MARINE BIOLOGICAL INVASIONS: THE DISTRIBUTIONAL ECOLOGY AND INTERACTIONS BETWEEN NATIVE AND INTRODUCED ENCRUSTING ORGANISMS

by

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Whether community membership is of limited or unlimited nature is a longstanding issue in ecology. Assembly studies have provided insight into the contributions of competition, diversity, and history on the development of community structure. In these studies however, the colonizers are drawn from the same species pool in which all members have had an evolutionary history. Thus interacting species have potentially evolved life history strategies in response to one another and have altered the resistance of native assemblages to species insertion.

The human-mediated introduction of species provides an opportunity to ask questions pertaining to the resistance or susceptibility of communities to invasion in the absence of co-evolved traits. Whether a co-adapted, potentially co-evolved species pool can resist the invasion of a species with which none of the community members have had evolutionary "experience" has rarely been experimentally examined.

The marine encrusting communities of Coos Bay estuary, Oregon, have been and continue to be inocculated by non-indigenous species from a range of donor regions. These communities form two distinct clusters dominated either by native species limited to marine sites in the lower bay or introduced species in the brackish waters of the upper bay.

The settlement phenologies of native and introduced species in both the lower and upper bay exhibit significant differences in the duration, timing, and density of settlement.

Questions pertaining to the resistance of native communities to invasion by non-indigenous species were examined in the face of catastrophic disturbance and established adult assemblages. In the presence of introduced species, disturbed patches (bare settlement panels) quickly attained a species equilibrium and diversity. In contrast native communities continued to gain species after 17mo.

Experimental manipulation of established native and invaded assemblages (14mo) such that native assemblages were placed in direct contact with invaded assemblages in 25%, 50% and 100% treatments allowed adult-adult interactions to be controlled. These manipulated assemblages were then reciprocally transplanted between the two sites. Early mortality of introduced species and lack of larval input at the native site resulted in reduced invader success. At the invaded site invasion success was correlated with two factors, initial native space occupancy and invaded assemblage treatment density.

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CHAPTER I

THE DISTRIBUTION AND ECOLOGY OF NATIVE AND INTRODUCED ENCRUSTING ORGANISMS IN THE COOS BAY ESTUARY

Introduction

Interest in the effect of introduced species on ecosystem function has risen since Elton's (1958) seminal monograph *The Ecology of Invasions by Plants and Animals*, as documented by the number of volumes dealing with this question published during the last decade (Groves and Burdon 1986; Mooney and Drake 1986; Kornberg and Williamson 1987; MacDonald et al. 1987; Joenje et al. 1987; Drake et al. 1989; di Castri et al. 1990; Groves and di Castri 1991; Rosenfield and Mann 1992; Mills et al. 1993; Nalepa and Schloesser 1993). Despite the broad geographic scope of these works (Britain, North America, Hawaii, Australia, South Africa, mainland Europe) this recent attention has focused in large part on freshwater and terrestrial systems, with little attention given to the nearshore marine environment (Carlton 1989, 1992b). In part this may be due to the lack of a clear consensus as to what constitutes the native biota in coastal ecosystems. Most biological surveys of coastal marine communities commenced well after many invasions occurred (Carlton 1979a, b, 1989, 1992b; di Castri 1989, 1990). Once biological surveys were conducted, the assumption that the organisms encountered were endemic until proven to be introduced has resulted in large numbers of widely distributed, "cosmopolitan" species whose biogeographic origins are largely unknown (cryptogenic species *sensu* Carlton 1979b; Chapman and Carlton 1991). Consequently our understanding of the degree to which marine communities in general have been biologically altered by human-mediated invasions is minimal.

Several general patterns that may or may not be transferable to the marine environment can be distilled from recent work on invasions in freshwater and terrestrial communities. That certain kinds of communities or ecosystems are more susceptible than others to invasion by non-native species is now well documented (Elton 1958; Carlton 1979a, b, 1989, 1992a, b; Fox and Fox 1986; Crawley 1987; Carlton et al. 1990). For example, islands, with their relatively depauperate faunas, are readily invaded by new species (Elton 1958; Pimm 1987). These island biotas are continually changing around an equilibrium number of species due to species' invasion and extinction events on the local (island) scale (MacArthur and Wilson 1967). Similarly, the effect of disturbance (both local and regional) in "resetting" a community to an earlier successional state has been linked to the success of invasions (Fox and Fox 1986). Species-poor regions such as the post-glacial Northwest Atlantic and the Laurentian Great Lakes (two regionally disturbed areas) have received considerable numbers of invaders (Vermeij 1991; Rosenfield and Mann 1992; Mills et al. 1993; Nalepa and Schloesser 1993).

The converse of this last pattern is that certain communities "resist" the invasion of exotics. Elton (1958) proposed that the ecological resistance of communities to invasion by exotics was related to native species diversity (i.e., richness). The Eltonian idea of ecological resistance is distinct from the dynamic equilibrium of MacArthur and Wilson (1967). Elton suggested that species rich communities will prevent the establishment of exotic species through an intricate series of synecological interactions including (but not limited to) competition with existing natives, predation by natives, parasitism and disease. Thus in this view recipient communities selectively allow entry into the system but are closed to the majority of invaders (closed systems: Roughgarden 1989). In contrast, MacArthur and Wilson (1963, 1967) proposed that communities were unlimited membership systems (Roughgarden 1989) in which the leading determinant of invasion success is not based on recipient community attributes, but on the dispersal ability of the invader species. Once a species has arrived in the new community, it is assumed that synecological assortative processes return the system to an "equilibrium" number of species.

On the Pacific coast the majority of biological introductions have been in bays and estuaries with relatively few successful open coast introductions (Carlton 1974, 1979a, b, 1989). The large estuaries of the Pacific Northwest are geologically young (10,000 - 15,000 yrs old; Atwater et al. 1977; Carlton 1979a, 1992b; Ricketts et al. 1985; Nichols and Pamatmat 1988) and consequently may have had an impoverished native brackish water fauna. It has been proposed that the "immature" (i.e., in the process of assembly), depauperate communities of these estuaries are more susceptible to the introduction of species from other regions of the world (Carlton 1974, 1979a, b, 1992b; Nichols and Thompson 1985) than the mature, species rich communities of the open coast. Alternatively, this apparent estuarine susceptibility may be an artifact of the availability of dispersal mechanisms (see below) that are more likely to transport estuarine species than than species from open coastal marine communities (Carlton 1979b, 1992b).

A faunal survey of the sessile, encrusting organisms (the "fouling" community) of Coos Bay, Oregon USA, was undertaken with two aims: 1) to determine the distribution of the native and introduced species along an estuarine gradient that is similar to those described for other Pacific coast estuaries; and 2) to discern any correlation between native and introduced species distributions within Coos Bay. Thirdly the monthly recruitment patterns in lower and upper bay communities were examined to detect differences in the phenology of recruitment for native and introduced encrusting species.

Study Site

The Coos Bay estuary, Oregon (43° 19' 30"N, 124° 19' 30"W) comprises two sub-estuaries: South Slough, a drowned syncline of the Empire Formation and the Coos River, an L-shaped bar-built estuary (see Figure 1). In the past these two estuaries had separate entrances but the southward extension of the sand spit (North Spit) shifted the Coos River mouth southward until it merged with South Slough. Combined, the present-day estuary covers approximately 10,000 acres (see Figure 1) and is classified as a well-mixed, drowned river mouth. The Coos River discharges between 90 and 5,500 c.f.s. seasonally, averaging 2,200 c.f.s. South Slough has few minor tributaries (Winchester Creek) from its watershed of 25,000 acres. Coos Bay is a heavily man-modified estuary and has lost approximately 90% of the tidal habitat (e.g., mud and sand flats, salt marshes) to land reclamation, diking and filling (Hoffnagel and Olson 1974).

Mechanisms of Biological Invasions

Four temporally distinct mechanisms of species introduction into Coos Bay have operated between 1850 and the present and have been elucidated for other estuaries such as San Francisco Bay (Carlton 1979b, 1987, 1989, 1992b). These mechanisms include I) wooden ship hull fouling/boring; II) Atlantic oyster (*Crassostrea virginica*) culture; III) Japanese oyster (*C. gigas*) culture; and IV) modern mechanisms which include ballast water transport, modern mariculture practices, and intra-coastal and intra-estuarine ship traffic. Table 1 summarizes the approximate periods of operation for each of these mechanisms and the areas of Coos Bay that have differentially been affected. Wooden-hulled vessels (mechanism I) operated between Coos Bay and San Francisco Bay, Portland, and Puget Sound between 1853 (initial settlement of Coos Bay by western

Table 1. Mechanisms of Encrusting Species Introduction into Coos Bay. Receiving areas are as follows: CR, Coos River; UB, Upper Bay; MB, Middle Bay; LB, Lower Bay; and SS, South Slough.

ID	Mechanism	Period	Range of Transport			Donor Region	Receiving Area in Coos Bay
			Inter-provincial >2000km	Regional 2000km> <20km	Local <20km		
I	Wooden Vessel Shipping	1850's - 1950's	☑	☑	☑	Atlantic, Europe	SS, LB, MB, UB
II	Atlantic Oyster Culture	1870's - 1930's	☑	☑	☑	Atlantic, Europe	SS,MB,UB
III	Japanese Oyster Culture	1930's - 1950's	☑	☑	☑	Japan/Asia	SS,MB,UB
IV	Modern Mechanisms						
	a) Ballast Water	1940's - present	☑	☑		Asia, Australia	LB,MB,UB
	b) Other Mariculture	present		☑	☑	-	SS,MB,UB
	c) Coastwise Shipping Fishing Boats Private Craft Replica Vessels	1850's - present		☑	☑	-	ALL

man) and the 1950's (Kemble 1957; Douthit 1986). This coastwise shipping (between bays and estuaries of the Pacific Coast) was initially restricted to the lower Coos Bay (Empire to the mouth) but in 1856 the waterfront of North Bend (a mill town) was developed for timber shipping to San Francisco Bay. The Collector of Customs for the Coos Bay harbor district reported that between 1867 and 1874 a total of 227 coastwise ships had arrived and departed Empire City - an average of 28 vessels per year. By 1883 the annual number of ships had risen to 167 (Douthit 1981, 1986; Case 1983).

The coastwise traffic increased to accommodate the coal and timber industries as well as passenger transport necessitating harbor improvements, including entrance jetties (North Jetty 1890's; South Jetty 1920's) and dredging up to Isthmus Slough. Over 100,000 tons of coal were extracted between 1896-1897, the bulk of which was shipped to San Francisco (Baldwin 1981; Case 1983). Much of the timber logged and milled in Coos Bay was shipped south in the earlier period by the lumber brigs due to their superior handling in the Coos Bay entrance, but as jetty placements stabilized the entrance they were soon replaced by coastwise lumber schooners (Kemble 1957). Consequently the intra-coastal trade may have distributed much of the San Francisco Bay exotic fauna to Coos Bay via hull fouling, until the late 1930's.

The first transoceanic vessel arrived in Coos Bay from Japan during 1921 (Case 1983). In the following years trade with Asian ports increased to a mean of 133,000 tons (s.d. = 29,000) until World War II. During the post-war years (1946 - 1952) foreign shipping in Coos Bay rose to a mean of 243,000 tons (s.d. = 80,000) with foreign imports remaining below 500 tons (Case 1983). Thus between the mid 1920's and the 1950's wooden hulled vessels had the potential to transport Asian hull fouling and boring organisms to Coos Bay directly.

Atlantic oyster culture (mechanism II) appears to have been limited to a single inoculation event at the entrance of South Slough in 1872 (Douthit 1986; P. Baker *pers.*

comm.), although numerous undocumented movements of this species may have occurred. Consequently while this mechanism may not have directly introduced species into Coos Bay, Atlantic oyster culture is known to have introduced scores of species to primary receiving regions including San Francisco Bay, Humboldt Bay, and Willapa Bay from 1890 to the 1930's (Carlton 1974, 1979b). From these primary receiving areas numerous encrusting species may have been secondarily spread via coastwise shipping traffic (wooden hulled fouling: mechanism I) and later, with Japanese oyster culture (mechanism III). This secondary invasion step would necessarily place additional filters or bottlenecks (Carlton 1979b, 1987) on the Atlantic species transported to Coos Bay and may explain the absence from Coos Bay of species that are present in San Francisco Bay or Willapa Bay.

The Japanese oyster, *Crassostrea gigas*, was first introduced to the larger bays of the Pacific Coast in 1919 (Steele 1964). These introductions of adult oyster communities (the oysters and encrusting and infaunal associates: mechanism III) continued until the 1950's when the practice of rearing spat negated the need to ship adults (Carlton 1979b; Qualman 1983). The sources of *C. gigas* material moved into Coos Bay have been varied and include Willapa Bay, Hood Canal, Netarts Bay, and to a lesser degree Humboldt Bay (Qualman 1983; P. Baker *pers. comm.*). The details of seeding and transport of oysters between the Pacific bays are mired in the lost records of the oystermen. The primary areas in Coos Bay used for the production of Japanese oysters are South Slough and Haynes Inlet. The muddy sand flats of Eastside (Figure 1) have also been used as oyster clearing grounds in the past (Qualman 1983; Douthit 1986).

The final group of transport mechanisms (mechanism IV) includes ballast water, recent mariculture plantings, and modern intracoastal and intra-bay small boat traffic. The transport of ballast water and associated plankton has been elucidated in general (Carlton 1985; Williams et al. 1988), and for Coos Bay specifically (Carlton and Geller 1993).

This water may be discharged as the vessel navigates the channel from the entrance to the primary docking areas in the upper bay (Figure 1, sites 7 and 12) but the bulk of the ballast (mean = 1.09×10^7 liters•ship^{-1}, s.d. = 2.7×10^6; Carlton and Geller 1993) is released at the docking facility and thus the upper bay is most likely to receive introductions.

The current mariculture plantings have occurred in the same regions as those used for *Crassostrea gigas* culture (mechanism III) and include the re-inoculation and subsequent re-establishment of the native Olympia oyster, *Ostrea conchophila (lurida)*. The Olympic oyster is native to the Pacific coast but it is herein treated as an introduced species into Coos Bay for the following reasons: 1) *O. conchophila (lurida)* went locally extinct from the Coos Bay estuary in prehistoric times due to a temporary change in siltation patterns (Stubbs 1973; P. Baker *pers. comm.*); 2) in the intervening period *O. conchophila (lurida)* did not naturally re-establish a viable population (P. Baker *pers. comm.*); and 3) it was re-inoculated in 1992 by local mariculturists. Having become re-established in Coos Bay, *Ostrea conchophila (lurida)* is now a member of an encrusting community newly composed of a large number of Atlantic and Japanese encrusting species that were absent when the oyster became extinct. For the resident community of invaders, *O. conchophila (lurida)* thus becomes an invader itself.

As opposed to the primary (1°) invasion mechanisms described above, the secondary (2°) introduction of species via intracoastal and intra-bay small boat traffic (commercial and private fishing vessels, sailing vessels, replica antique vessels) continues to redistribute species introduced originally to primary receiving areas (e.g., San Francisco Bay and Willapa Bay). These vessels have the propensity to develop lush hull fouling due to lack of upkeep (Crisp 1958; Crisp and Southward 1959, Skerman 1960; Carlton and Scanlon 1985; Carlton and Hodder 1993). The primary mode of transport within the Coos Bay region was historically by water. Until the 1940's a variety of within bay vessels operated as far up the Coos River as Alleghany and down into the South Slough, acting as passenger and cargo carriers. These small vessels may have moved organisms introduced by coastwise or foreign shipping (mechanism I) from the larger shipping docks to areas throughout the bay.

Carlton and Hodder (1993) studied species transport between Pacific Coast bays by the *Golden Hinde II*, a replica of Sir Francis Drake's vessel *Golden Hinde*. They demonstrated that a variety of species were collected and transported between estuaries and bays on the hull of this replica vessel, despite the application of copper based antifouling paints. Species were transported between each adjacent pair of bays studied (Yaquina Bay → Coos Bay → Humboldt Bay → San Francisco Bay) as well as in an additive fashion between all bays.

Materials and Methods

Coos Bay Transect

Physical Measurements

Temperature and salinity (conductivity) were characterized at four sites in Coos Bay (sites 2, 9, 12 and 15 of Figure 1; see also Table 2) during spring low tide series of each month from September 1988 to September 1990. A fifth site in South Slough was sampled by researchers conducting studies in the National Estuarine Research Reserve (site 18 of Figure 1 and Table 2) over the same time period and the data are presented for comparison. Salinity and temperature were collected with a YSI temperature-salinity meter. Measurements were taken at approximately -2.0' Mean Lower Low-Water (MLLW). An additional bay wide (0 to 32 km) transect was conducted during flood tide in July 1990, in which temperature and salinity measurements were collected at one mile intervals (Figure 2).

Table 2. Sample Sites within Coos Bay. Transect names are CB, Coos Bay and SS, South Slough. Region of the bay follows codes in Table 1.

Site ID#	Transect	Region	Site Name	River Mile	Km	Substrate	Physical Measurement Site
1	CB	LB	Coos Head	1.25	2	Rock	
2	CB	LB	Ocean Station	1.5	2.4	Shell, Rock	☑
3	CB	LB	North Jetty	2.25	3.6	Rock	
4	CB	LB	Fossil Point Jetty	2.5	4	Rock	
5	CB	MB	Sitka Dock	4	6.4	Panels, Pilings	
6	CB	MB	Coos Bay Dredge	6	9.6	Shell	
7	CB	MB	Weyerhauser Dock	8	12.8	Panels, Piling, Rock	
8	CB	MB	Pony Slough	9	14.4	Floats, Pilings	
9	CB	UB	Haynes Inlet	10	16	Pilings, Rock	☑
10	CB	UB	Larson Slough	12	19.2	Rock	
11	CB	UB	City Dock	14	22.4	Floats, Pilings	
12	CB	UB	Isthmus Slough Float	15	24	Floats, Floating Logs	☑
12	CB	UB	Isthmus Slough Dredge	15	24	Shell, Rock, Bark	
12	CB	UB	Isthmus Slough Panels	15	24	Panels	
13	CB	CR	Coos River	20	32	Floats	
14	SS	SS	Point Adams Jetty	2	3.2	Rock	
15	SS	SS	Charleston Boat Basin	2.75	4.4	Floats, Pilings	☑
16	SS	SS	Hallmark Fisheries Dock	3	4.8	Floats, Pilings	
17	SS	SS	Port of Coos Bay Dock	4	6.4	Floats, Pilings	
18	SS	SS	South Slough	5	8	Oyster Shells, Logs	☑

Biological Communities

The distributions of encrusting (i.e. sessile) organisms in the Coos Bay estuary were surveyed along two estuarine transects: Coos Bay (CB) and South Slough (SS). Fourteen sites were selected (nine in the CB transect and five in SS) based in part on the consistent presence of hard substrate, accessibility and location relative to other sites (Table 2). Long term settling or "fouling" panels of sanded black acrylic plexiglass ($200cm^2$) were placed at three sites, Sitka Dock, Weyerhaeuser Dock, and Isthmus Slough to supplement the availability of retrievable hard substrate. At each subsequent sampling (roughly six month intervals between September 1988 and 1990) a species list was compiled for the more obvious fauna (macro-fauna) during a qualitative site survey. Approximately 400 cm^2 of the encrusting community from each site was collected, placed in seawater and transported to the Oregon Institute of Marine Biology (OIMB), where samples were examined under dissecting microscopes to aid in species detection and identification of the less obvious species.

Species were scored for presence or absence at each site. Site species lists were then compared between sample times and collapsed so that a single list was obtained for each site where species were scored for presence at any sample time. This results in liberal (maximum) distributions of species within the bay without regard to temporal fluctuations. Surveyed substrates included rock (basalt jetty materials and conglomerate material surrounding tide gates), cobble, live and dead shell material, wood and bark, pilings and floating docks (see Table 2). All collections were made between 0.0' and -2.5' MLLW. Three additional dredge sites (-20.0' to -30.0' MLLW) were sampled in November 1988 and October 1989 in the lower (site 2: 2.4 km), middle (site 6: 9.6 km), and upper (site 12: 24 km) portions of the bay.

Species presence and absence were compared between sites by calculating a Sørensen's similarity coefficient (1948) and constructing a similarity dendrogram. The Sørensen's similarity coefficient compares the number of species shared between two samples versus the total number of species in those samples. All between-site similarities were calculated and a similarity dendrogram was derived based on a hierarchical clustering technique, the unweighted pair grouping method (UPGMA; Wilkinson 1990).

Recruitment Phenologies and Abundances

Two sites, one in the upper bay (Isthmus Slough, site 12, Figure 1) and one in the lower bay (Charleston Boat Basin, site 15, Figure 1), were selected to study the recruitment dynamics of native and introduced species. At each site four sanded, black acrylic recruitment panels 50 cm^2 (7.2cm X 7.2cm) were exposed horizontally at -1.0' MLLW for 30 days, at which time the panels were collected and replaced by a clean set. The collected panels were placed in seawater, transported to OIMB and the bottom surface examined with a dissecting microscope. All organisms were identified to species or if species identification was not possible an illustration was made for future reference and the settlement panel was placed in running seawater and examined until identification was possible. In this fashion a catalogue of identification illustrations was developed for use with early recruits. After recruitment panels were examined they were cleaned and sanded for reuse.

This experiment continued at the two sites from August 1988 to December 1990. Due to differences in the number of days between collections, the species recruitment data were standardized over a 30-day month and averaged over the four replicate panels ($recruits \bullet panel^{-1} \bullet mo^{-1}$). The data include the phenology or timing of recruitment (number of $species \bullet mo^{-1}$), number of months in which recruits were observed for each individual species (mo•species^{-1}), and the rates of larval recruitment on bare substrate (recruits•panel^{-1}•mo^{-1}). Monthly samples were averaged over years (January to July = 2 years, August to December = 3 years) in order to calculate the duration and abundances of recruitment. As the numbers of native and introduced species are greatly different at each site, the values (number of species•mo^{-1}) were converted to percentages within group (native or introduced). These data (percent of group•mo^{-1}) were arcsine transformed and compared within site by t-test. Length of recruitment period for each species (mo•species^{-1}) was compared between groups at each site by t-test. Seasonal variation patterns in native and introduced species recruitment abundances (recruits•panel^{-1}•mo^{-1}) were found to violate assumptions of homogeneity of variances (F_{max} test) after log (n+1) transformation and thus were analyzed by a Kruskal-Wallis non-parametric two-way ANOVA (Sokal and Rohlf 1981; Zar 1984).

Results

Coos Bay Transect

Physical Measurements

Temperature and salinity measurements are presented in Figures 3 through 7 as both line graphs and "hydroclimagraphs" (*sensu* Hedgpeth 1957) of monthly means for each sampled site. Temperature and salinity of the lower bay station (site 2, Figure 3) vary little throughout the year, ranging between 7° and 13°C and 28 and 33‰ (parts per thousand) (see Table 3). In contrast, the Charleston Boat Basin (site 15, Figure 4) experiences seasonal reductions in salinity (17‰ in January). The Charleston Boat Basin sample station is located on the OIMB dock adjacent to a stream outlet feeding an anadromous

Table 3. Physical Measurements for Coos Bay Stations.

Site ID	Name	Salinity (ppt)				Temperature (°C)			
		Mean	SD	Min	Max	Mean	SD	Min	Max
2	Ocean Station	31.3	1.5	29	33	10.6	1.4	8.4	13
15	Charleston Boat Basin	25.5	5.7	17	32.5	11.5	1.5	9.3	13.5
18	South Slough	25.1	8.1	12	33	13.1	4.0	7	18.5
9	Haynes Inlet	17.1	8.7	2.9	30	14.1	2.7	10	18
12	Isthmus Slough	17.6	8.0	4.5	29	14.9	5.3	4.5	22

fish ladder. The December through March reductions in salinity reflect a slight delay from the peak precipitation period for the Pacific Northwest (rain year begins October).

South Slough (site 18, Figure 5) experiences a wide range of salinities (12 to 33‰). Similarly, South Slough experiences summer warming of the shallows as demonstrated by the mid-summer elevated temperatures (18°C) returning to oceanic temperatures in winter (7° to 10°C).

