes in sediment grain size, organic content, and shear strength (Chapters 5 and 6). Through this habitat modification other species are affected

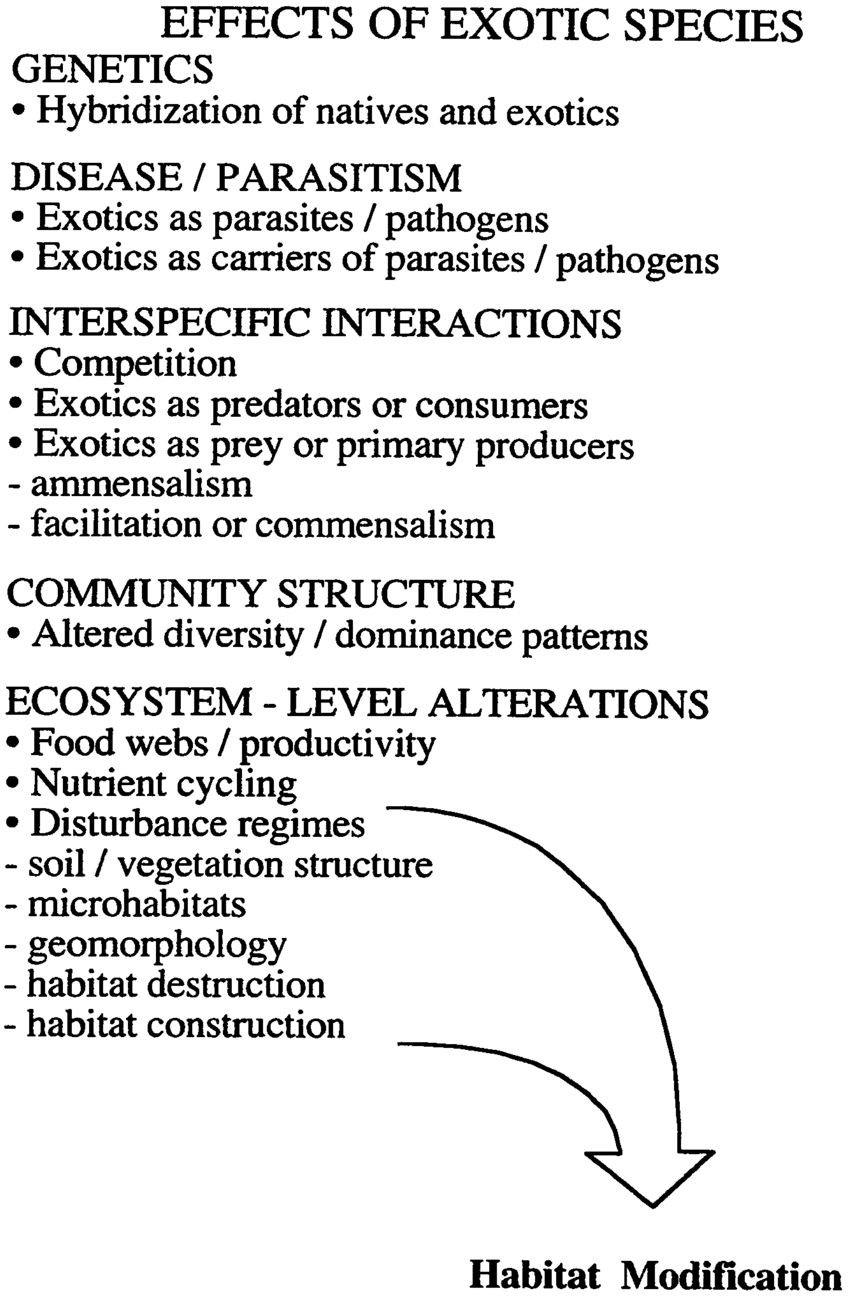
(Chapters 5 and 6). Although there are a number of other examples of habitat-altering exotics in the literature (Table 7-2), the general idea that exotics can fundamentally modify ecosystems and affect resident biota by constructing, destroying, or otherwise modifying the physical nature of habitats (sometimes termed ecosystem engineering *sensu* Jones et al. 1995, 1997) has yet to be incorporated into invasion biology. The recognition of this concept provides a valuable framework with which to view the effects of exotics. It encompasses alteration of disturbance regimes as well as other assorted ecosystem-level affects. In the case of *M. senhousia* and other exotics that create physical structure, this habitat creation may benefit resident biota (Chapter 6).

Conservation and Management Implications

Because this research has emphasized exotic species in an urbanized system, the findings have important conservation and management implications. Overall, it is important that scientists and managers maintain a broad and dynamic view of issues related to biological invasions. Exotic species can have a wide variety of effects, both negative and positive (Table 7-1). Although a biological invasion may be a natural process, the human-mediated mass movement of species is homogenizing the earth's biota and having undesirable ecological and technological effects (Cairns and Bidwell 1996; Williamson 1996; Vitousek et al. 1997). The introduction of exotic species must therefore be an important consideration in our efforts to conserve the natural integrity and biodiversity of ecosystems.