The upper bay sites, Haynes Inlet (site 9, Figure 6) and Isthmus Slough (site 12, Figure 7), experience salinity variations from 3‰ in mid-winter to 29-30‰ in summer. This wide variation is due in large part to the riverine input of the Coos and Millicoma Rivers whose outflows increase during the rain year. Haynes Inlet experiences a temperature range (10° to 18°C) approximately equal to that of South Slough. Isthmus Slough however reaches elevated summer temperatures above 20°C and winter lows of <10°C (Figure 7).

The bay-wide transect conducted in July of 1990 demonstrated strong relationships between distance from the ocean (river mile) and temperature (positive) and salinity (negative; Figure 2). The environmental change along the estuarine gradient is described by the variation or range of temperature and salinity values as presented in Figures 8 and 9. Temperature range increases linearly with distance (km) from the ocean ($\Delta\text{temp} = 0.51(\text{dist}) + 3.66$), and salinity range increases with the exponent of distance ($\Delta\text{salinity} = 8.04\, e^{(\text{dist})} + 2.48$).

Biological Communities

During the course of this study the regional diversity or γ-diversity was 106 species of encrusting (sessile) organisms, 84 native (Table 4), 16 introduced and 6 cryptogenic species (Table 5). In the Coos Bay transect 101 species were collected (84 native,

Table 4. Native Species List for Five Regions of Coos Bay. Region codes follow Table 1. Asterisks identify possible introductions.

		Region				
PHYLUM	Species	SS	LB	MB	UB	CR
Cirripedia						
	Balanus crenatus	☑	☑			
	Balanus glandula	☑	☑	☑	☑	
	Balanus nubilus		☑			
Cnidaria						
	Aglaophenia spp	☑	☑			
	Anthopleura elegantissima		☑			
	Anthopleura xanthogrammica	☑	☑			
	Epiactis prolifera	☑	☑			
	Garveia annulata		☑			
	Hydroid (Phialella?)	☑	☑	☑		
	Metridium senile	☑	☑	☑		
	Obelia spp	✱	☑	☑		
	Sarsia spp	☑	☑			
	Scyphistomae (Aurelia spp?)	☑	☑	☑		
	Tubularia indivisa	☑	☑			
	Tubularia marina	☑	☑	☑		
	Urticina crassicornis	☑	☑	☑		
	Zanclea spp	☑	☑			
Ectoprocta						
	Aetea anguina		☑			
	Alcyonidium polyoum?	☑	☑	✱		
	Bugula californica		☑			
	Bugula pacifica	☑	☑	☑		
	Callopora armata		☑			
	Callopora circumclathra	☑	☑			
	Callopora horrida	☑	☑			
	Callopora inconspicua		☑			
	Caulibugula ciliata	☑	☑	☑	☑	
	Cauloramphus spiniferum		☑			
	Cheilopora praelonga	☑	☑			
	Coleopora gigantea	☑	☑			
	Conopeum reticulum	☑	☑			
	Costazia costazii	☑	☑			
	Cribrilina annulata	☑	☑	☑		
	Crisia occidentalis	☑	☑	☑		
	Dendrobeania lichenoides	☑	☑			
	Electra crustulenta	☑	☑	☑		
	Electra crustulenta var arctica	☑	☑			
	Eurystomella bilabiata		☑			
	Fenestrulina malusii var. umbonata	☑	☑			
	Filicrisia franciscana	☑	☑			
	Flustrellidra corniculata		☑			
	Heteropora alaskensis		☑			
	Hippothoa divaricata		☑			
	Hippothoa hyalina	☑	☑	☑	☑	

Table 4. (Continued).

				Region		
PHYLUM	Species	SS	LB	MB	UB	CR
Ectoprocta (cont.)						
	Lichenopora verrucaria		☑			
	Microporella californica	☑	☑			
	Microporella ciliata	☑	☑			
	Oncousoecia ovoidea	☑	☑			
	Parasmittina trispinosa	☑	☑			
	Porella columbiana	☑	☑			
	Rhamphostomella costata	☑	☑			
	Smittoidea prolifica	☑	☑	☑	☑	
	Tegella robertsonae		☑			
	Tricellaria erecta	☑	☑			
	Triticella spA	☑	☑			
Entoprocta						
	Barentsia discreta		☑			
	Barentsia gracilis		☑			
	Barentsia ramosa		☑			
	Loxosoma sp	☑	☑			
	Pedicellina cernua	☑	☑			
Mollusca						
	Hinnites gigantea	☑	☑			
	Mytilus californianus	☑	☑			
	Mytilus trossulus	☑	☑	☑	☑	
	Pododesmus cepio	☑	☑			
Annelida						
	Crucigera zygophora	☑	☑	☑		
	Eudistylia polymorpha	☑	☑			
	Eudistylia vancouveri	☑	☑			
	Pseudochitinopoma occidentalis	☑	☑			
	Serpula vermicularis	☑	☑			
	Spirorbids	☑	☑			
	Terebellid spp	☑	☑			
Porifera						
	Halichondria panicea	☑	☑			
	Haliclona spp	*	☑			
	Leucosolenia sp	☑	☑			
	Myxilla sp	☑	☑			
	"Ophlitaspongia" spp	☑	☑			
Chordata (Urochordata)						
	Ascidia ceratodes	☑	☑			
	Boltenia echinata		☑			
	Chelyosoma productum		☑			
	Cnemidocarpa finmarkiensis	☑	☑			
	Distaplia occidentalis	☑	☑			
	Perophora annectens	☑	☑			
	Pyura haustor	☑	☑			
	Styela gibbsi	☑	☑			
	Styela montereyensis	☑	☑			

12 introduced, 5 cryptogenic) while in South Slough 78 species (66 native, 8 introduced, 4 cryptogenic) were observed. The encrusting species of Coos Bay are divided among eight phyla (Figure 10): Ectoprocta (bryozoans), Cnidaria, Chordata (tunicates), Annelida, Porifera, Entoprocta, Mollusca, and Arthropoda. The percentages of species in each phylum when contrasted between native and introduced groups are surprisingly similar (Figure 11). With the exception of the Annelida (no introduced species in the Coos Bay fauna) every group is represented by both native and introduced species in similar proportions with no significant difference between native and introduced proportions ($G_{[7]} = 2.58$ adjusted for small sample size, n.s.). Cryptogenic species are represented by six taxa in three phyla, four species of ectoprocts, one cnidarian and one sponge (Figure 12).

As discussed above and in Table 1, the introduction mechanisms moving species into the Coos Bay estuary have differentially inoculated various regions of the bay. Figure 13 represents the number of introduced (or cryptogenic) species in each of five regions of the bay by the probable mechanism of earliest introduction (Table 5). The species associated with the most historically obscure invasion event, wooden vessel hull fouling (mechanism I), appear to have spread throughout Coos Bay with minor concentrations in South Slough (SS) and the upper bay (UB).

The history of Atlantic oyster culture (mechanism II) is somewhat patchy for the Coos Bay region and consequently no good predictions concerning localized impact can be made. It should be noted, however, that the upper bay was the first common oyster ground and this area appears to have the only substantive concentration of introduced species associated with Atlantic oysters. As predicted from the historical practice of oyster farming, the South Slough region has the greatest number of species associated with Japanese oyster culture (mechanism III). Oyster associated encrusting species include the colonial tunicates *Botryllus schlosseri* (Atlantic oysters) and

Table 5. Introduced and Cryptogenic Species List for Five Regions of Coos Bay. Region codes follow Table 1. Asterisks identify possible natives.

PHYLUM	Species	Region					Origin	Mechanism
		SS	LB	MB	UB	CR		
Cirripedia								
	Balanus improvisus			☑	☑	☑	NW Atlantic	I,II,III
Cnidaria								
	Cordylophora caspia				☑	☑	Southern Europe	I,II,III
	Haliplanella lineata				☑		Asia	I,II,III
	Tubularia crocea				☑		NW Atlantic	I,II,III
Ectoprocta								
	Bugula neritina	☑					Europe	I,II,III
	Conopeum tenuissimum	☑	☑	☑	☑	☑	NW Atlantic	I,II,III
	Schizoporella unicornis	☑					Japan	III
	Watersipora edmonsonii?	☑					Southern California	IV
Entoprocta								
	Barentsia benedeni				☑	☑	Europe	I,II,III
Mollusca								
	Crassostrea gigas	☑		☑	☑		Japan	III
	Ostrea conchophila (lurida)				☑		Pacific Coast	IV
Porifera								
	Halichondrea bowerbanki	☑	*		☑		NW Atlantic	I,II,III
Chordata (Urochordata)								
	Botrylloides violaceus	☑		☑	☑		Japan	III
	Botryllus schlosseri	☑					Europe	I,II,III
	Diplosoma mitsakurii				☑		Japan	IV
	Molgula manhattensis	☑			☑		Northeast Atlantic	I,II
Cryptogenic species								
Cnidaria								
	Obelia spp	*	*		☑		??	I,II,III,IV
Ectoprocta								
	Alcyonidium sp	*			*		Japan?	IV
	Bowerbankia gracilis	☑	☑	☑	☑	☑	Europe?	I,II,III
	Cryptosula pallasiana	☑	☑				Atlantic?	I,II,III
	Triticella spB	*	*		☑		Japan?	III,IV
Porifera								
	Haliclona sp	*	*		☑		Northwest Atlantic?	I,II,III

Botrylloides violaceus (Japanese oysters; see Van Name 1945; Boyd et al. 1990), and the Japanese bryozoan *Schizoporella unicornis* (Powell 1970; Ross and McCain 1976; see also Miyazaki 1938).

The last group of invasion mechanisms, ballast water and others (mechanism IV), has potentially affected all regions of the bay, although the primary region of ballast water discharge is adjacent to the lumber and mill docks of the middle (MB) and upper (UB) bay. Additionally, the movements of species by within-bay or intra-coastal (coastwise) transport are included in this group. These movements which will not impact any particular region of the bay. South Slough (SS), MB and UB have species that are associated with this mechanism.

During the course of this study several invasion events were observed via modern transport mechanisms (mechanism IV). In June 1990, a private dock was towed from Joe Ney Slough (an arm of South Slough) to Isthmus Slough (site 12). In the process the bryozoan, *Schizoporella unicornis*, the ascidian, *Botrylloides violaceus* (both Japanese), and the Atlantic ascidian, *Botryllus schlosseri*, were transplanted during a period when the physical conditions (Figure 7) were within the physiological limits of these three species. This is also the period of greatest reproductive output for all three species (Figures 25 through 28). Approximately 15 days after transport to Isthmus Slough all three species were still present on the transported dock, occupying approximately equal percent cover totalling >80%. By September 1990, *S. unicornis* colonies had bleached (turned white) and were presumably dead, while the colonies of *B. schlosseri* had regressed and were not abundant (together occupying <5% on the transplanted dock). The colonies of *Botrylloides violaceus* however had grown considerably. In addition newly recruited colonies on adjacent docks and floating logs increased the percent space covered by *B. violaceus* to 60% on the transplanted dock and about 20% in the adjacent encrusting community.

Over the course of the ensuing years *Botrylloides* has overwintered and successfully insinuated itself into the Isthmus Slough introduced-species community. Densities in subsequent years have dropped to 5 - 10% of the total space. I have followed the spread of *Botrylloides* down the bay over the years 1991, 1992 and 1993 by its appearance at each of the Coos Bay transect sites. The rate of spread is approximately 2 km•yr^{-1} (Table 6) reaching the Pony Slough (site 8) after three years. Measurements of water flow at Isthmus Slough at peak ebb tide convert to approximately 3.6 km•yr^{-1}, and Japanese studies of the large (>1mm) lecithotrophic tadpole larvae of *Botrylloides violaceus* have shown that settlement can occur up to 10 hr after release (Saito et al. 1981; Boyd et al. 1990). Berrill (1949) has shown that in congeners settlement occurs between 5 min and 12 hr after release (mean of 1 hr in the laboratory). Thus the rate of spread is well within the capability of a single cohort.

As previously discussed, the native Olympia oyster, *Ostrea conchophila (lurida)*, was re-established in Isthmus Slough by mariculture in the summer of 1992. As with *Botrylloides*, *O. conchophila (lurida)* has spread down the bay and is presently found in Pony Slough (site 8).

The Isthmus Slough community has also been the receiving area for a second ascidian, *Diplosoma mitsakurii*. The native *D. macdonaldi* has recently been synonymized with *D. listerianum* (G. Lambert *pers. comm.*), and the common Japanese *D. mitsakurii* may be indistinguishable from *D. listerianum*, although Nishikawa (1990) retained the species name. The combined factors of the absence of a *Diplosoma* from any site in the bay between 1988 - 1991, the sudden appearance of common colonies (>15% cover) in the summer of 1992, and the presence of ascidian tadpole larvae in ballast water (Carlton and Geller 1993) lead me to view this species as *D. mitsakurii*, a Japanese ballast water introduction.

Table 6. *Botrylloides violaceus* Dispersal Following Secondary Introduction. Mechanism codes follow Table 1.

	Distance(km)	Furthest Spread				
Date	Spread	Site ID#	Site Name		Donor Region	Mechanism
unknown	-	18	South Slough	1° invasion	Japan	III
June, 1990	20km	12	Isthmus Slough	2° invasion	South Slough	IV
June, 1991	1.6km	11	City Dock	expansion	Isthmus Slough	-
June, 1992	3.2km	-	Coast Guard*	"	Isthmus Slough	-
May, 1993	4.8km	8	Pony Slough	"	Isthmus Slough	-

* - Coast Guard Cutter Citrus Dock at 19.2km

This may have been a transient invasion since it disappeared from permanent panels in Isthmus Slough, and has not been collected since September 1992 (subsequent collections in November 1992, February and April 1993). A second potential Japanese ballast water invader is the bryozoan *Alcyonidium* sp. collected once from Isthmus Slough. Carlton and Geller (1993) reported *Alcyonidium* larvae in Japanese ballast water. They were able to isolate and culture these cyphonautes larvae in the lab and induce settlement (J. Carlton *pers. comm.*). It is impossible to distinguish a transient (failed) invasion event of Japanese *Alcyonidium* sp. from the seasonal colonization of the upper bay by native *Alcyonidium polyoum*? due to the morphological similarity of *Alcyonidium* species.

In the Charleston Boat Basin (site 15), the bryozoan *Watersipora edmondsonii*? (identification by W. Banta, *pers. comm.*) is a new introduction to this community. Between 1988 and the appearance of *W. edmondsonii*? in 1990, extensive surveys of the Charleston fouling community had not detected its presence, nor was it found in surrounding habitats (Point Adams Jetty, site 14). *Watersipora*, a deep maroon to burgundy red bryozoan, reached moderate abundance in 1990 (5% space) and in the following years was found at nearby sites (sites 14 and 17) until September 1992. Since then the abundance of *Watersipora* has declined (<1% space) and it is now absent from Point Adams Jetty (site 14). The intracoastal traffic between California ports and Coos Bay is the most probable mechanism responsible for this introduction. In spring 1992 a *Watersipora* sp. that is morphologically very similar to the Coos Bay species appeared in the San Francisco Bay encrusting communities (J. Carlton pers. comm.).

The native species richness (α-diversity or point diversity) declines in highly significant exponential decay curves along the South Slough ($r^2 = 0.54$, $p<0.001$) and Coos Bay ($r^2 = 0.73$, $p<.001$) estuarine transects (Figure 14). The South Slough transect proceeds from a high of 66 native species to 12 in the oyster beds (*Crassostrea gigas*) of South Slough, while the Coos Bay transect declines from 84 native species at the North

Jetty (site 3) to 0 at 32 km (site 13). The response of native species richness to the estuarine gradient is not significantly different between transects and can be described by a single regression (pooled regression $r^2 = 0.64$, $n = 17$, $p<.001$; $\ln(\text{native species richness}) = -0.2(\text{km from ocean}) + 3.65$).

An estimate of β-diversity (*sensu* Whittaker 1960,1972) can be calculated from the mean similarities between sites along the length of the gradient. Since the within-site salinity range (max‰ - min‰) changes with the exponent of distance from the ocean an estimate of the estuarine gradient used here is the difference in salinity ranges between two sites. Figure 15 illustrates the reduction in native species diversity as a function of the (estimated) annual range of salinity at a site (pooled regression $r^2 = 0.64$, $n = 20$, $p<.001$). South Slough and Coos Bay transects follow similar patterns. The β-diversity plot (Figure 16) of mean similarity (Sørensen's Index: proportion of species in two samples shared between two samples) versus gradient change illustrates the rate of species turnover in the Coos Bay and South Slough transects (β-diversity = 0.10).

The introduced percentage of the total community increases in a linear fashion with the estuarine gradient (SS: $r^2 = 0.86$, $n = 5$, $p<.001$; CB: $r^2 = 0.94$, $n = 15$, $p<.001$; Figure 17). These two transects however, can again be described by a single, significant regression line (pooled regression $r^2 = 0.90$, $n = 20$, $p<.001$; $(\text{introduced species }\%) = 3.32(\text{km from ocean}) + 1.19$).

The introduced percentage of all species in the community decreases with native species richness (Figure 18) both in the South Slough (SS) transect and the Coos Bay (CB) transect. The pooled regression is significant and thus a single exponential line sufficiently describes both transects ($r^2 = .69$, $n = 20$, $p<.001$; $\ln(\text{introduced species }\%) = -0.04(\text{native species richness}) + 4.03$).

The encrusting communities of the Coos Bay estuary are divided into two distinct groups by similarity dendrograms (Figure 19). The upper bay communities between site 7 and 13 (Coos River) are largely introduced, estuarine derived species (7 native, 12 introduced, 4 cryptogenic) whereas sites 1 to 6, and 14 to 18 (SS) are predominately native, marine derived communities (83 native, 15 introduced, 4 cryptogenic).

Recruitment Phenologies and Abundances

The timing of native and introduced species settlement is graphically illustrated in Figure 20 for the communities of organisms in Isthmus Slough (site 12) and the lower bay (site 15) between August 1988 and December 1990. Species are listed according to taxon and native or introduced origin.

Throughout the year a relatively constant number of species continued to recruit in the lower bay (Figure 21), fluctuating around a mean of 24.2 species•mo^{-1} (s.d. = 4.59). Approximately three times as many native species recruited per month (mean = 18.08, s.d. = 4.54) than introduced (mean = 6.08, s.d. = 1.08). Comparisons of the mean percent of species per group (native or introduced) recruited per month demonstrate that a significantly higher proportion of the introduced species pool settled on a month to month basis ($t_{[22]}$= 4.22, p<.001; Table 7). In Isthmus Slough a strong reduction in recruitment occured during the winter months (Figure 22) and was reflected in increased variation in the number of species recruited per month for both native (mean = 1.08, s.d. = 1.51, n = 5) and introduced (mean = 4.25, s.d. = 3.49, n = 10) species (Table 7) resulting in significantly different settlement patterns between native and introduced species groups ($t_{[22]}$= 3.67, p<.01).

The mean settlement period (i.e., number of months in which recruitment occurred) for natives (mean = 5.9 mo, s.d. 3.9, n = 35) and non-natives (mean = 8.6 mo, s.d. = 4.8, n = 9) in the lower bay was not significantly different ($t_{[42]}$= 1.56, n.s.). Further examination of the patterns in Figure 20 suggests that there are three groups of native

Table 7. Percentage of Total, Native and Introduced Species Recruiting Per Month in the Lower and Upper (Isthmus Slough) Coos Bay Estuary.

	Number of Species Recruiting Per Month			Percent of Group		
SITE	Mean	S.D.	N	Mean	S.D.	CV
Lower Coos Bay						
Total Species	24.17	4.59	44			
Native Species	18.08	4.54	35	80.23	1.75	2.18
Introduced Species	6.08	1.08	9	97.16	1.78	1.83
Upper Coos Bay						
Total Species	5.33	3.75	15			
Native Species	1.08	1.51	5	39.79	22.07	55.47
Introduced Species	4.25	3.49	10	66.29	20.14	30.38

species with similar settlement periods; it also appears that the introduced species were divided into two groups whose settlement periods differ (Figure 23). In Isthmus Slough however, a significant difference between the mean length of recruitment period for natives (mean = 2.3 mo, s.d. = 1.9, n = 5) and non-natives (mean = 5.6 mo, s.d. = 2.1, n = 10) was detected ($t_{[13]} = 3.10$, $p < .05$).

Kite diagrams of settlement abundances (mean number of recruits•panel^{-1}•month^{-1}) of common native and all introduced species are presented in Figures 24 and 25. Of the introduced species present in the lower bay, the Japanese bryozoan, *Schizoporella unicornis* and tunicate, *Botrylloides violaceus*, exhibit strong settlement peaks between July and September in the lower bay (means of 22.5 and 41.1 recruits•panel^{-1}•mo^{-1}, respectively), although *S. unicornis* continues to settle throughout the year (Figures 26 and 27). The Atlantic tunicate *Botryllus schlosseri* peaks earlier in the summer between May and July (mean = 6.87 recruits•panel^{-1}•mo^{-1}) with occasional recruits into the fall (Figure 28). *Conopeum tenuissimum*, an Atlantic bryozoan, exhibits a bimodal pattern (Figure 29) in which peaks in July (mean = 0.81 recruits•panel^{-1}•mo^{-1}) and September (mean = 0.76 recruits•panel^{-1}•mo^{-1}) are approximately of equal height. May appears to be the beginning of the recruitment year for all four introduced species discussed here.

The cryptogenic bryozoans *Bowerbankia gracilis* and *Cryptosula pallasiana* exhibit broad settlement periods from January to September with no single discernible peak in abundance (Figures 30 and 31).

In contrast to the apparent overall pattern of settlement within the introduced species, or even the broad pattern of the cryptogenic species, there is no single pattern in the native group. *Alcyonidium polyoum*, *Distaplia occidentalis*, and *Balanus glandula* exhibit a late summer-fall group of peaks, while *Bugula pacifica*, *Cheilopora praelonga*, and spirorbids appear to form a cluster with settlement beginning in April-May and continuing until August (November for *C. praelonga*) (Figure 24; see individually Figures 32 to 37).

Serpulids appear to have a haphazard settlement, although if one takes the highest recruitment levels as an indication of pattern, the settlement peaks are in winter (February) and late summer (August, Figure 38). Similarly *Hippothoa hyalina* exhibits a bimodal pattern of recruitment with a peak in June and a second, shallower peak in October (Figure 39).

A Kruskal-Wallis two-way test of settlement abundance, in which species origin (native and introduced/cryptogenic) and time were the main effects, found significant differences between ranked settlement abundances based on species origin ($H = 8.70$, $df = 1$, $p < .05$, $n = 24$) with introduced species recruiting at higher densities. Neither the main effect of time (month) ($H = 3.346$, $df = 11$, n.s., $n = 24$) nor the interaction between origin and time was significant ($H = 13.74$, $df = 11$; Table 8).

Discussion

Elton's (1958) suggestion that species rich communities have the emergent property of *ecological resistance* to invasions and its inverse, that species poor communities are susceptible (invasible), lends itself to the examination of the native and introduced species in communities in the bays and estuaries of the Pacific Northwest. The pattern of decreasing native species diversity with distance from the ocean found in the encrusting communities of Coos Bay (Figures 14 and 15) and also found in the encrusting (Carlton 1979a, b) and soft substrate (Nichols and Pamatmat 1988) communities of San Francisco Bay suggests that these upper bay communities are susceptible to invasion by non-native species.

Carlton (1979b, 1992b) has reviewed three possible explanations for the apparent absence of native fauna in the brackish water portions of bays in the Pacific coast: 1) an absence of

Table 8. Non-parametric ANOVA Table Comparing Ranked Native and Introduced Recruitment Rates And Month.