The recognition of lag times in the population explosions of exotics demonstrates that it is potentially dangerous to assume the status of an invader as it appears at one time (even if considered to be in "equilibrium") accurately reflects what will occur in the future. The attributes of an invader, its population dynamics, and its role in invaded systems can change suddenly and dramatically (Chapter 4). Another sort of lag is also becoming evident. Researchers are often slow in recognizing new exotic species because in many cases effective means of detecting and identifying invasive species are not in place and adequate lists of native species do not exist (Chapter 4). In San Diego, for example, many exotics almost certainly remain undetected. Another related class of lag involves our delayed response to invasions. Responses may involve control of the vectors of exotic species introductions or management of already established populations (Hobbs and Humphries 1995). For example, despite decades of experience with harmful exotics in the Great Lakes, not to mention explicit warnings about the potential threat caused by the invasion of the zebra mussel, substantive actions to limit ballast water invasions were taken too late (Nalepa and Schloesser 1993). In the case of managing already established exotics, delays in instituting possible and appropriate measures of control or extirpation, which typically appear to be very difficult under the best of circumstances, can make such controls ineffective if the invasive population grows overly large (Chapter 4). In marine systems, control of invasive populations appears very difficult, although biocontrol by natural enemies may offer some promise (Lafferty and Kuris 1996). Another possible approach could involve using the observed relationship between pollution or disturbance and the presence of exotic species (e.g., Chapter 4). This would suggest that decreasing pollution loads in a system, a desirable endeavor in its own right, may lead to decreased success of exotics.

One important, overriding factor in our consideration of Mission Bay, and many other areas with which humans are associated, is that the ecological interactions we are observing are occurring in systems that are distinctly different from what they were before anthropogenic intervention. An indication of this can be provided by examining the historical ecology of large, relatively well-known taxa like bivalves (Chapter 2). The undocumented alteration of ecosystems may bias our view of anthropogenic impacts, because many consequences of habitat loss, pollution, over-exploitation of species, and introductions of exotics, may have already occurred (Dayton 1998; Dayton et al. 1998). Unfortunately, many unrecognized changes (both undesirable and favorable) are probably still occurring in these ecosystems, which will not only hinder efforts to make comparisons with the past but also compromise our ability to provide accurate benchmarks for the future. Added attention to basic descriptive research (e.g., natural history, ecological surveys, and taxonomy) in these sensitive and threatened ecosystems is required if we are to enact effective measures of stewardship and conservation.



EFFECTS OF EXOTIC SPECIES

GENETICS
- Hybridization of natives and exotics

DISEASE / PARASITISM
- Exotics as parasites / pathogens
- Exotics as carriers of parasites / pathogens

INTERSPECIFIC INTERACTIONS
- Competition
- Exotics as predators or consumers
- Exotics as prey or primary producers

\- ammensalism
\- facilitation or commensalism

COMMUNITY STRUCTURE
- Altered diversity / dominance patterns

ECOSYSTEM - LEVEL ALTERATIONS
- Food webs / productivity
- Nutrient cycling
- Disturbance regimes

\- soil / vegetation structure
\- microhabitats
\- geomorphology
\- habitat destruction
\- habitat construction

Habitat Modification

Figure 1. Commonly considered effects of exotic species, and recognition of habitat modification as a major class of ecosystem-level alteration. Sources include Elton 1958; Carlton 1979; Jarvis 1979; Simberloff 1981; Mooney and Drake 1986; DiCastri 1990; Vitousek 1990; Lodge 1993; Cushman 1995; Caughley and Gunn 1996; Hunter 1996; Williamson 1996; and Meffe and Carrol 1997.

Table 1. Reported effects of *Musculista senhousia.*

Effect	Description	Reference
Carrier of parasite	Intermediate host to unidentified species of flatworm parasites (final host is probably a fish or shorebird).	Crooks 1992; P.S. Perkins pers. comm.
Competition	Inhibits suspension-feeding bivalves such as *Chione undatella* and *C. fluctifraga.*	Chapter 2 & 3
	Negative effects on vegetative spread of eelgrass.	Reusch & Williams 1998
Exotics as predators	May consume plankton through filtration of water column.	Cloern 1983
Exotics as prey	Consumed by fish (e.g. yellowfin and spotfin croakers, sargo).	Crooks 1992
	Consumed by snails (*Pteropurpura festiva*).	Reusch 1998
	Consumed by shorebirds (e.g. willets and godwits) and ducks.	Carlton et al. 1990; Crooks pers. obs.
Ammensalism	May inhibit subsurface deposit feeders and some tube-builders.	Chapters 3, 5 & 6
Facilitation	Facilitates small infauna within mats (mediated by habitat creation).	Chapters 5 & 6
	Benefits eelgrass blade growth by biodeposition.	Reusch & Williams 1998
Community structure	Increases local species richness & density of individuals.	Chapters 5 & 6
	Increases spatial heterogeneity of tidal flat.	Chapter 5
Habitat modification	Creation of byssal mats on soft sediments - increases structural complexity, shear strength, and amounts of fine sediments & organics	Chapters 5 & 6

Table 2. Examples of habitat-modifying exotic species.

Species	Location	Effects	Reference
Japanese eelgrass (*Zostera japonica*)	Pacific Northwest mudflats	Creates intertidal beds, facilitates macrofauna	Posey 1988
Water hyacinth	Lake Victoria	Clogs bays, increases anoxia, creates snail habitat & predation refuge for fish	Ogutu-Ohwayo 1996
Mesquite	South African savanna	Forms thickets, decreases dung beetle diversity and abundance	Steenkamp & Chown 1996
Tank bromeliads	Florida	Creates aquatic habitat for *Aedes* spp. mosquitoes	O'Meara et al. 1995
Goats, sheep	Channel Islands, California	Overgrazes vegetation, increases erosion	VanVuren & Coblentz 1987
Periwinkles (*Littorina littorea*)	East coast of U.S.	Bulldozes sediments, inhibits algae & cordgrass	Bertness 1984
Zebra mussels	Lakes & rivers of N. America, Europe	Filters water column, increases light penetration & macrophyte growth, shells provide habitat for macrofauna	Lowe et al. 1995
Carp, goldfish	N. America and elsewhere	Destroys submerged vegetation, increases turbidity in ponds	Richardson et al. 1995

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