Source	df	SS	F	Critical Value
Native/Introduced	1	240869	8.70 **	3.84
Month	11	92686	3.35	19.68
Interaction	11	380533	13.74	19.68
TOTAL	23	714089		

a diverse euryhaline native estuarine fauna due to a) physiological restrictions of marine derived stenohaline species (Jones 1940; Ricketts et al. 1985) and b) the lack of an evolved native euryhaline fauna; 2) the presence of a native estuarine fauna which was lost due to man's activities (habitat loss and degradation: dredging, pollution, tideland reclamation); and 3) the establishment of novel physical habitats (e.g., man-made pilings, docks, jetties) for which no native species were pre-adapted.

In Coos Bay 100% of the native encrusting γ-diversity is found in the marine dominated communities of the lower bay. All native species (84) are found within the first 4km of the Coos Bay entrance, 80 at the North Jetty (site 3), 48 at Fossil Point Jetty (site 4), and 66 at Point Adams Jetty (site 14; Figure 1). These sites consist of stable basalt and mudstone substrates of ages varying from about 100 yrs (construction of site 3 began in 1900 and was rebuilt in 1920, site 4 construction began in 1880; COE 1979) to about 20 yrs (site 14, 1974). Though less than 1.5km away, the native encrusting community at Point Adams is a subset (79%) of the communities found at the other two sites.

The pattern of decreasing native species richness along the estuarine transects of South Slough and Coos Bay (Figure 14) is highly correlated with physical changes in the range and values of temperature and salinity (Table 3, Figure 15). The calculated β-diversity (= 0.10; Figure 16) associated with the environmental gradient of annual salinity range supports the first of Carlton's (1979b) hypotheses, that the estuaries of the Pacific have a depauperate native fauna due to physiological constraints on the distributions of native marine species. Minimum salinity determines the distributions of many organisms (Ricketts et al. 1985) and may set the upper distribution limits within the bays and estuaries of the Pacific Northwest for many native, marine derived species (Carlton 1979b). The same argument of a depauperate native euryhaline fauna has been used by Wolff (1972) and Leppäkoski (1984) to explain the large numbers of successful northern European estuarine (or brackish water) invasions by introduced species.

It has been demonstrated that the larger bays of the Pacific coast are between 10,000 and 15,000 yrs old (Atwater et al. 1977). This has resulted in insufficient time to have evolved a diverse native euryhaline biota (Ricketts et al. 1985). The few euryhaline species appear to have evolved in smaller streams and river mouths. These include predominately mobile fauna such as isopods, amphipods, and mysid shrimp (Carlton 1979b). No native euryhaline encrusting organisms are known from Pacific coast estuaries (Smith and Carlton 1975; Carlton 1979b).

Human activities have drastically altered the bays and estuaries of the Pacific coast and may have caused large scale defaunation of native estuarine biotas. Conomos (1979), Nichols and Thompson (1985), and Nichols et al. (1986) have discussed the human mediated alterations to San Francisco Bay that include the diking and filling of tidal lands, increased sedimentation due to hydraulic mining, waste and sewage disposal, and diversion of freshwater inflow. It has been proposed that these large scale disturbance events occurred prior to the arrival of many successful introductions (Carlton 1979b).

Coos Bay has similarly been altered by human activities. More than 90% of the Coos Bay tidal lands have been filled, diked or reclaimed (Hoffnagle and Olson 1974). Logging and log rafting practices, which have been shown to drastically alter benthic communities either directly by physical disturbance and indirectly by pollution, resulted in increased siltation and pollution in Isthmus Slough (Case 1983). Pollution in the form of raw sewage, and industrial and agricultural chemicals has been demonstrated to alter community structure elsewhere (Moran and Grant 1989a, b) and has reduced water quality in Coos Bay historically (Hoffnagle and Olson 1974). Thus these human mediated alterations may have caused the large scale decimation of a native marine encrusting fauna, however no evidence supports the historical presence of such a community.

The establishment of novel man-made habitats is a result of the increasing urbanization of bays and estuaries (Conomos 1979). The destruction of native habitat, through the processes of dredging, diking, and filling (land reclamation) discussed above is accompanied by the installation of wharfs, pilings, and floating docks, and the establishment of jetties and sea walls. These structures have attributes that may be different from natural habitats. Pilings, wharfs, and docks provide large quantities of fixed wood which may not have been historically available (Carlton 1979b). Similarly floating docks provide permanently subtidal but near-surface habitats not comparable to any natural substrate. In general however, the appearance of large quantities of hard substrate in bays and estuaries where little previously existed should not preferentially favor an introduced over native encrusting fauna, except that the arrival of introduced fauna was associated predominately with these structures. Thus this hypothesis is rejected as the sole mechanism explaining the lack of a native biota in the estuaries of the Pacific northwest.

A fourth possibility, that the introduced species themselves may have competitively excluded native species from bays and estuaries is rejected as the sole cause of a lack of native fauna for several reasons. First, regional extinction due to competitive exclusion has been documented in closed systems of freshwater and terrestrial environments such as lakes and forests (see Baker and Stebbins 1965), yet has rarely been demonstrated in the open systems of the marine environment (Carlton 1976; Carlton et al. 1991). The vertical displacement of the native mud snail, *Cerithidea californica,* by the introduced mud snail, *Ilyanassa obsoleta* has been documented, but has not led to bay-wide extinction due to the presence of spatial refugia (Race 1982). Nor has the competitive dominant invading Red Sea mussel, *Brachidontes variabilis*, been able to eradicate the native Mediterranean mussel, *Mytilus minimus* from Isreali intertidal shores (Safriel and Sasson Frostig 1988).

Similarly, the benthic soft-bottom communities of the upper San Francisco Bay (San Pablo Bay, Suisan Bay, and Grizzley Bay) have recently been invaded by the Asian clam, *Potamocorbula amurensis* (Carlton et al. 1990). These communities, comprised largely of introduced species (Nichols and Pamatmat 1988), appear to be in the process of competitive displacement (not replacement) due to ecosystem alterations by *P. amurensis* (Nichols et al. 1990). The interactions between the native Hawaiian stomatopod *Pseudosquilla ciliata* and the introduced species *Gonodactylus falcatus* and *G. hendersoni* (Kinzie1968, 1984) in coral heads has been widely cited as an example of native species replacement by an introduced species. Yet this too is an example of a native species being displaced by an introduced species from a specific habitat type, and has not resulted in the regional extinction of the native species (Kinzie 1968).

These are striking examples of the competitive abilities of invaders, yet in spite of the "remarkable" alterations neither case has resulted in the bay-wide eradication of a species. Furthermore one would expect that due to random processes, some bays and estuaries would retain relict populations of native species. From this perspective it is improbable that competitive displacement alone explains the apparent lack of a native estuarine fauna.

The occasional settlement of native species in upper bay (Isthmus Slough) communities is confined to three species (*Hippothoa hyalina*, *Smittoidea prolifica*, and *Mytilus trossulus*) which, with the exception of *S. prolifica*, settle in the lower bay during the same period (Figure 20). *Hippothoa hyalina* and *S. prolifica* are transient members of the upper bay community, rarely covering less than 1% of area. The mussels, abundant members of the community in Isthmus Slough, (up to 90% of primary space, *pers. obs.*), have been identified as the native *M. trossulus* by Geller using mtDNA analyses (Geller et al. 1993), although the morphologically similar *M. galloprovincialis* has been consistently documented in Japanese ballast water released within 1km of this site (Carlton and Geller 1993; Geller et al. 1993) and is known from Asian waters (Lee and Morton 1985).

The linear increase in the introduced species percentage with distance from the ocean (and therefore, with the correlated factors of temperature and salinity; see Figures 13 and 17) supports Elton's hypothesis of community susceptibility with decreasing native richness. Fox and Fox (1986, Figure 5) present data from two studies of shrublands of Western Australia (Abbott 1980; Aplin et al. 1983a, b) which relate the introduced percentage of the shrubland community with native species richness. These data demonstrate highly significant negative exponential decay curves. Fox and Fox (1986) concluded that species richness was significantly negatively correlated with invasion success. The Coos Bay transect (Figure 18) exhibits a similar exponential decay curve.

While the pooled regression of percentage of introduced species in the community on native species richness in both Coos Bay and South Slough transects taken together is highly significant, the South Slough transect has more than the expected percent introduced species at high native species richness (Figure 18). The Point Adams Jetty (site 14) and Charleston Boat Basin (site 15), have diverse native faunas (66 and 31 species, respectively) as well as high numbers of introduced species (8 and 11). Both sites are of recent construction (approximately 20 yrs) and the Charleston Boat Basin is heavily affected by human activity (pollution, fuel and waste discharge, fish processing plant discharge). Disturbance has been linked to invasion success in many systems (Ewel 1986; Moyle 1986) and has been proposed to be the primary determinant of invasion success in terrestrial systems (Fox and Fox 1986) through alteration of the community resource base.

In encrusting systems, space is often the limiting resource (Stebbing 1973; Jackson 1977; Osman 1977; Keough 1983, 1984a, b). The increased levels of disturbance due to pollution and mechanical abrasion (boat impacts, dock and hull cleaning) will act to increase open space. The Charleston Boat Basin has a constant flow of small craft and moderate sized fishing vessels, many of which move from port to port along the Pacific coast with the potential to act as secondary transport mechanisms (Table

1, mechanism IV). This boat traffic and the proximity of the oyster grounds in South Slough with their introduced fauna combine to increase the pool of introduced species, while the level of disturbance increases the likelihood that space is available for settlement. It may be for these reasons that the Charleston Boat Basin (site 15) and the adjacent Point Adams Jetty (site 14; Figure 1) have elevated numbers of invaders despite the presence of high native diversity.

The recent invasions of Isthmus Slough (and subsequent spread of these species) demonstrate the apparent continued susceptibility of the community to invasion (Figure 13). At present these upper bay communities have 18 species covering more than 80% of the substrate during the period between March and November. Each of the observed recent invasion events occurred during the summer when space was at a premium and settlement by existing species is high (Figure 22), and yet two of the six invasions have resulted in the insertion of new species into the community with no apparent alteration of existing community patterns (*pers. obs.*). Three species (*Schizoporella unicornis, Botryllus schlosseri,* and *Diplosoma mitsakurii*) and possibly a fourth (*Alcyonidium sp.*) have so far failed to establish in the upper bay communities.

The percentage of introduced species that succeed or fail is not known (Simberloff 1981). Di Castri (1990) has suggested rough estimates based on previous literature: for every a) 100 species transported to an environment, b) 10 will colonize, c) 5 will establish reproductive populations and d) fewer than 3 will spread and expand their range. Of the six species that colonized Isthmus Slough initially (b), two (33%) successfully established populations and spread (c and d). This agrees surprisingly well with di Castri's (1990) estimates in which for every 10 species that colonized, three (30%) would become established and spread.

The recruitment periods for introduced species in Coos Bay are different from those of native species. A higher proportion of the introduced species pool settles in any given month than of the native species pool. Similarly introduced species settle in significantly higher numbers (number of recruits•panel^{-1}•mo^{-1}). Sutherland (1977b, 1978) suggested that three life history attributes of "ideal" invaders exist. His definition of an invader was a species that is able to insert itself into an assemblage where it is not presently found. The three attributes are: a high recruitment rate; the ability to settle on occupied substrate (on top of a competitor); and a long lifespan. Of these three attributes Sutherland (1977b) suggested that two are sufficient for a species to become a competitive dominant in the system.

In this chapter the ecological attributes of species have been subsumed under the grouping of historical status (native or introduced). These broad categories cross phyla and, for non-natives, biogeographic origin. To treat native species as a unit is not without precedent (Tyser and Worley 1992). The action of diffuse coevolution in structuring community patterns (Fox 1988; Dunning et al. 1992) has been poorly studied but is increasingly entering the arena of ecological theory (Gilpin and Hanski 1991; Rummel and Roughgarden 1983, 1985; Wilson 1992). Native species by definition have evolved in the environments of the Pacific Northwest and, presumably, with one another. The treatment of non-native species as a group without regard to biogeographic origin may make an erroneous assumption, yet it is a conservative one for purposes of statistical comparison.

There are significant differences between these two groups. Introduced species tend to dominate the upper reaches of Coos Bay in areas of seasonal salinity fluctuations, possibly a consequence of native species being restricted to marine habitats. In the lower bay introduced species tend to recruit over long periods (recruit for more months of the year) at higher mean monthly densities than natives (Figure 20, Figure 23 and 25). Although several native species settle at high densities and for long periods of time (Figure 20, Figure 24), a greater number have limited settlement periods (Figure 23).

Thus as space becomes available due to the disturbances mentioned above, non-native species have a higher probability of recruitment and subsequent establishment than natives.

In both computer simulations and empirical investigations, a species' success in terms of space occupied is a function of both its local competitive abilities and its dispersal capabilities (Sutherland 1977a, b, 1978; Sutherland and Karlson 1977). Species with the attributes of good competitive abilities and dispersal abilities would be expected to be space dominants in a majority of spatial patches. These "super-species" (Hanski 1982) do exist but that they are prevented from dominating entire landscapes by the stochastic processes of disturbance and recruitment (Chesson 1985; Chesson and Case 1986; Chesson and Ellner 1989; Chesson and Huntly 1989).

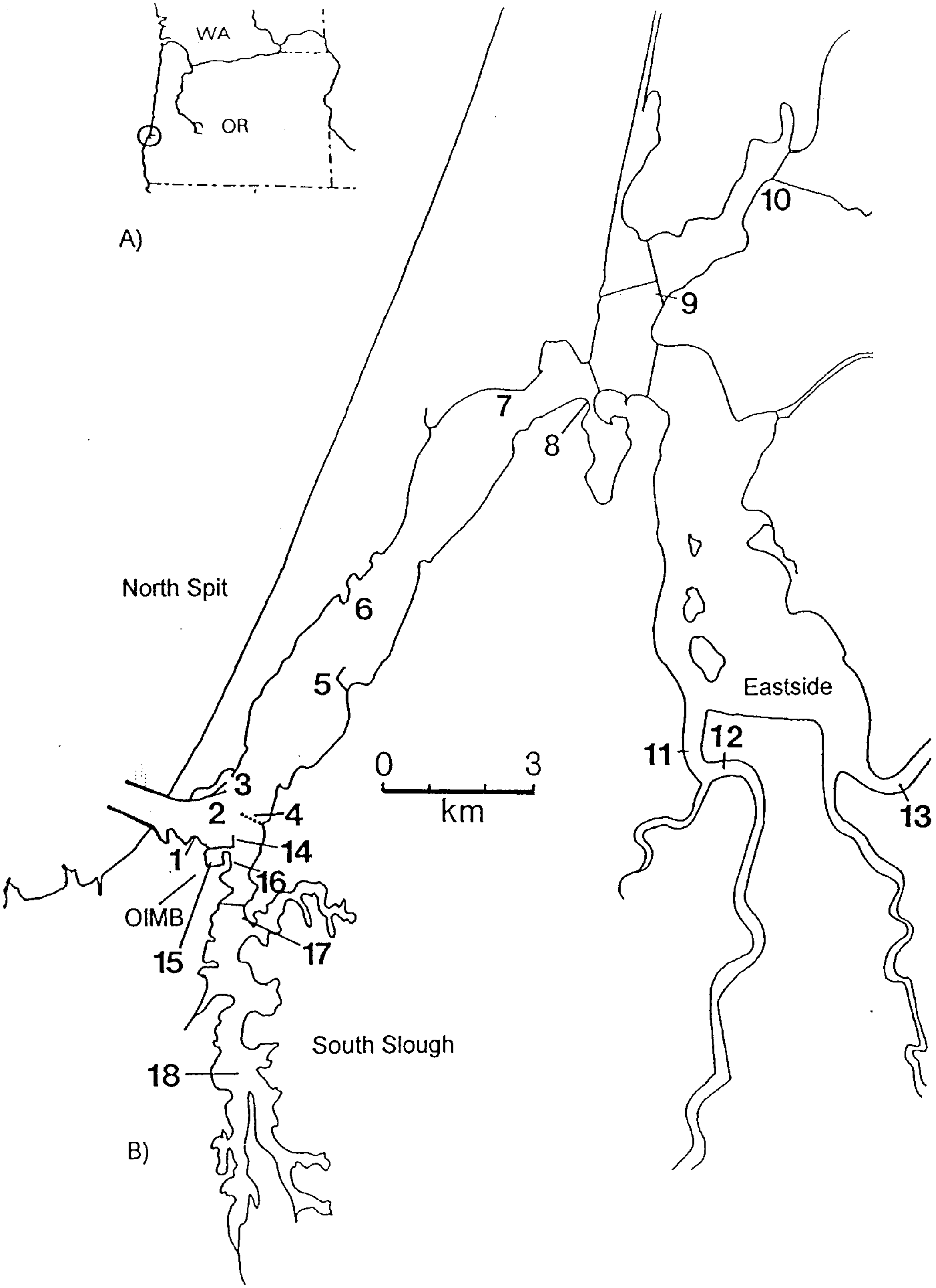


Figure 1. Inset Map (A) of Oregon with Coos Bay Circled. Map of Coos Bay (B) with Sample Stations and Major Geographical Locations. Sample Station Codes Follow Table 2. Scale Equals 3 km.

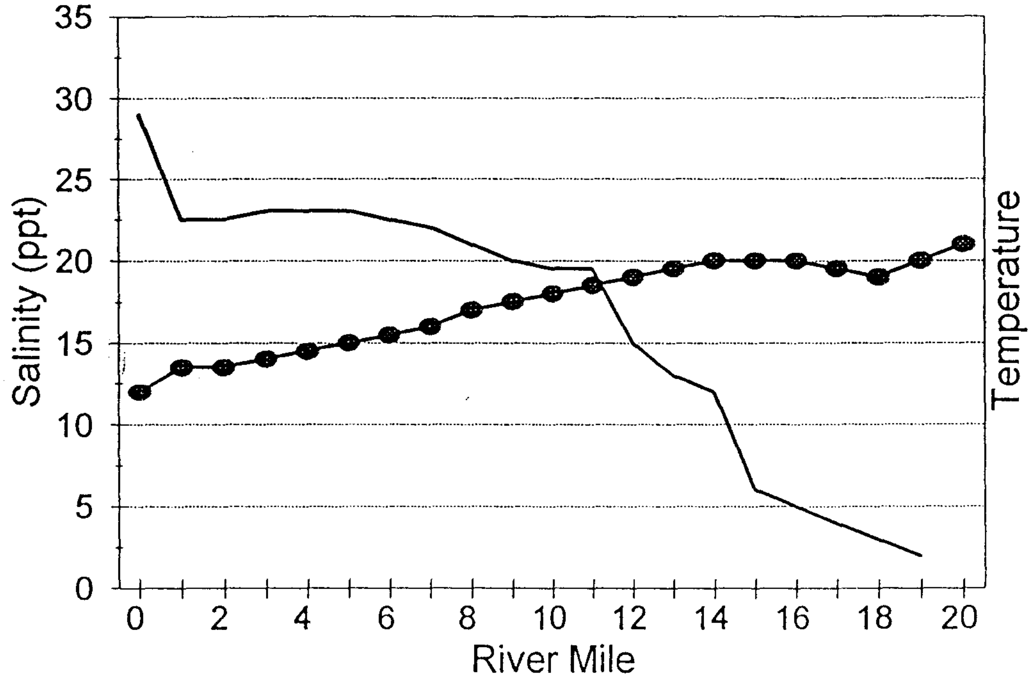
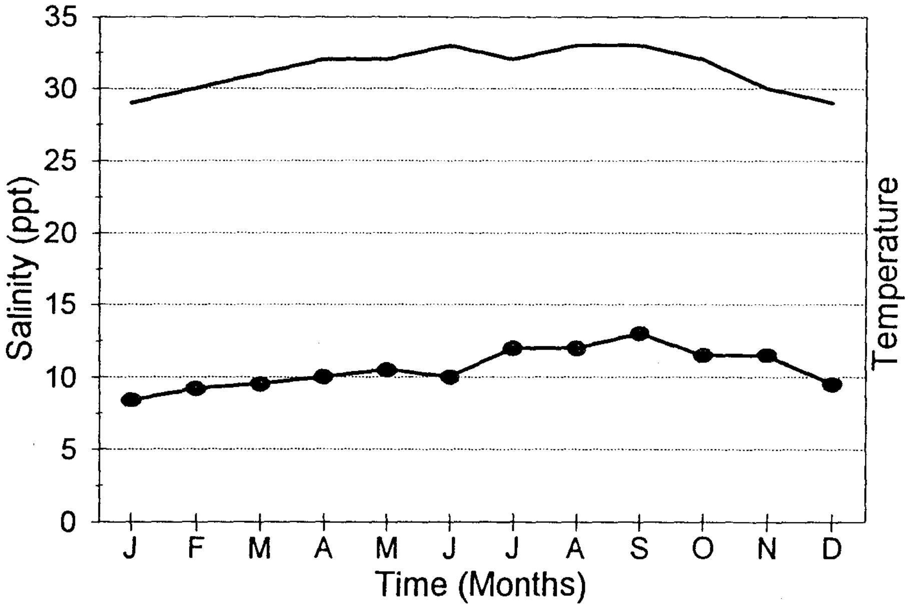


Figure 2. Average Temperature and Salinity Measurements Along the Coos Bay Transect During July 1989. Solid Line Represents Salinity (ppt) and the Line with Closed Circles Represents Temperature (°C).

Figure 3. Physical Measurements from the Ocean Station (Site 2): a) Average Temperature and Salinity Data by Month (Solid Line Represents Salinity and the Line with Closed Circles Represents Temperature °C); b) Hydroclimagraph of Site 2, January (1) and December (12) are Labelled.

A)


35
30
25
20
15
10
5
0
Salinity (ppt)
Temperature
J
F
M
A
M
J
J
A
S
O
N
D
Time (Months)

B)

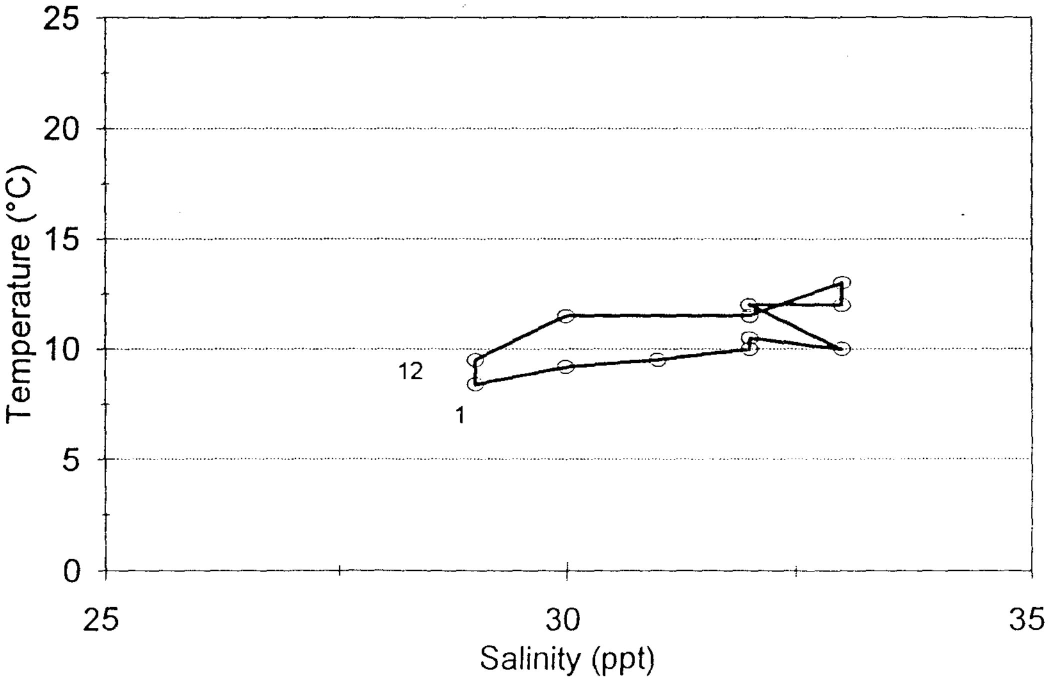
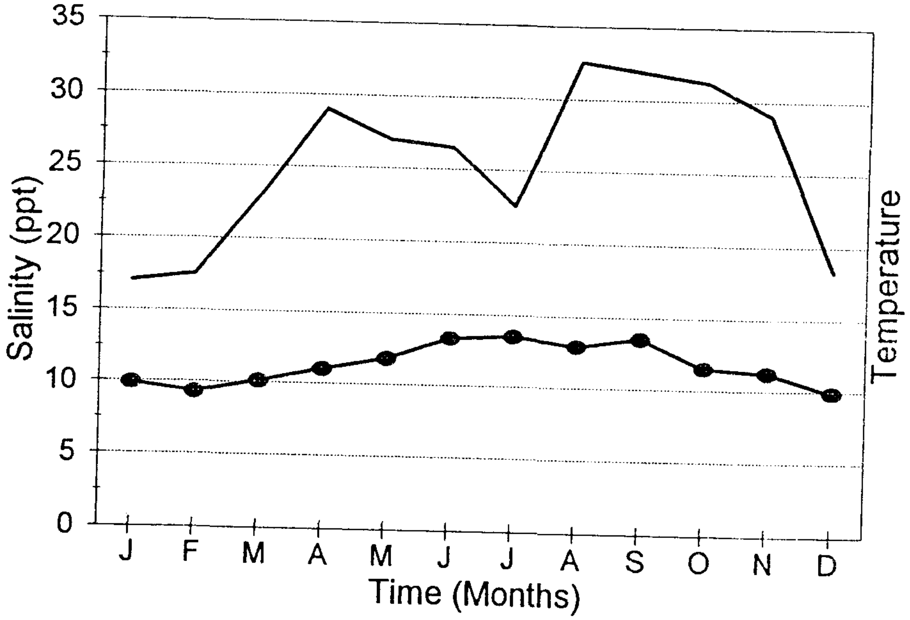

25
20
15
10
5
0
Temperature (°C)
12
1
25
30
35
Salinity (ppt)

Figure 4. Physical Measurements from the Charleston Boat Basin (Site 15): a) Average Temperature and Salinity Data by Month (Solid Line Represents Salinity and the Line with Closed Circles Represents Temperature °C); b) Hydroclimagraph of Site 15, January (1) and December (12) are Labelled.

A)


35
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0
Salinity (ppt)
Temperature
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F
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J
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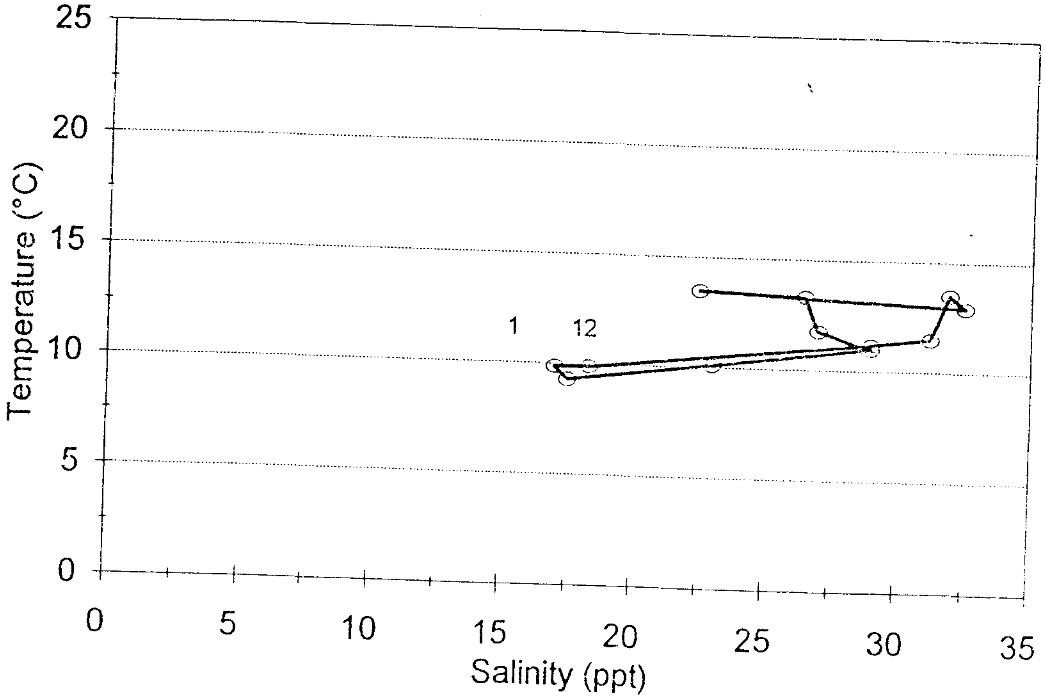
D
Time (Months)

B)


25
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15
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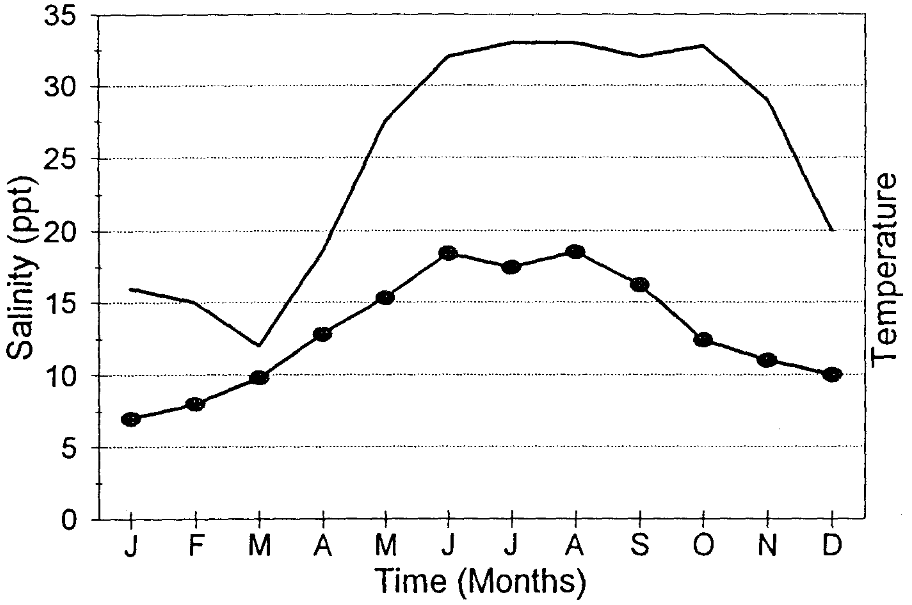
5
0
Temperature (°C)
1
12
0
5
10
15
20
25
30
35
Salinity (ppt)

Figure 5. Physical Measurements from the South Slough (Site 18):
a) Average Temperature and Salinity Data by Month (Solid Line Represents Salinity and the Line with Closed Circles Represents Temperature °C); b) Hydroclimagraph of Site 18, January (1) and December (12) are Labelled.

A)


35
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5
0
Salinity (ppt)
Temperature
J
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J
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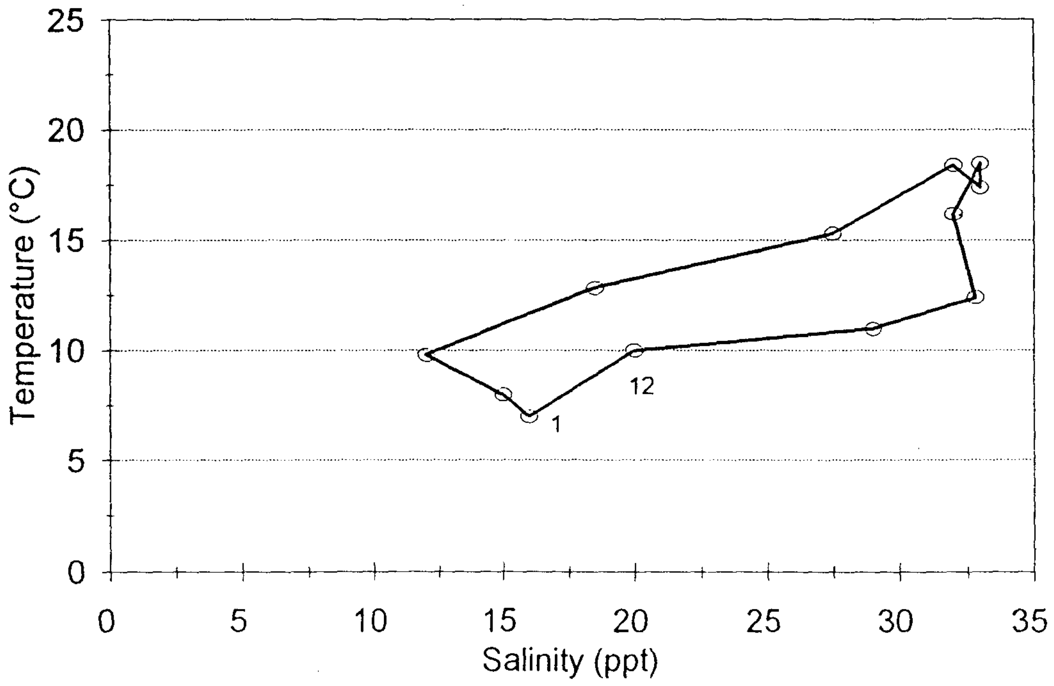
D
Time (Months)

B)


25
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Temperature (°C)
12
1
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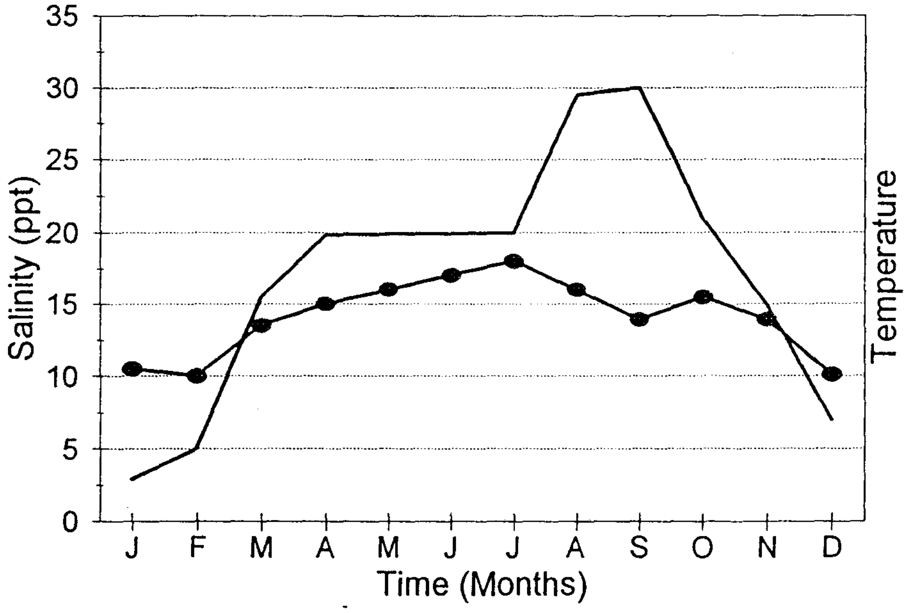
20
25
30
35
Salinity (ppt)

Figure 6. Physical Measurements from the Haynes Inlet (Site 9): a) Average Temperature and Salinity Data by Month (Solid Line Represents Salinity and the Line with Closed Circles Represents Temperature °C); b) Hydroclimagraph of Site 9, January (1) and December (12) are Labelled.

A)


35
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Salinity (ppt)
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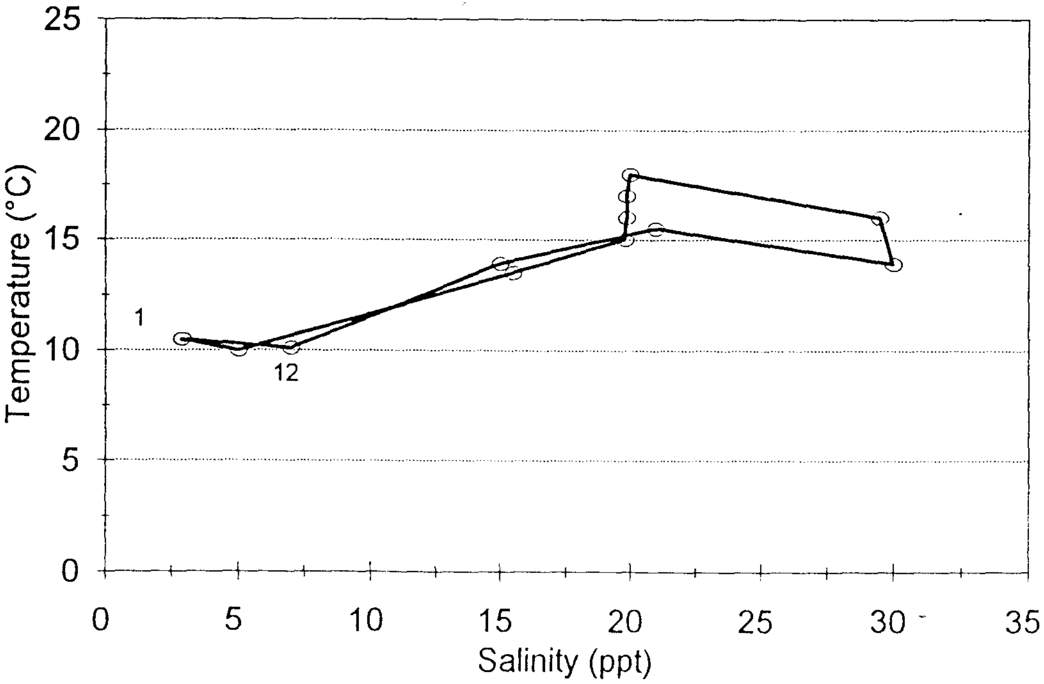
Time (Months)

B)


25
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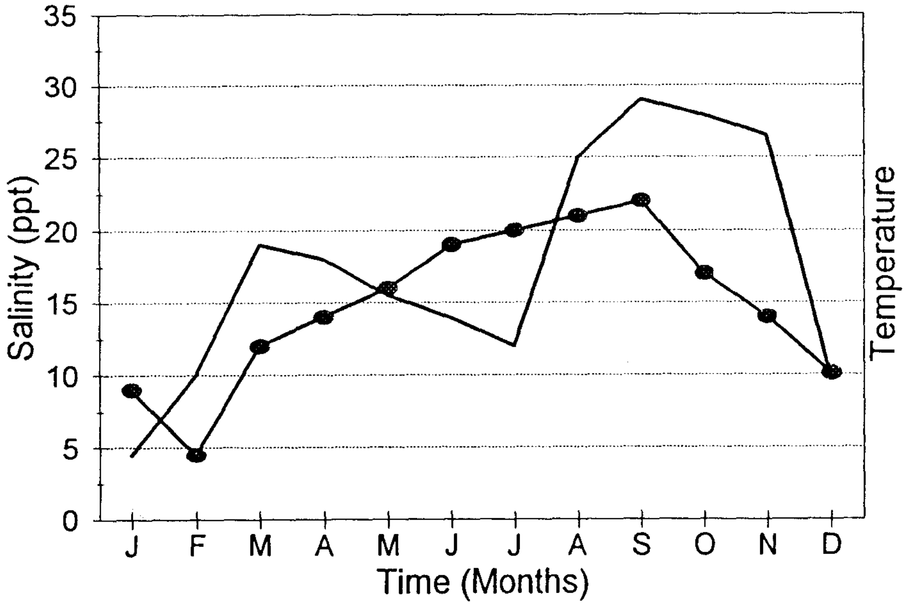
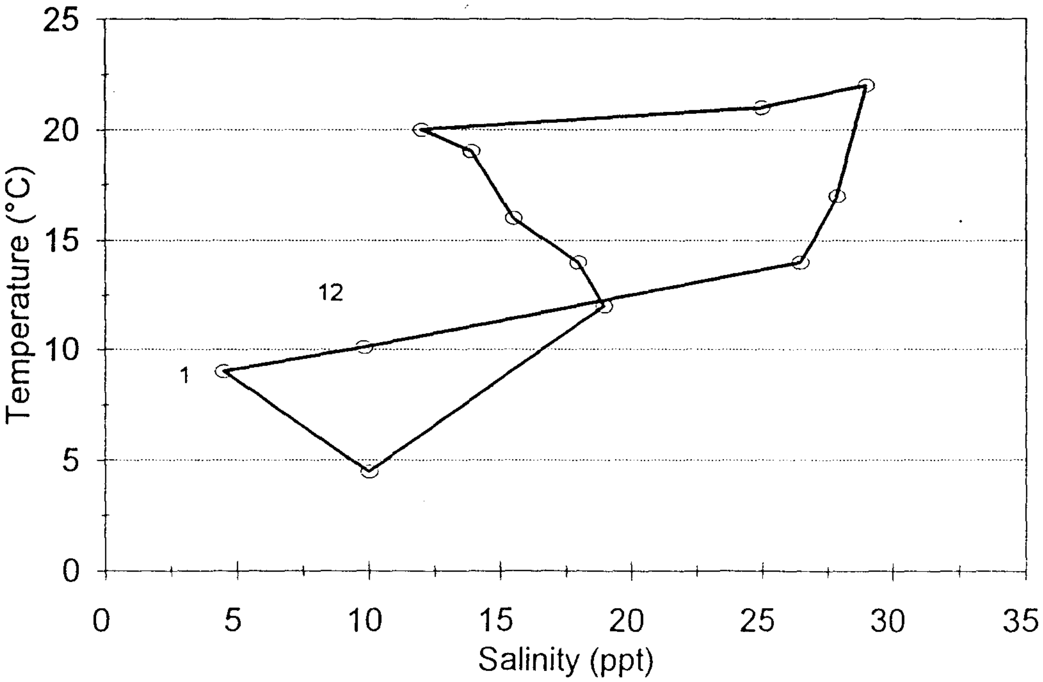
0
Temperature (°C)
1
12
0
5
10
15
20
25
30
35
Salinity (ppt)

Figure 7. Physical Measurements from the Isthmus Slough (Site 12): a) Average Temperature and Salinity Data by Month (Solid Line Represents Salinity and the Line with Closed Circles Represents Temperature °C); b) Hydroclimagraph of Site 12, January (1) and December (12) are Labelled.

A)


35
30
25
20
15
10
5
0
Salinity (ppt)
Temperature
J
F
M
A
M
J
J
A
S
O
N
D
Time (Months)

B)


25
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Temperature (°C)
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1
0
5
10
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20
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30
35
Salinity (ppt)

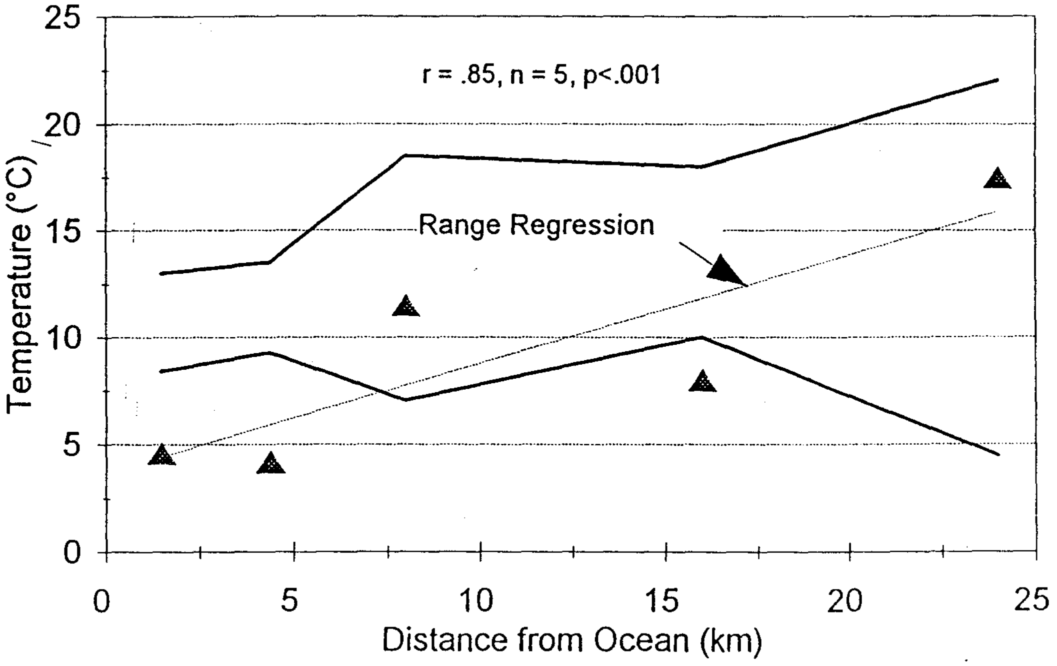


Figure 8. Maximum and Minimum Annual Temperature Values (Solid Lines) and Temperature Range (Triangles and Dotted Regression Line) as a Function of Distance from Ocean. (temperature range = 0.51•distance + 3.66).

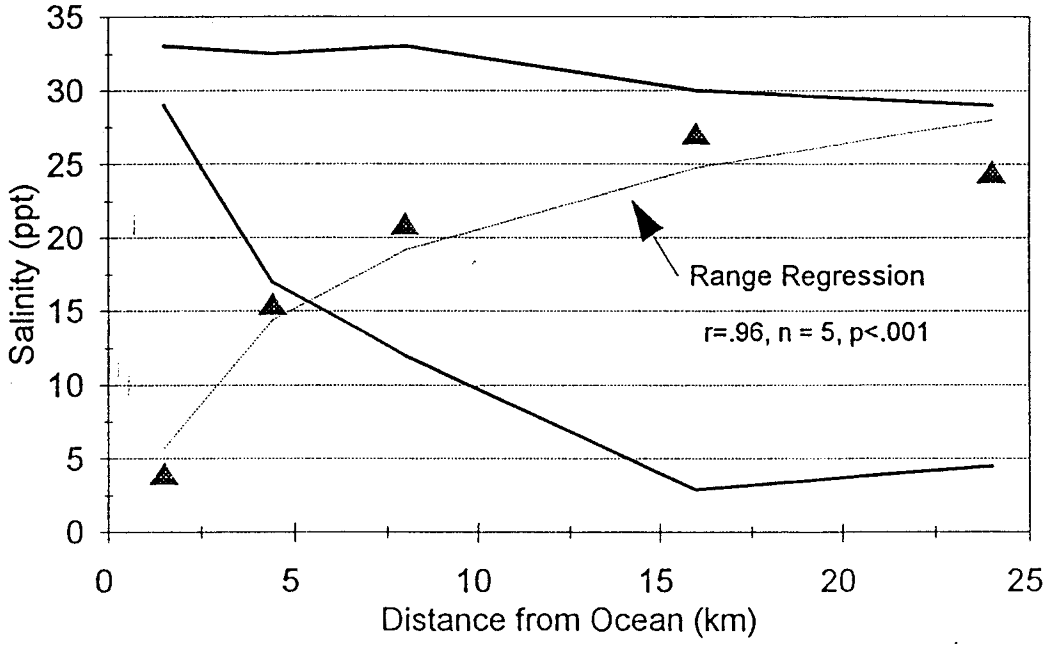


Figure 9. Maximum and Minimum Annual Salinity Values (Solid Lines) and Annual Salinity Range (Triangles and Dotted Regression Line) as a Function of Distance from Ocean. (salinity range = $8.04 \bullet e^{(\text{distance})} + 2.48$).

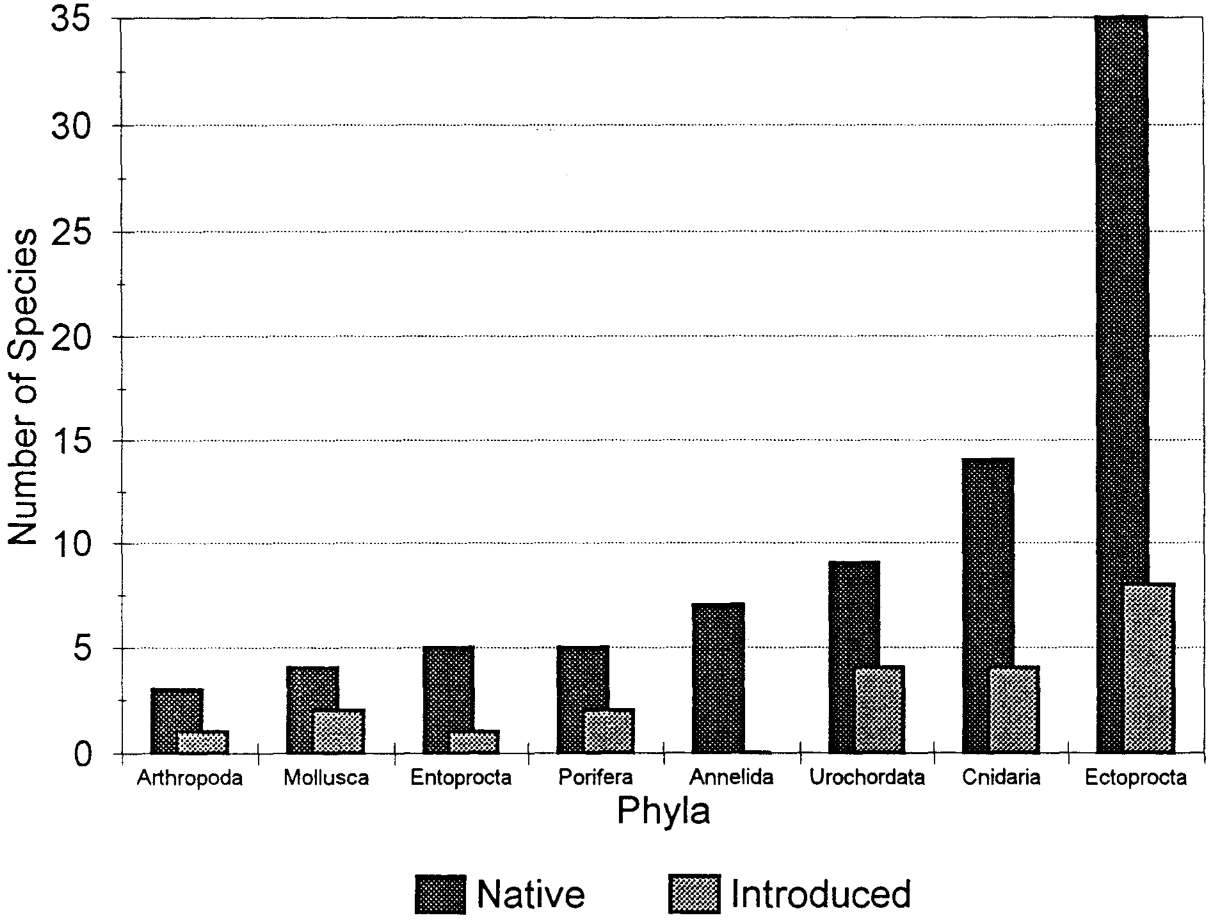
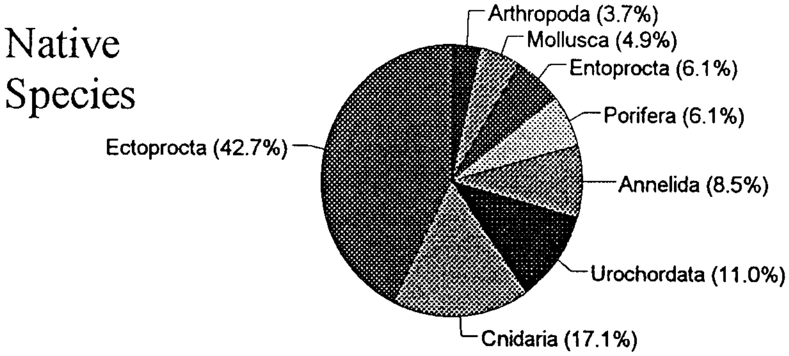


Figure 10. Frequency of Native and Introduced (and Cryptogenic) Encrusting Species by Taxa.


Native Species

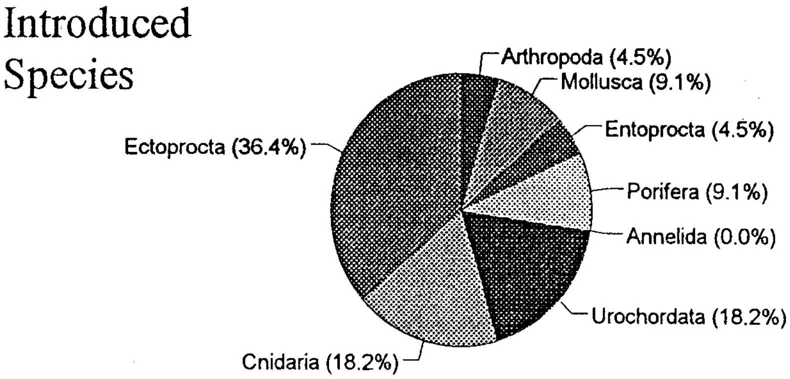

Introduced Species

Figure 11. Pie Diagrams of Native and Introduced (and Cryptogenic) Encrusting Organisms by Taxa.

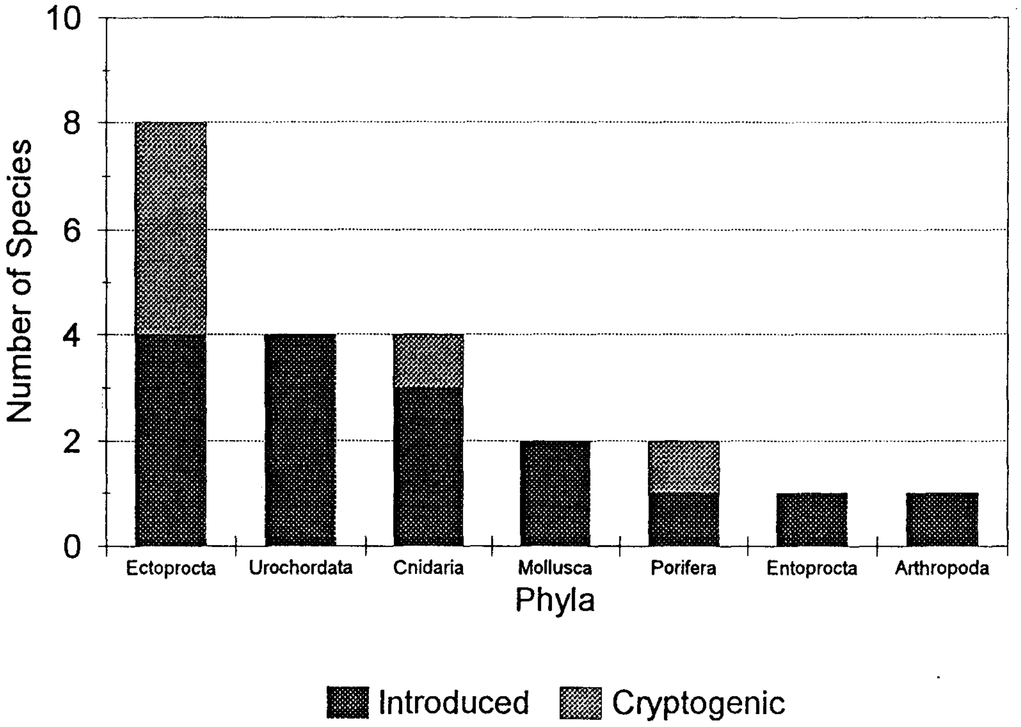


Figure 12. Frequency of Introduced and Cryptogenic Species By Taxa.

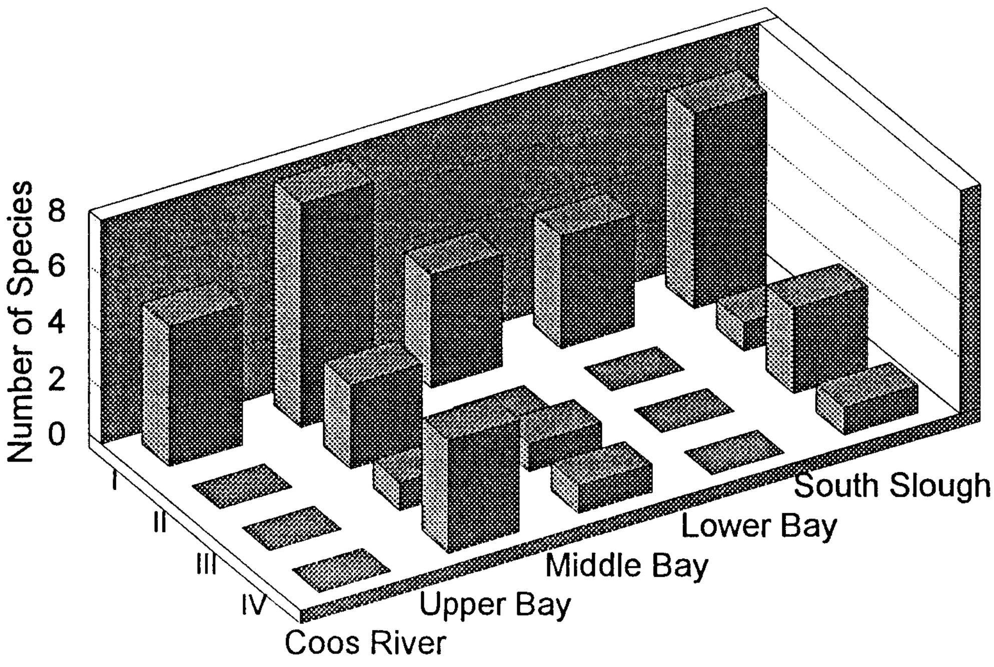


Figure 13. Introduced Species Abundances in Five Regions of Coos Bay According to Their Affinities with Specific Introduction Mechanisms. Mechanisms: I, Wooden Hulled Vessel Fouling; II, Atlantic Oyster Culture; III, Japanese Oyster Culture; IV, Modern Introduction Mechanisms (See Text).

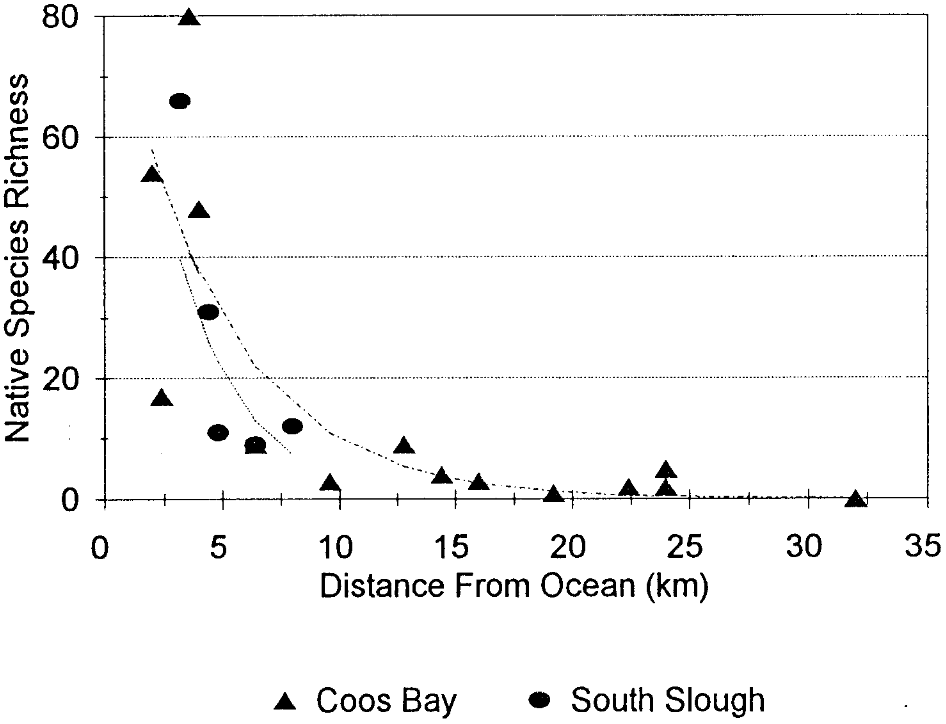


Figure 14. Native Species Richness Correlated with Distance (km) from the Ocean (pooled $r^2 = 0.65$, $n = 20$).
$\ln(\text{Native Spp Richness}) = -0.2(\text{km from Ocean}) + 3.65$.

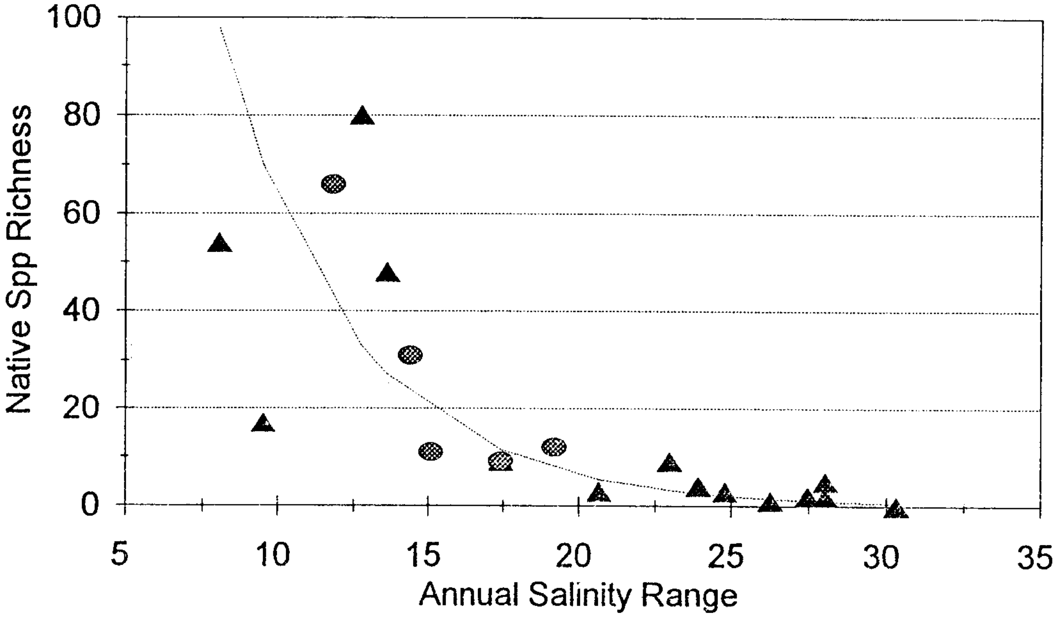


Figure 15. Native Species Richness as a Function of Annual Salinity Range at Each Site (pooled $r^2 = 0.64$, $n = 20$).
ln(Native Spp Richness) = -0.2(Salinity Range) + 6.43.

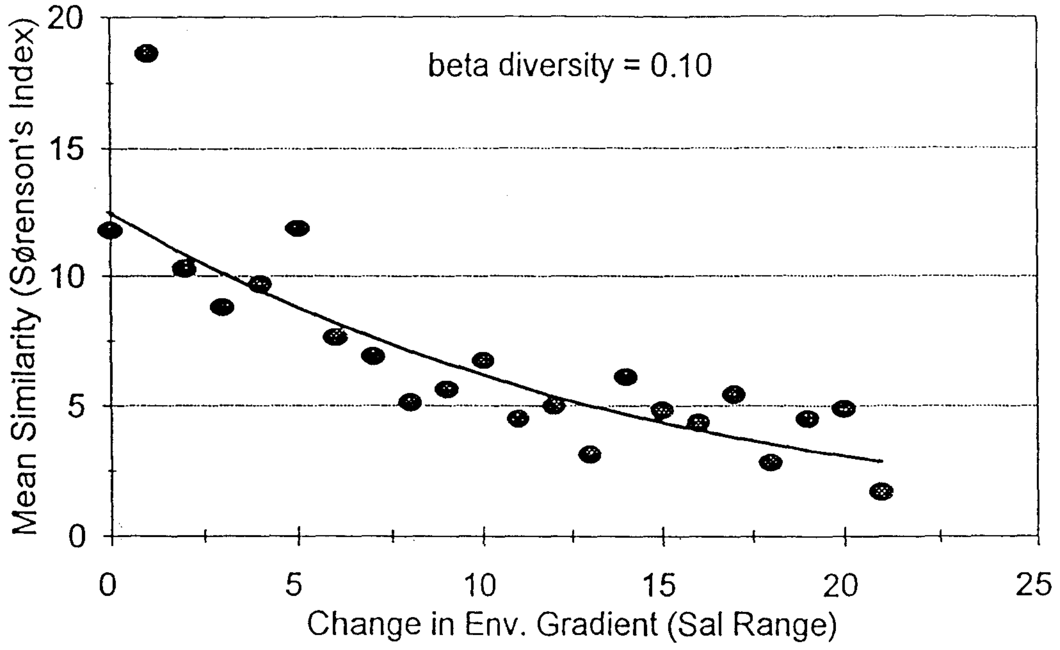


Figure 16. Coos Bay Encrusting Community β-Diversity. Sørensen's Between-Site Similarity as a Function of the Difference Between Site Specific Annual Salinity Range.

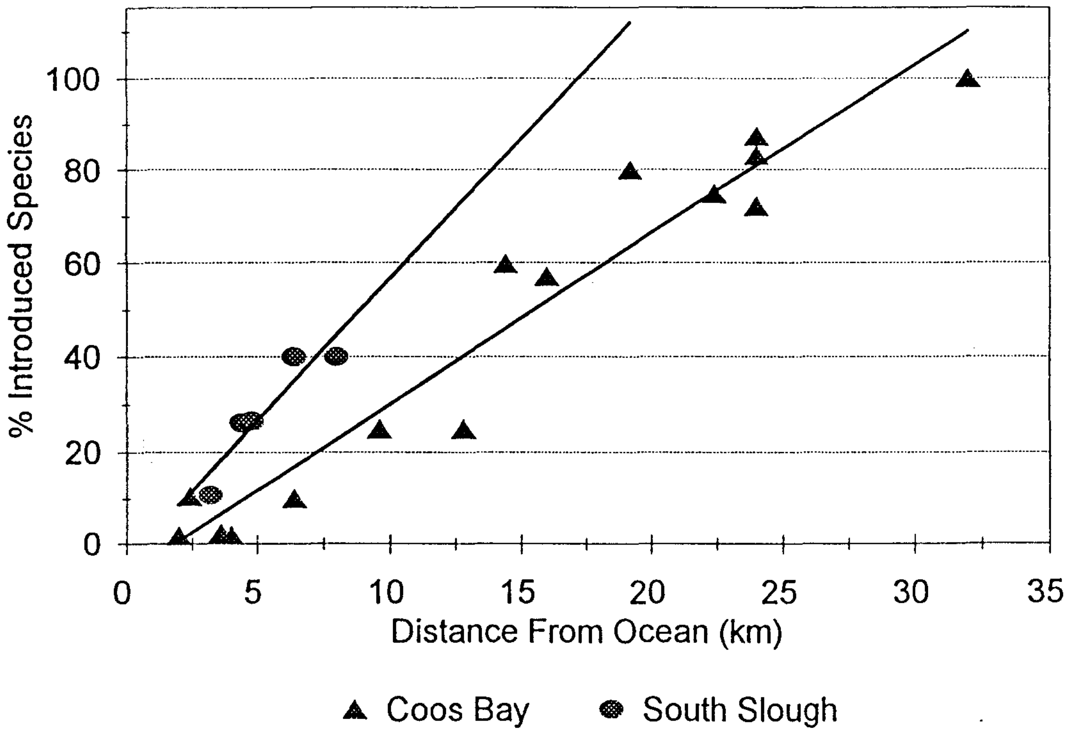


Figure 17. Introduced Percentage of the Community as a Function of Distance From the Ocean (pooled $r^2 = 0.95$, $n = 20$).
(Introduced Spp %) = 3.32(km from Ocean) + 1.19.

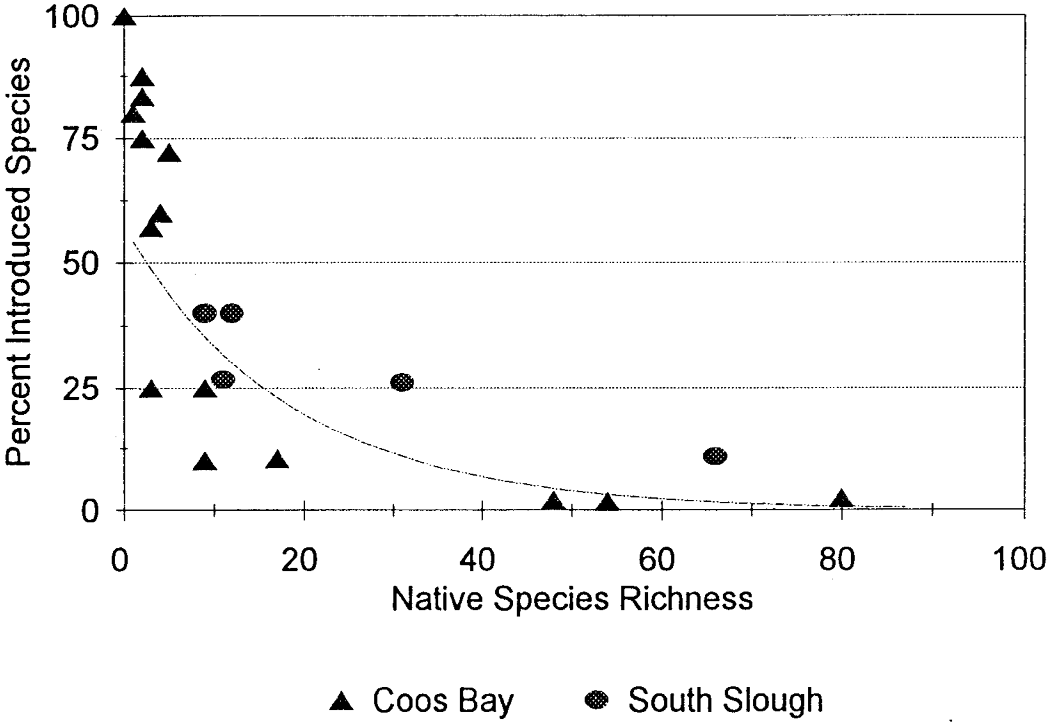


Figure 18. Introduced Percentage of the Community as a Function of Native Species Richness (pooled $r^2 = 0.70$, $n = 20$).
ln(Introduced Spp %) = -0.04(Native Spp Richness) + 4.03.

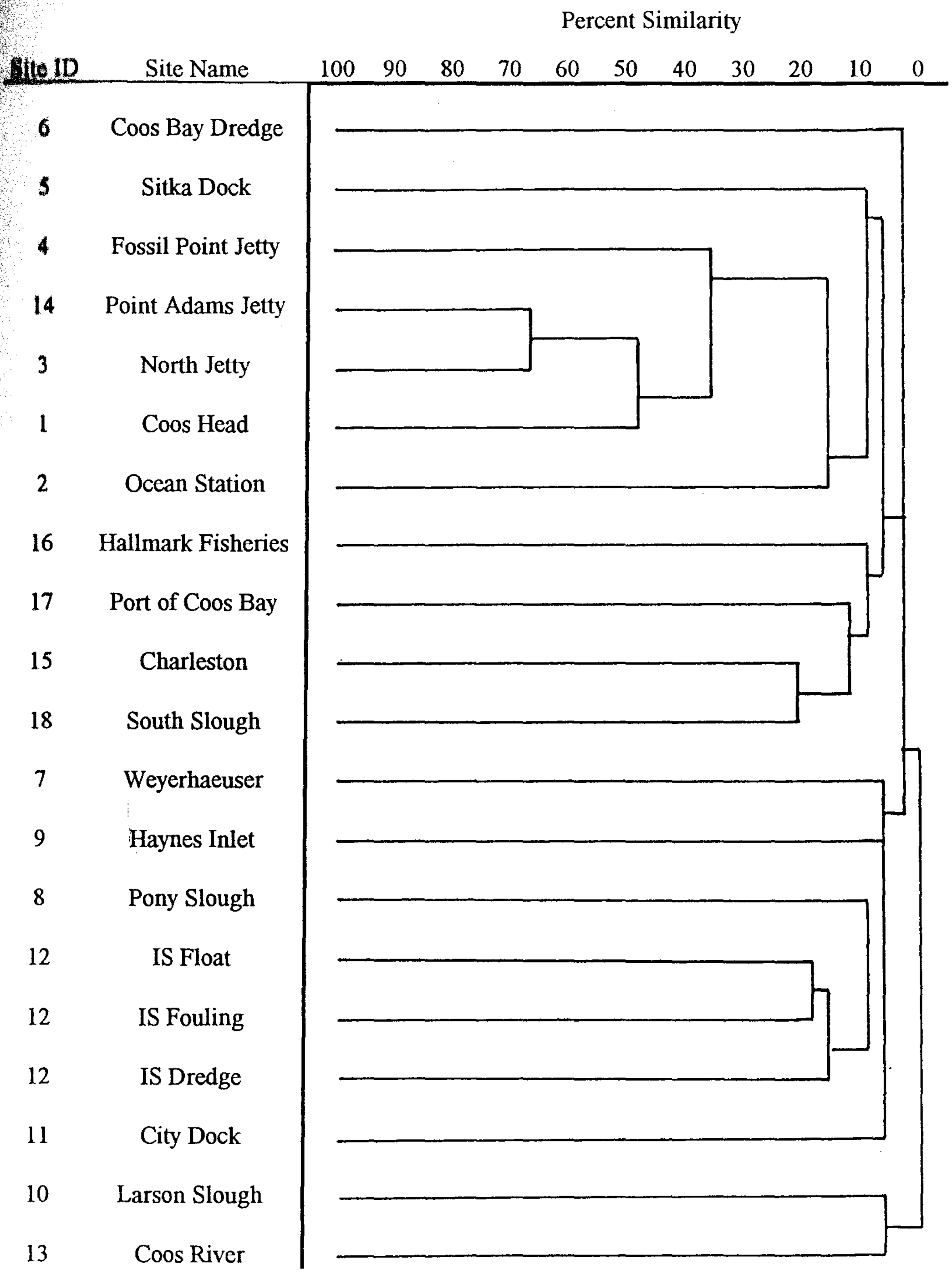
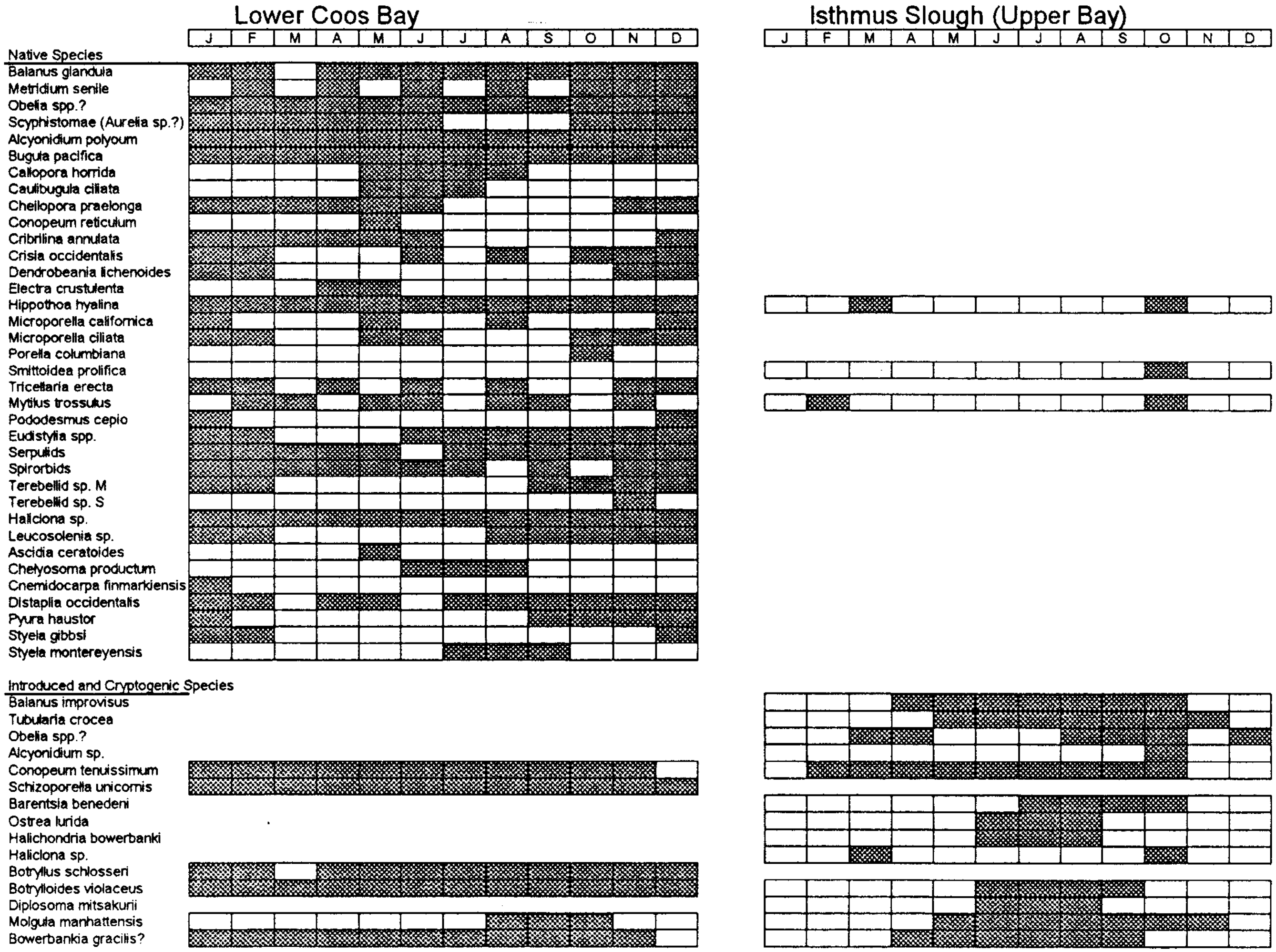


Figure 19. Similarity Dendrogram Based on Sørensen's Similarity Measure Comparing Species Presence/Absence Data for all Sites in Coos Bay. Site Codes Follow Table 1. Dendrogram was Constructed Using UPGMA Clustering Technique.

Figure 20. Monthly Recruitment Phenologies of Native and Introduced Encrusting Organisms in Lower Coos Bay and Isthmus Slough (Upper Bay). Species Recruitment During the Study is Represented by Filled Boxes.


Lower Coos Bay
Isthmus Slough (Upper Bay)
J
F
M
A
M
J
J
A
S
O
N
D
Native Species
Balanus glandula
Metridium senile
Obelia spp.?
Scyphistomae (Aurelia sp.?)
Alcyonidium polyoum
Bugula pacifica
Callopora horrida
Caulibugula ciliata
Cheilopora praelonga
Conopeum reticulum
Cribrilina annulata
Crisia occidentalis
Dendrobeania lichenoides
Electra crustulenta
Hippothoa hyalina
Microporella californica
Microporella ciliata
Porella columbiana
Smittoidea prolifica
Tricellaria erecta
Mytilus trossulus
Pododesmus cepio
Eudistylia spp.
Serpulids
Spirorbids
Terebellid sp. M
Terebellid sp. S
Haliclona sp.
Leucosolenia sp.
Ascidia ceratoides
Chelyosoma productum
Cnemidocarpa finmarkiensis
Distaplia occidentalis
Pyura haustor
Styela gibbsi
Styela montereyensis
Introduced and Cryptogenic Species
Balanus improvisus
Tubularia crocea
Obelia spp.?
Alcyonidium sp.
Conopeum tenuissimum
Schizoporella unicornis
Barentsia benedeni
Ostrea lurida
Halichondria bowerbanki
Haliclona sp.
Botryllus schlosseri
Botrylloides violaceus
Diplosoma mitsakurii
Molgula manhattensis
Bowerbankia gracilis?

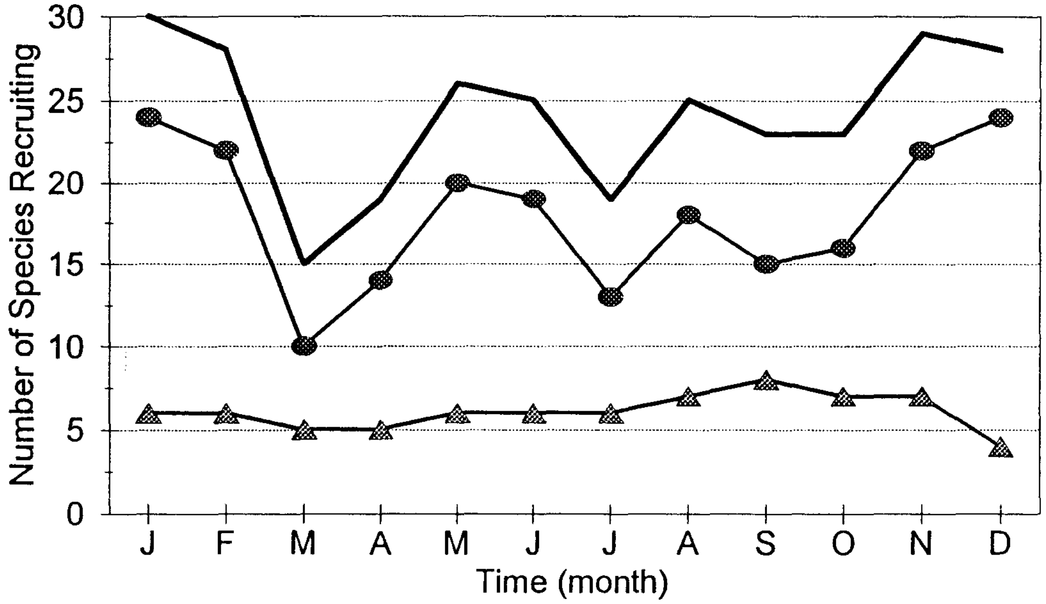


Figure 21. Average Number of Species Settling per Month in the Lower Bay Between August 1988 and December 1990. Solid Line Represents all Species, Triangles Represent Introduced Species and Circles Represent Native Species.

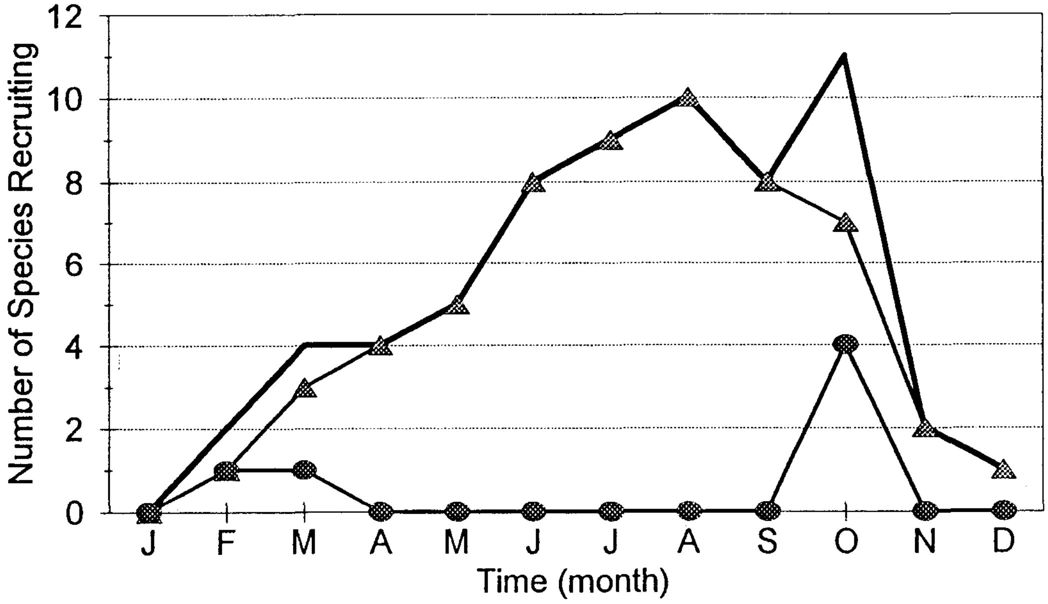


Figure 22. Average Number of Species Settling per Month in the Upper Bay Between August 1988 and December 1990. Solid Line Represents all Species, Triangles Represent Introduced Species and Circles Represent Native Species.

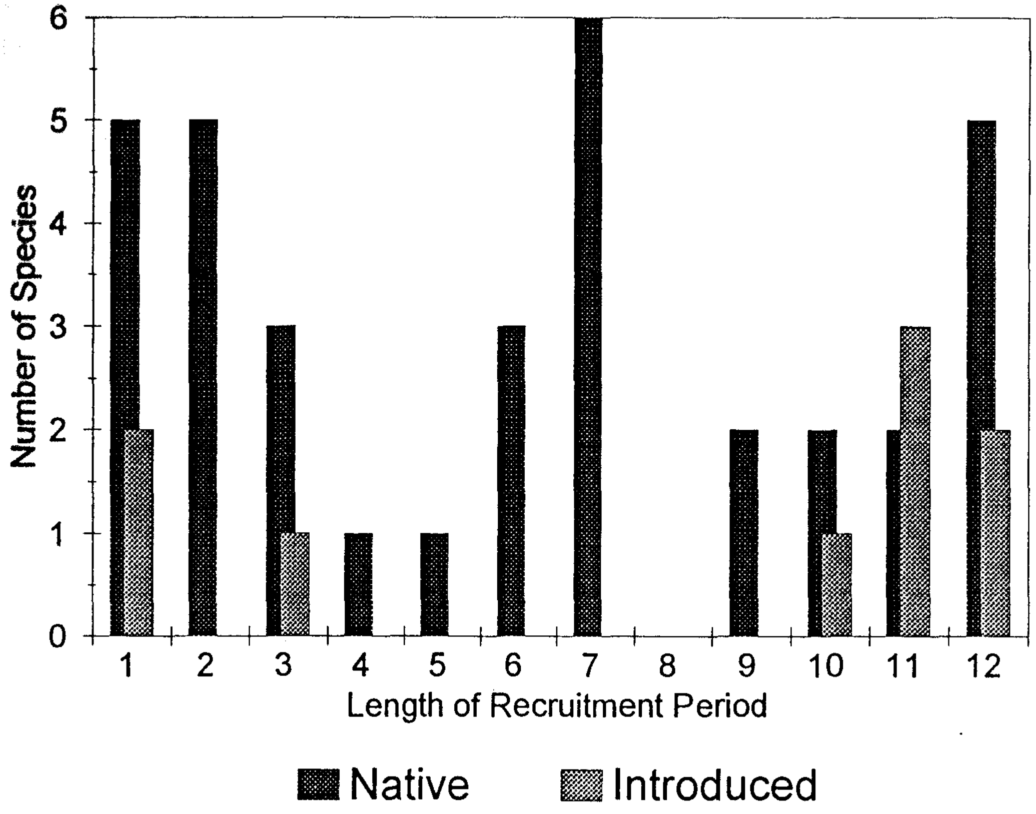


Figure 23. Frequency of the Length of the Recruitment Period for Native and Introduced Species.

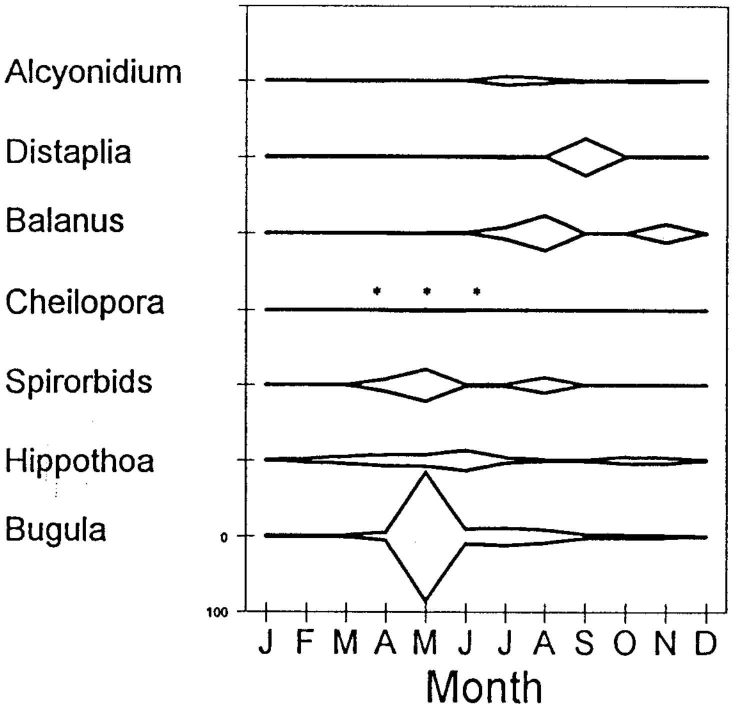


Figure 24. Kite Diagram of Average Recruitment Rates (Recruits•Panel^{-1}•Mo^{-1}) for Native Species in the Lower Bay. All Species are Represented at the Same Scale, Asterisks Represent Recruitment at Low Densities.

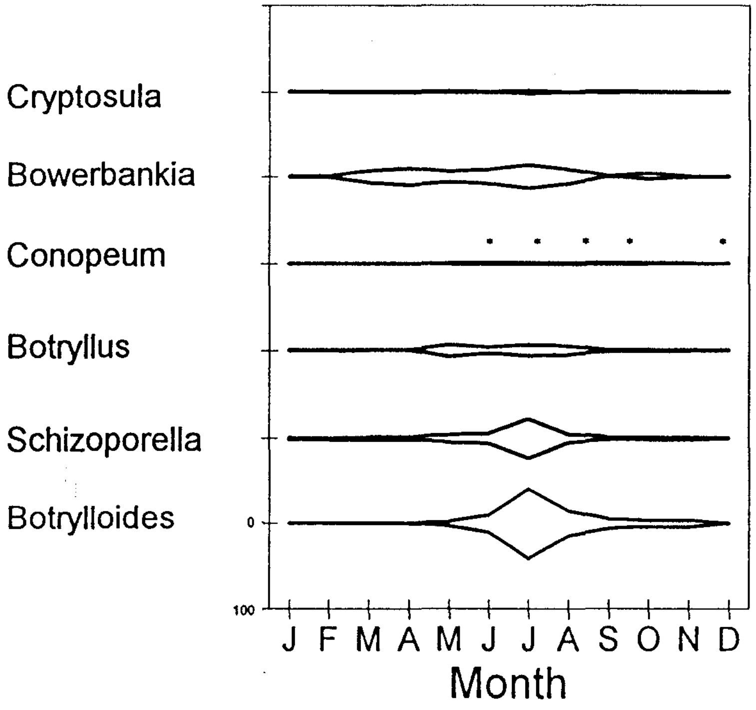


Figure 25. Kite Diagram of Average Recruitment Rates (Recruits•Panel^{-1}•Mo^{-1}) for Introduced Species in the Lower Bay. All Species are Represented at the Same Scale, Asterisks Represent Recruitment at Low Densities.

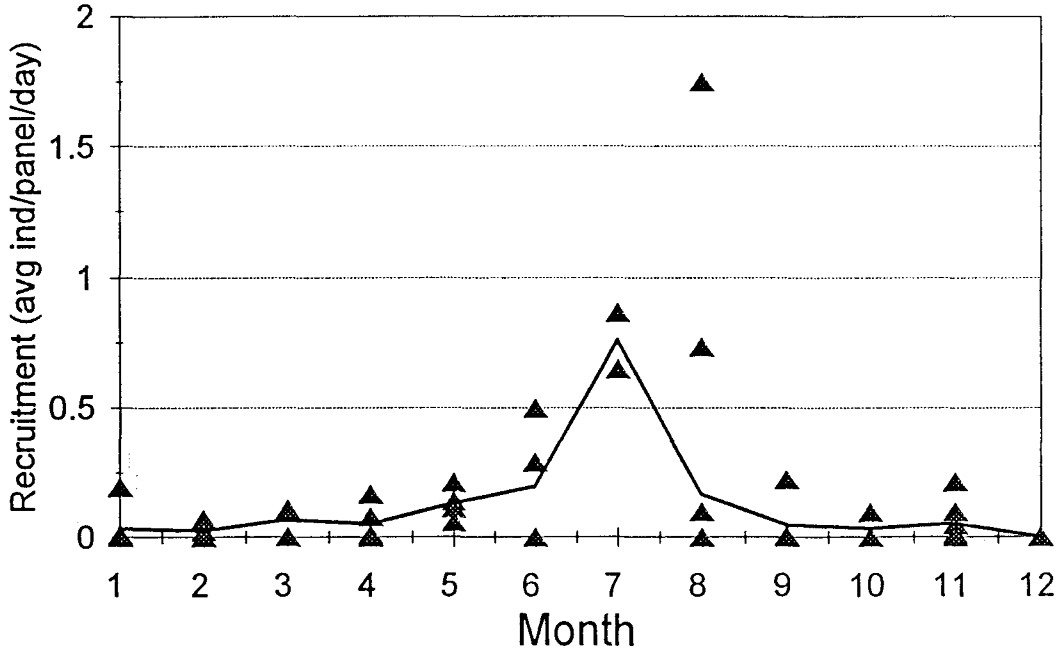


Figure 26. *Schizoporella unicornis* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

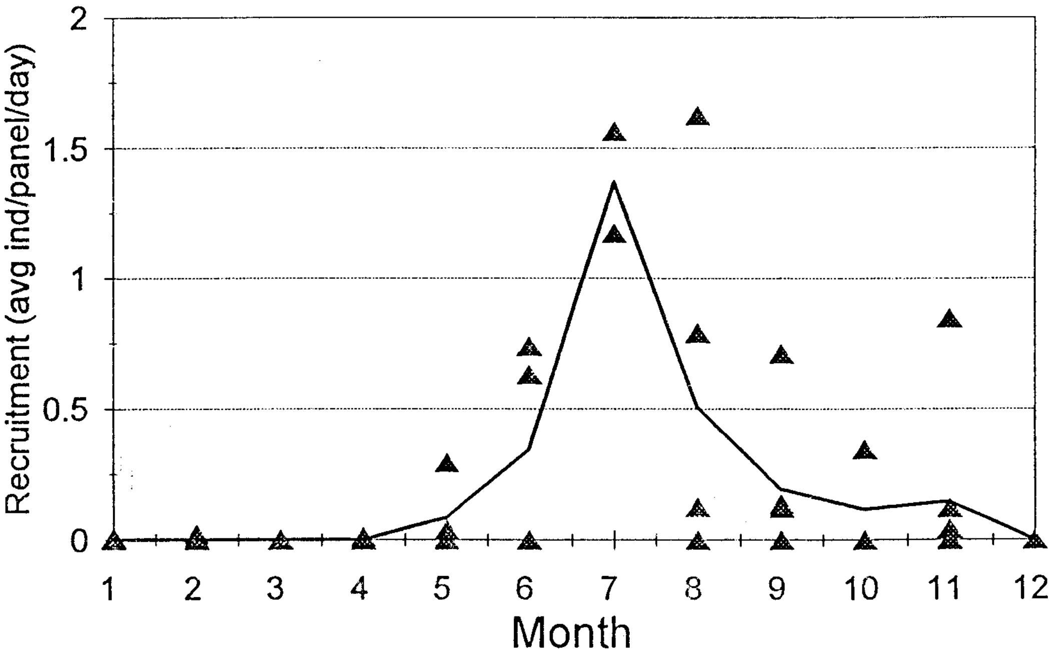


Figure 27. *Botrylloides violaceus* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

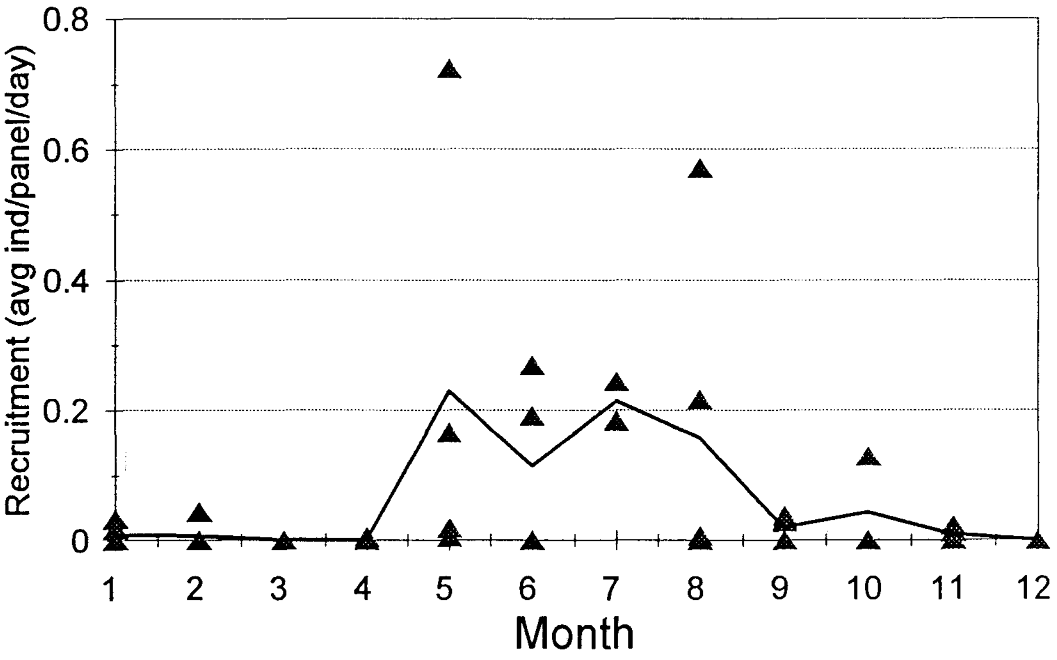


Figure 28. *Botryllus schlosseri* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

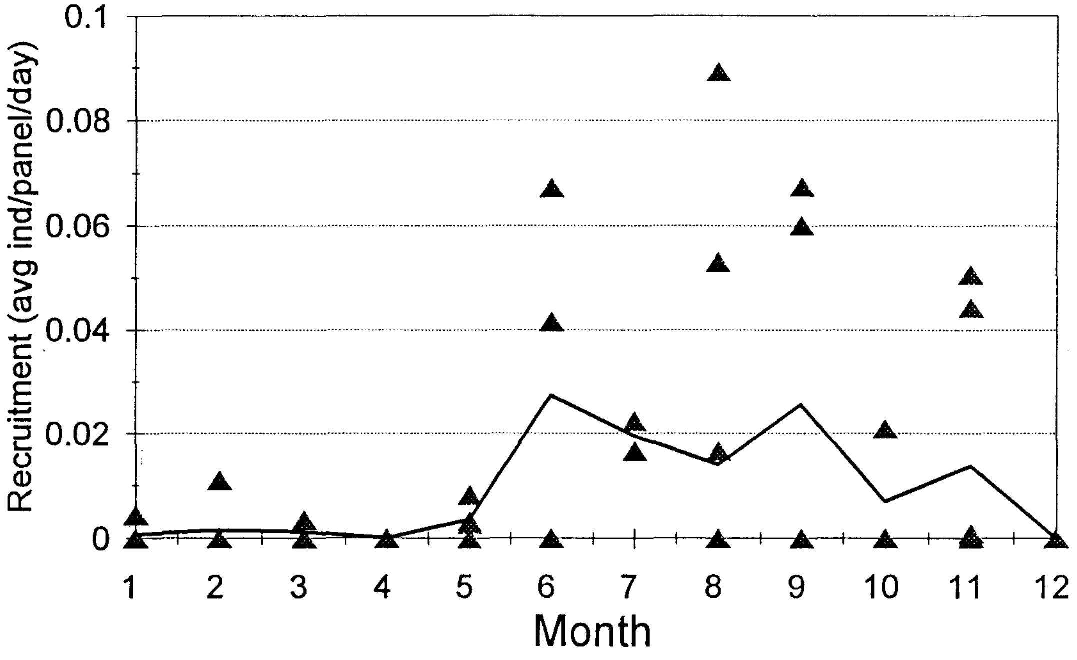


Figure 29. *Conopeum tenuissimum* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

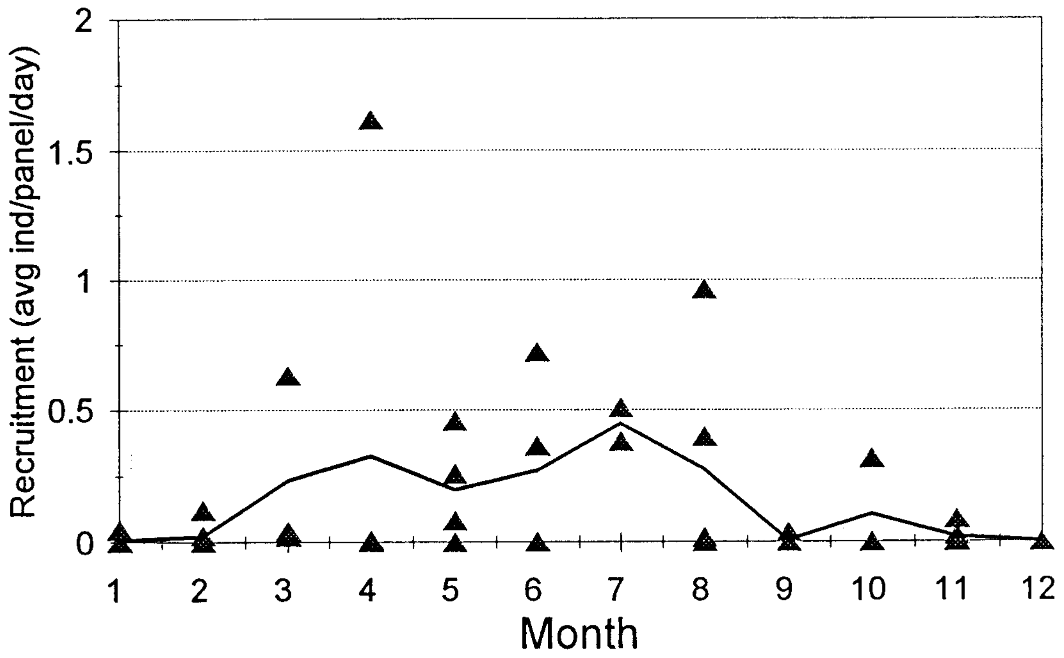


Figure 30. *Bowerbankia gracilis* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

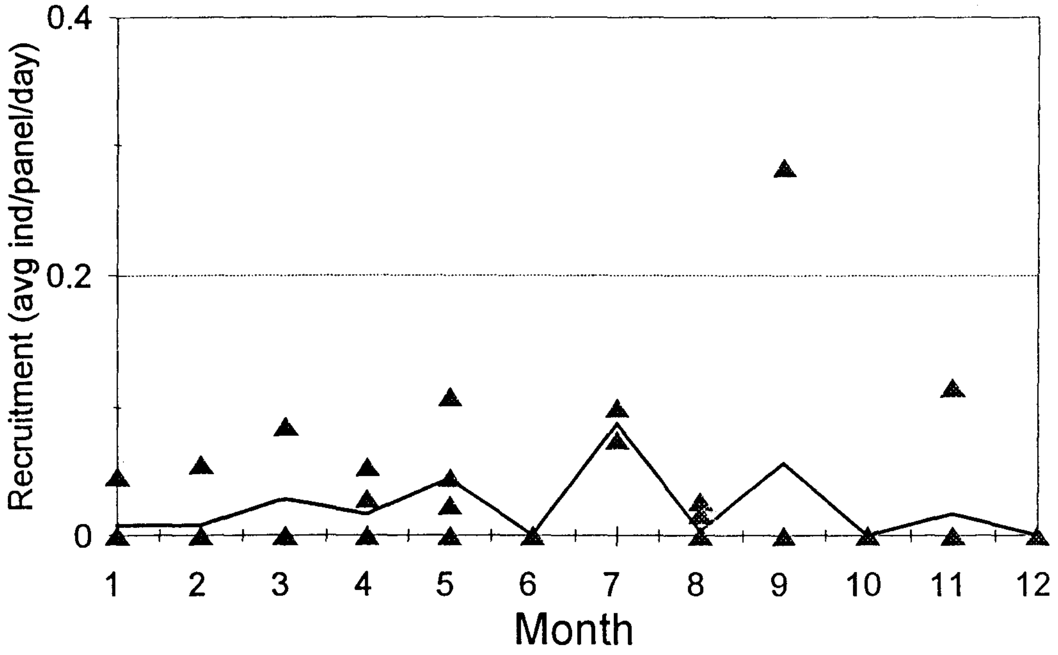


Figure 31. *Cryptosula pallasiana* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

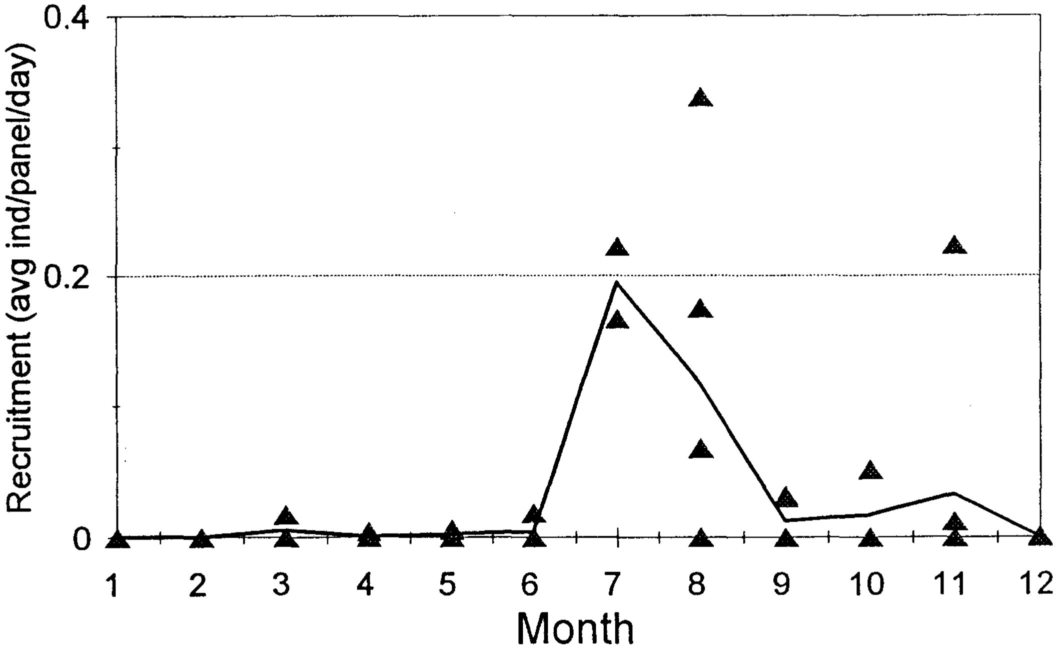


Figure 32. *Alcyonidium polyoum* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

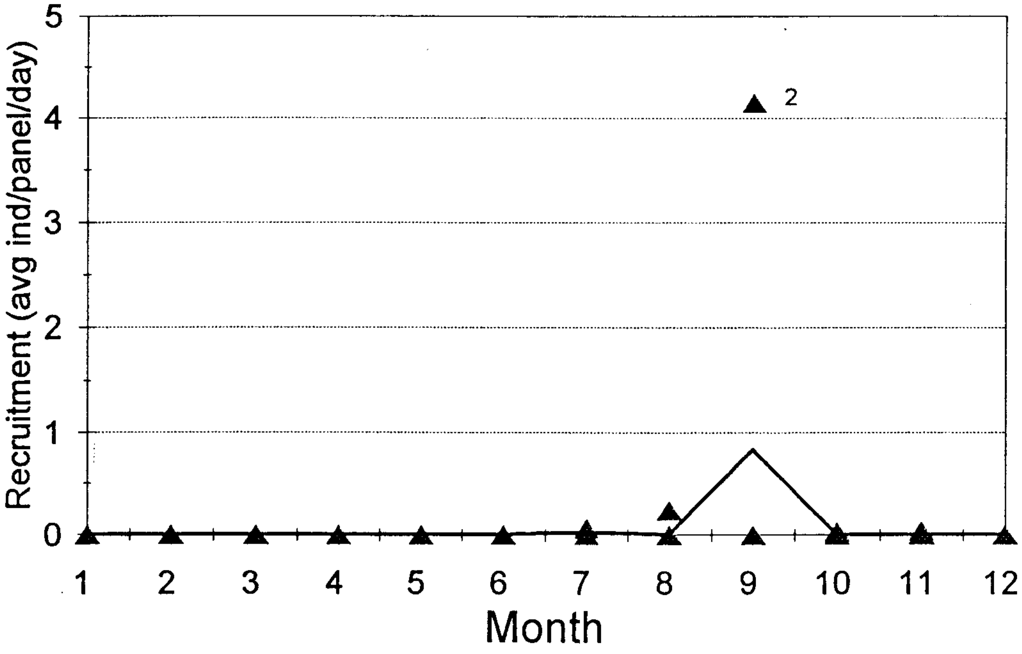


Figure 33. *Distaplia occidentalis* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years. Numbers Adjacent to Symbols Represent the Number of Replicates at that Position.

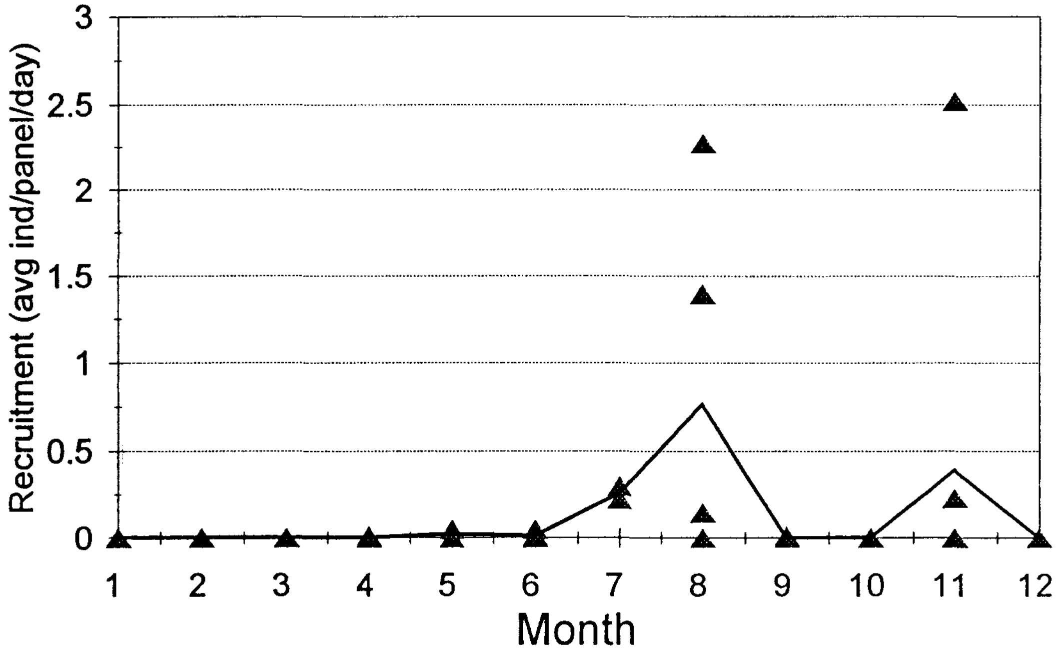


Figure 34. *Balanus glandula* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

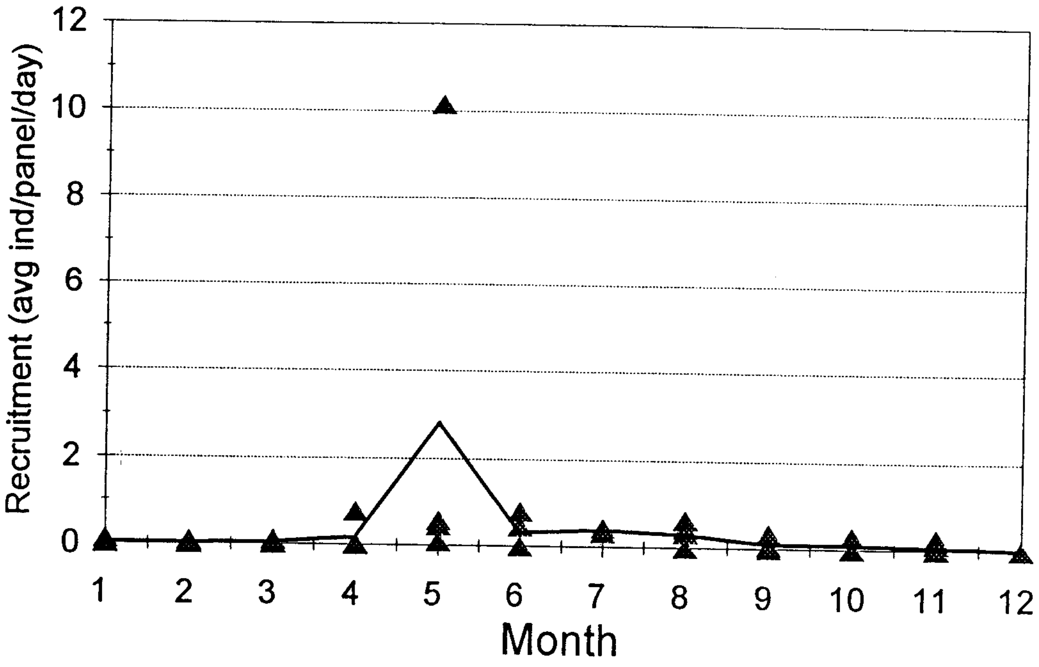


Figure 35. *Bugula pacifica* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

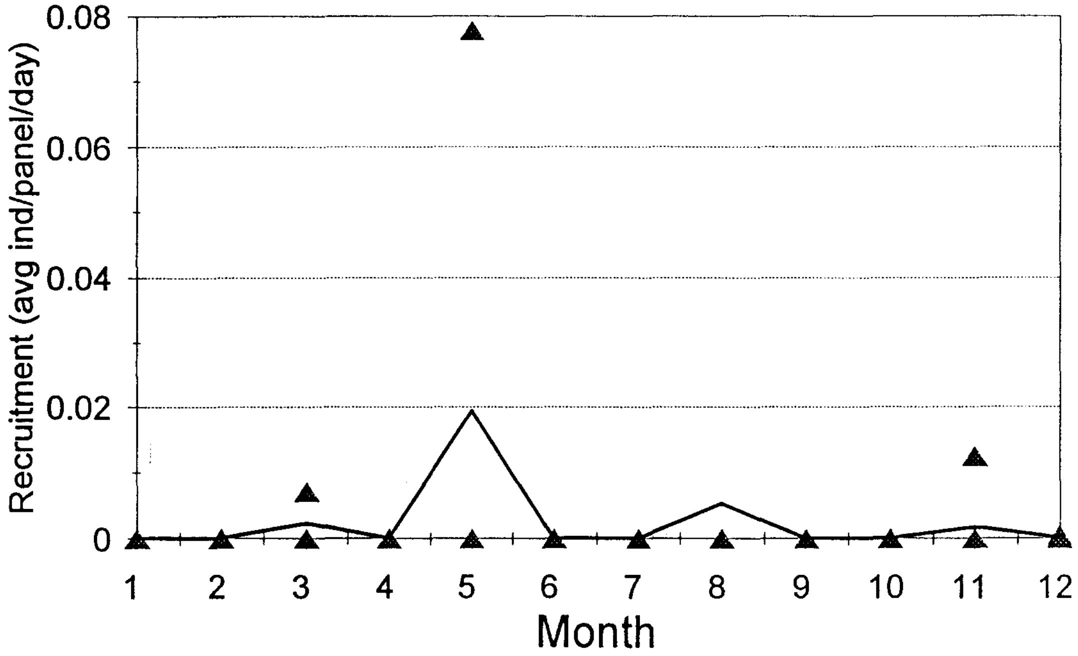


Figure 36. *Cheilopora praelonga* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Year.

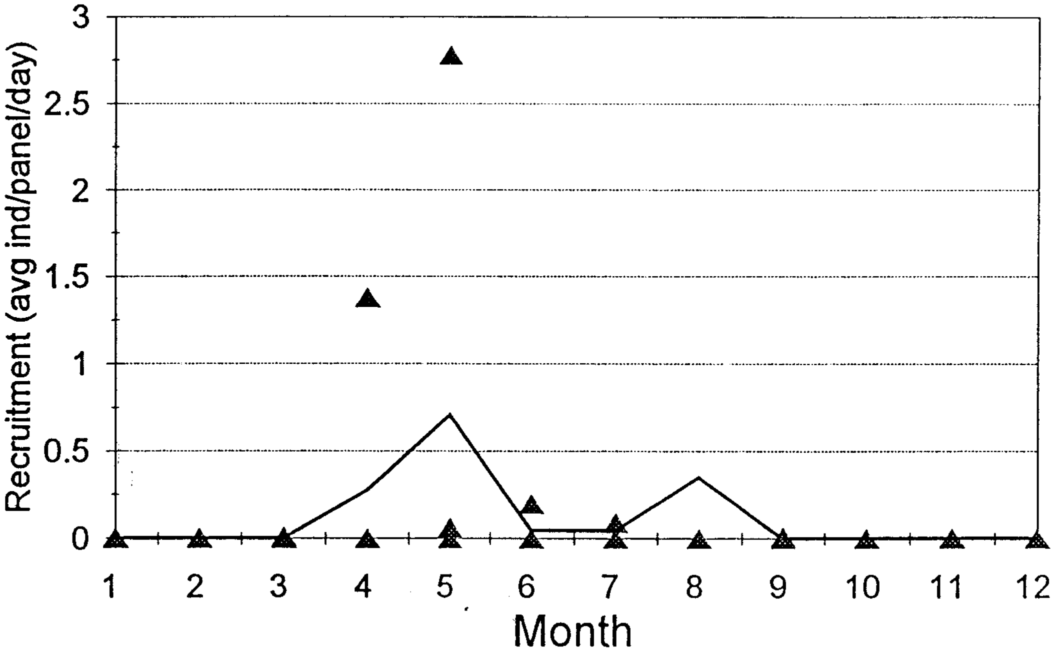


Figure 37. Spirorbid spp. Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Year.

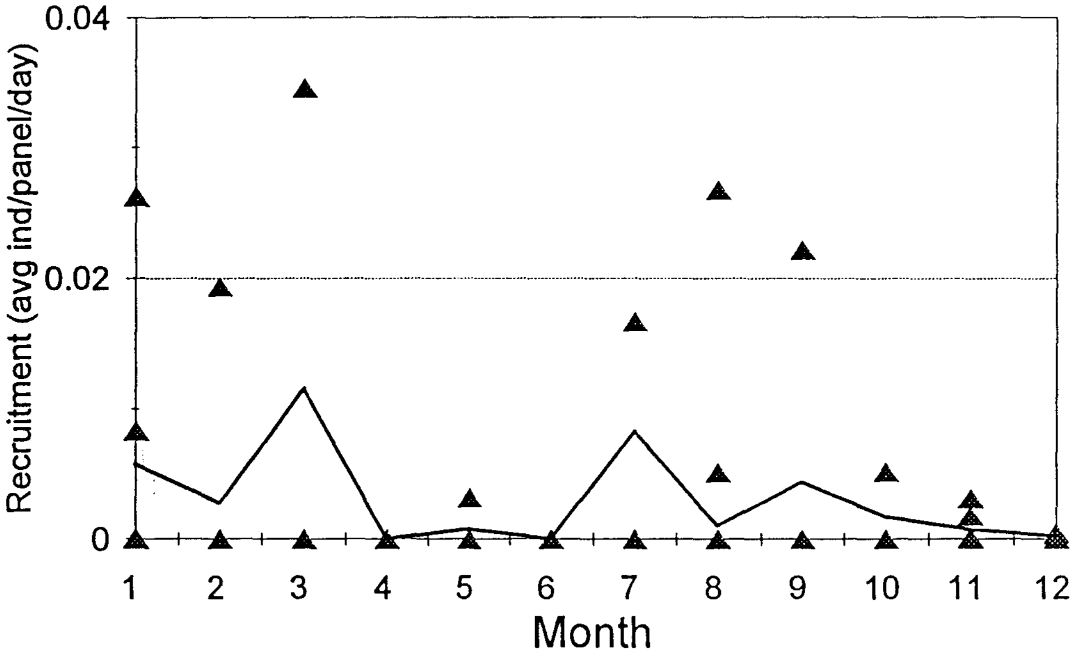


Figure 38. Serpulid spp. Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

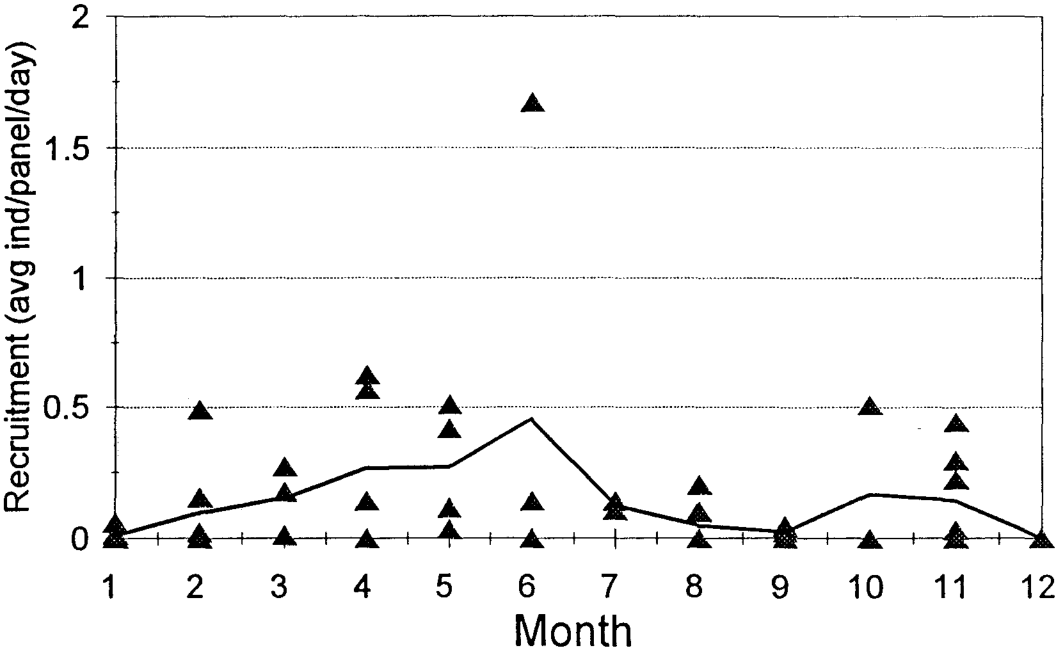


Figure 39. *Hippothoa hyalina* Recruitment (Average Number of Recruits•Panel^{-1}•Mo^{-1}) by Month Between August 1988 and December 1990. Triangles Represent Means of Four Replicate Samples During One Sample Period (Approximately 30 Days), Solid Line Represents the Average of Monthly Recruitment Rates Between Years.

CHAPTER II

THE ASSEMBLY OF ENCRUSTING COMMUNITIES IN THE LOWER COOS BAY ESTUARY

Introduction

The patterns of community development have long interested ecologists (e.g., Clements 1916; MacArthur and Wilson 1963, 1967; Drury and Nisbet 1973; Pimm 1984, 1991). In the face of catastrophic disturbance, such that all species in a patch are driven locally extinct, the trajectory of community assembly will be determined by species colonization from adjacent (or regional) patches. The resulting variation in community structure may be examined from a variety of perspectives, including community richness (diversity), and composition.

The conceptual model of island biogeography, developed by MacArthur and Wilson (1967), predicts that through the processes of immigration and extinction a dynamic equilibrium of species number will exist for a given community. Large perturbations may drive all organisms in a patch to local extinction, but the patch will proceed to accumulate species according to patch size, distance from source pool of species (immigration), and as the community develops, the extinction rate of species present in the patch. There is no intrinsic assumption that the developing community is more or less closed to portions of the donor species pool (Roughgarden 1989). Instead the turnover model of island biogeography presents the community as open to all colonists, that is the community has unlimited membership.

This non-interactive model has been modified to include the alteration of extinction rates due to competitive exclusion by resident species (Wilson 1969) while maintaining the quality of unlimited membership (interactive model). Additionally, Wilson postulated that two further stages in the shifts of community equilibria might exist in ecological and evolutionary time. With increased time the species combinations will result in stable patterns (assortative equilibria) and as these species combinations persist through evolutionary time they will co-adapt (to environmental conditions) and co-evolve (to one another) resulting in reduced extinctions from competitive interactions. While Wilson proposed that both assortative and evolutionary equilibria would increase the species equilibrium ($\hat{S}$), it has been suggested (Goodman 1975; Osman and Whitlach 1978) that it is equally likely for the species equilibrium ($\hat{S}$) to decrease.

Many authors have tested the species equilibrium in a variety of insular habitats (Simberloff 1974). These include oceanic islands (MacArthur and Wilson 1963, 1967), lacustrine islands (Kadmon and Pulliam 1993), defaunated mangrove islands (Simberloff 1969; Simberloff and Wilson 1969, 1970; Wilson and Simberloff 1969), caves (Culver 1970), artificial substrates in aquatic (Patrick 1967, 1968, 1975) and marine (Osman 1977, 1978; Schoener 1974 a, b) systems, and laboratory microcosms (Dickerson and Robinson 1985, 1986). The marine encrusting community has proven to be a model system with which to test concepts of insular faunal buildup (Schoener 1974a, b; Osman 1977, 1978). In most studies the results have supported the predictions of the model, although a few exceptions have resulted in further development of the theory (Brown 1971; Brown and Kodric-Brown 1977). Robinson (1981) has discussed the inapplicability of assembly experiments (i.e., defaunated island, artificial substrate, island microcosms) to study the assortative and evolutionary equilibria of Wilson (1969), but has demonstrated the ability of these same studies to assess the robustness of the interactive and non-interactive aspects of the theory.

Alternatively, the temporal patterns of species composition have been examined in an effort to predict community change. Given the same set of potential colonists, will all communities converge on "stable" community states or is the sequence of species accumulation non-deterministic, resulting in a general lack of pattern? Three successional models were reviewed by Horn (1974) and Connell and Slatyer (1977). These included the "facilitation," "tolerance," and "inhibition" models of community development.

Facilitation is the classical Clementsian view of community succession: a single climax community will be approached only after passing through earlier stages of community development (Clements 1916; Margalef 1968; Odum 1969). In each stage the resident species "prepare" the way for the next rank of colonists (Clements 1916; Horn 1974). In the second model of succession the early colonizers will "tolerate" the appearance of later arrivals (Horn 1974; Connell and Slatyer 1977). Early colonists are ephemeral species which are not resistant to the appearance of longer lived species but are negatively affected by the presence of these late arrivals. As the early recruits die either due to natural mortality or through competitive interactions, the later arrivals dominate the community; the result is a community which is resistant to the early recruiting species. The third model predicts that all colonists arrive at random with no predictable sequence. These early arrivals however are hypothesized to actively inhibit the recruitment of new colonists by exploitative competition (Connell and Slatyer 1977).

Of the three models of succession, the inhibition model has received the greatest level of support in marine communities (e.g., Sutherland 1974, 1977a, b, 1978; Woodin 1976; Connell and Slatyer 1977; Dean and Hurd 1980; Smedes and Hurd 1981). Thus the history of species accumulation is capable of determining subsequent additions or deletions of species in the community. Robinson and Dickerson (1987) and Drake (1990b) have empirically demonstrated that in aquatic laboratory microcosms the order (sequence) of species immigration can drastically alter the ultimate community composition. These alterations can be either deterministic or non-deterministic such that several alternate community states are possible from identical species trajectories

(Drake 1990b). Similarly, Sutherland (1974, 1978, 1981) and Sutherland and Karlson (1977) have demonstrated that in the encrusting communities at Beaufort, N.C., the resident species of specific assemblages are highly resistant to subsequent larval recruitment. In these examples the arrival at one of several ultimate community states is greatly influenced by historical effects of species arrival.

The discussion of community assembly and successional change in species composition has concerned systems in which all potential colonists are drawn from the same source pool of regional biota. It has been proposed that these systems have, through evolutionary time, developed coevolutionary constraints such that specific assembly pathways are closed (Ehrlich and Mooney 1983; Rummel and Roughgarden 1983, 1985; Drake 1990a, b). Thus the "ghosts" of past competitive interactions may have altered the assembly states away from unstable trajectories resulting in generally stable communities (Lewontin 1969; Jackson 1981; Sutherland 1981).

The phenomenon of introduced species, that is the addition of new species to a regional pool by human-mediated mechanisms, has resulted in drastic alterations (additions and subtractions) in local if not regional species pools. The addition of new species to the species pool may be viewed as a permanent perturbation experiment (Sutherland 1981; Pimm 1984, 1987, 1991) in which an alteration in the trajectory of community development and ecosystem function may be observed (Vitousek et al. 1987; Vitousek 1990; Moulton and Pimm 1983, 1986; see also Mooney and Drake 1986, Drake et al. 1989).

Carlton (1979b, 1987, 1989) has reviewed the mechanisms and patterns of human-mediated species introduction to the marine communities of the Pacific coast of North America. The majority of successful introductions have been in bays and estuaries with relatively few invaders on the open coast. It has been suggested that the geologically young bays and estuaries of the Pacific coast (Atwater et al. 1977) aboriginally had a depauperate native fauna (Carlton 1979b; Ricketts et al. 1985) and were as a consequence readily invaded by introduced species (Elton 1958; Carlton 1979b, 1989, 1992b). In contrast the absence of introduced species on the open coast has been proposed to be a function of the ecological resistance (Elton 1958) of the species rich native marine communities.

The communities of the Coos Bay estuary have been and continue to be invaded by non-indigenous species (Carlton 1979b, 1987, 1989; Chapter 1). Within the Coos Bay estuary a changeover occurs from native species dominated, marine communities near the ocean to introduced species dominated, brackish water communities in the upper bay. In the lower bay however communities exist which have comparable native species richness, but only one of these has been successfully invaded by nine introduced species (Chapter 1). Elton (1958) proposed that species rich communities would resist invasions, but that if a successful invasion did occur the novel species would cause a drastic alteration of the community structure, and significantly alter the trajectory of community development (Pimm 1984, 1987, 1991; Vitousek et al. 1987; Vitousek 1990).

In this chapter, I examine the development of these native-species rich, native and invaded communities in the lower bay of Coos Bay, Oregon. The following questions are asked:

1) Does the pattern of community assembly differ between the native and invaded sites?

2) Are there successional or directional patterns in species accumulation in communities at either site?

Study Sites

Two study sites, the North Jetty and Point Adams Jetty (Figures 1 and 40), were selected in the lower portion of the Coos Bay estuary (43° 19' 30"N, 124° 19' 30"W) based on the distributions of native and introduced species described previously (Chapter 1). These sites are separated by less than 2km, and are physically similar, with similar temperature and salinity regimes. Both are basalt rock jetties of varying ages: the North Jetty is approximately 100 yrs old (construction began ~1900) and the Point Adams Jetty is 20 yrs old (constructed in 1974). The North Jetty has a diverse native marine fauna of 83 species. Two additional species of unknown biogeographic origin (cryptogenic species) occupy less than 1% of the total space (Carlton 1979, 1989; Chapman and Carlton 1991). The Point Adams Jetty has 66 native species (and the two cryptogenic species), a subset of the North Jetty fauna. This site has been invaded by 9 species of sessile invertebrates.

The disjunct distribution of non-native species at these sites may be due in large part to dispersal limitation (i.e., a lack of intra- and trans-bay transport mechanisms). Velocity field diagrams of the lower bay (developed by COE 1979) for maximum flood (Figure 41) and maximum ebb (Figure 42) tides illustrate the difficulty a passively dispersing planktonic larva would have in crossing the channel between the North Jetty and Point Adams Jetty. Preliminary support for this was obtained from an exploratory experiment conducted in July 1989 where 10 oranges were dropped 50m from the Point Adams Jetty during a moderate ebb tide. Within 30 min all 10 oranges had passed less than 30m from the OIMB boathouse (Figures 1 and 40) shore. Oranges are useful drogues. They are positively buoyant and float just under the water-air interface; they are passively dispersing; and they are highly visible.

Materials and Methods

In order to assess the under rock encrusting community, settlement panels of black acrylic sanded to approximate a natural surface were placed amidst the low intertidal (-1.5' to -2.0' MLLW) jetty rocks of the two selected study sites. These panels consisted of four 50cm^2 (7.2cm X 7.2cm X 0.6cm) subpanels (quadrants) arranged in a 2x2 array such that each quadrant could be individually removed, but as a unit they represent a single 200cm^2 settlement surface. It has been shown that surface anomalies (e.g., barnacles, Leggo™ bumps, bolt heads) alter the settlement patterns of many invertebrates (Barkai and Branch 1988; Dean 1981; Walters and Wethey 1991). In order to create modular panels without attachments breaking the planar settlement surface the following design was developed. Each subpanel has a permanently attached 3cm stainless steel machine screw cemented (Poly-Poxy™ underwater cement) into a centered 0.3cm countersunk hole in the back. Four subpanels are then fitted and attached to a back panel (with appropriate holes) using wing nuts for ready field removal. Two 10cm stainless steel flathead bolts are attached to the back panel and face away from the subpanels (Figure 43).

The entire array (back panel with four subpanels) is placed (with the settlement surface down) inside one space of a concrete building block (15cm X 15 cm X 32 cm) which has been prepared by drilling two holes on either top surface of either side. The bolts are threaded through the drilled holes and attached with stainless steel wing nuts (for easy field removal). Plastic spacers maintain the panel at the mid-point of the space and approximately 1.5cm from the walls. Thus each concrete block has two panel arrays, one on either side (Figure 43). To reduce or prevent the action of mobile benthic fauna (e.g., crabs, seastars, and fish) the concrete block openings were covered by 0.7 cm VEXAR™ plastic mesh. One side had permanently attached mesh cemented to the concrete block.

On the opposite side of the block the mesh was cemented on the bottom side, the remaining three sides had VELCRO™ hook strips sewn to the mesh with the VELCRO™ loop strips cemented to the concrete blocks providing easy access.

Experiment 1

In order to assess the effects of mesh on settlement patterns, a series of no mesh (neither side covered), partial mesh (mesh on the bottom half of both sides), and complete mesh (both sides) treatments was conducted over a sixteen month period between April 1989 and August 1990. Treatments (mesh cover) were randomized between and within concrete blocks such that microsite differences in block placement were not confounded with treatment. Each treatment was replicated three times at the two study sites. A single subpanel (one quadrant of each panel array is equal to $50cm^2$) was randomly selected as the focal panel and the back marked for later identification. This focal panel was the sample unit in each panel array for the duration of the experiment.

At each sample period the concrete blocks were examined and panel arrays were carefully removed in the field. The presence or absence of benthic mobile fauna (cancrid crabs, fish and seastars), the degree of mesh obstruction due to algae or encrusting organisms, and the degree of siltation were noted. The mobile fauna and accumulated sediment were removed and the mesh coverings cleaned before the blocks were replaced. Thus any disturbance-mediated larval release would occur during the 24 to 48 hr period in which the settlement substrates were in the lab. These panel arrays were then transported to the Oregon Institute of Marine Biology (OIMB), and maintained in running seawater. The focal panel was identified for each panel array by subpanel markings, examined with a dissecting microscope and returned to the field within 24 to 48 hr. Species lists were constructed for each panel array (replicate) from the focal panel.

Experiment 2

In a second study, conducted from September 1990 to February 1992, all concrete blocks were 100% mesh treatments (mobile fauna exclosures). All panels were replicated four times at the two sites and the frequency of sampling increased to 13 samples over 17 mo (mean = 38.5 days, s.d. = 14.3). As in experiment 1, a single subpanel (50cm^2) was randomly selected for each panel array as the focal panel for the duration of the experiment and was marked for future identification. At each sample period during the spring low tides, the concrete blocks (with two panels in place) were examined (as above for the presence of mobile fauna, mesh obstruction, and siltation), collected from the field, brought to the OIMB docks and the panels carefully removed. This procedure lessened the disturbance effect of panel removal from the blocks. These panels were then transported to OIMB, and maintained in running seawater while high resolution videotapes were made of each panel for later analysis. The panel arrays were returned to the field during low tide within 24 to 48 hr.

In order to avoid contamination of native site panel arrays with introduced species from the invaded site the following measures were taken: 1) site collections were staggered over four to six days in which the native site panels were collected during the low tide, videotaped, and redeployed during the following low tide (24 to 48 hr later); the following day the invaded site panels were collected at low tide, video-taped, and redeployed during the subsequent low tide (24 to 48 hr later); 2) the running seawater tables used to hold panels were drained and scrubbed between sample periods (28 to 70 days); and 3) the site panels were consistently held in two separate water tables over the course of the study. The timing of the sample regime described above allowed panel arrays and blocks to be repaired if necessary. During the 24 to 48 hr period, subpanels whose holding screws were loose could be re-cemented and cured out of the water, while the organisms on the opposite side of the panel were still under water.

While the concrete blocks were on the OIMB dock, repairs to the mesh and VELCRO fastener system were conducted. In addition the blocks were scraped clean during each tide cycle, and then repeatedly subjected to high-pressure freshwater, with the intent that the concrete blocks not contribute significantly to larval supply.

High resolution videotapes (sVHS) were made with a copy-stand mounted sVHS Panasonic color CCD camera with a 50mm zoom macro lens. The entire panel array ($200cm^2$) was placed in a container that allowed the movement of the panel along registered guides. At each sample period the identical physical placement of the panel was obtained. Images of each subpanel ($50cm^2$) in a $200cm^2$ array were videotaped (four shots) and sixty-four overlapping macroshots (approximately $6cm^2$ each) were made for the entire $200cm^2$ panel. In this fashion the video-resolution was approximately $1mm^2$ and the accuracy of species identification from the video was > 90% for most taxa. To further aid in subsequent species identification, a continuous audio recording was made on the videotape in which newly settled, obscured, or unusual colonies (or individuals) were identified. Similarly, arborescent bryozoans and hydroids were moved during the videotaping such that all primary space could be both easily viewed and accounted for. Only the area of basal attachment, rather than the canopy area, was recorded for arborescent species. Similarly, the settlement of a species or growth of vine-like (runner) species on top of another was counted for both species. However, overgrowth by sheet-like species was counted only once for the apparent "winner" of the outcome, but through time the result of the overgrowth interaction was followed and scored. Thus more than $50cm^2$ (greater than 100%) could be counted on a given plate. "Winner" is here defined in sheet-like species' encounters as the species which overgrows more than 5mm onto the "losing" colony (Buss and Jackson 1979; Quinn 1982; Buss 1986).

High resolution video-images were digitized using the JAVA image analysis software (Jandel Scientific, Corte Madera, California) installed on a 33 Mhz 486DX computer. Individual (or colony) areas of each species were digitized. At each time period maps of the focal panel were made with individual or colony identification and location, thus individual growth and mortality could be assessed. Similarly the recruitment and immigration (lateral growth from adjacent subpanels) of individuals (or colonies) could be distinguished between time periods.

Video analysis however presents some difficulty. The difficulty in distinguishing three serpulid species, *Crucigera zygophora, Pseudochitinopoma occidentalis,* and *Serpula vermicularis*, with the sampling method used, prevented species level identification and thus "serpulids" was the least discernible taxonomic unit. Similarly "spirorbids" may refer to a species group (Blake 1975). The difficulty of counting percent cover of runner or vine-like species (Jackson 1977) makes it more reliable to use estimates in 5% intervals (equal to $2.5cm^2$).

Terebellids are not truly sessile organisms but were included in this study due to their consistent presence on panels to which they had recruited and the high densities attained at specific times. While capable of leaving the tube, terebellids are functionally sessile much of the time. As with serpulids and spirorbids, the group "terebellid" may have several species. In contrast, "introduced species" does not describe a taxonomic unit but describes the biogeographic origins of the species included in the group. As a group, these species represent an addition to the species pool (an increase in the regional γ-diversity) which may alter the rates of species immigration into and extinction from local patches (in this case settlement substrates). Thus, it is desirable to examine their effect as a unit on native species immigration and extinction processes.

Community Structure

Colonization curves of species richness (S) were calculated from the summary statistics for each panel at each sample period based on the qualifications for species identification stated above. Additionally the following community indices were calculated from the areas (cm^2) occupied by sessile organisms for each panel at each sample period. The Shannon-Weaver information index (H'; Shannon and Weaver 1949) was calculated for species contribution to live cover (total space occupied by living organisms), as

$$H' = -\sum p_i \ln(p_i),$$

where p_i is the proportion of all occupied space occupied by the i-th species (area of the i-th species/sum of occupied area for all species). The Evenness Index (J') was calculated from the Shannon-Weaver diversity (H') as

$$J' = H'/H'_{\max},$$

where $H'_{\max} = \ln(S)$ (Pielou 1966).

Two measures of dominance were calculated, McNaughton's index (MD) is defined as the ratio of the space occupied by the two dominant species (greatest and second greatest areas covered) to the total space occupied by all species (McNaughton 1967). A second index used by Osman (1977) is defined as the smallest number of species that, taken together, account for 75% of the occupied space.

Community Dynamics

Species immigration and extinction curves (number of species newly immigrating or going extinct per month) relative to the number of resident species were generated for panels at the two sites. The development of the native component of the community was examined as well at the invaded site, such that native species immigration and extinction rates were compared against the total number of species (native and introduced). From these curves estimates of $\hat{S}$ were generated for comparison with the colonization curves developed earlier.

A primary tenet of the theory of island biogeography is that species numbers in any given patch are determined by a balance between the rates of species immigration and extinction (MacArthur and Wilson 1967). As Chesson (1978) has argued, deterministic concepts of stability are inappropriate for the assessment of this dynamic equilibrium. Instead he has proposed the concept of stochastic boundedness. A bounded system is one in which upper and lower limits (bounds) exist such that at some arbitrary probability they are not exceeded. As Keough and Butler (1983) have pointed out, it is not sufficient to know that a system has bounds, but it is necessary to evaluate the width of the bounds. They have proposed a statistical criterion for "narrow" boundedness to evaluate the degree of stochastic fluctuation. There exist upper and lower bounds for any data set such that the probability of exceeding those bounds is $<\varepsilon$ and the width of the bounded region is $\leq 2\omega\mathbf{X}$, where ω is a constant defining the width of the band and **X** is the mean of the variable of interest (e.g., species number of a sample through time). In Keough and Butler (1983) the values for $\varepsilon = 0.05$ (representing the 95% confidence interval for **X**), and $\omega = 0.2$ were proposed as a definition for narrow boundedness.

Osman and Dean (1987) suggested that $\omega = 0.2$ is too restrictive, particularly with richness less than 10 species; instead they proposed $\omega = 0.3$ which is used here. The statistical test they developed compares the degree of change in a random variable (community statistic) through time according to the following statistic:

$$t = \frac{CV_X - (100\omega / 1.96)}{SE_{CV}} \quad \text{with (n-1) degrees of freedom}$$

where n = sample size, CV_X = the coefficient of variation of the variable of interest (**X**), and SE_{CV} = the standard error of the $CV_X = (CV_X/\sqrt{2n})\bullet(1+(CV_X/100)^2)$ (Keough and Butler 1983; Kay and Butler 1983). With $\omega = 0.3$ the null hypothesis becomes $CV_X \leq 15.3$. Alternatively the calculation of ω allows one to compare the degree of sample boundedness for different communities (Keough and Butler 1983).

In order to compare the similarity of community compositions, Bray-Curtis similarity coefficients (denoted 1 - BC) were calculated between each replicate panel combination both between and within sites. This distance measure is a standardized Manhatten metric (Bray and Curtis 1957):

$$1 - BC = \frac{\Sigma \mid X_{ij} - X_{ik} \mid}{\Sigma \mid X_{ij} + X_{ik} \mid},$$

where X_{ij} is the abundance of species i in sample j and X_{ik} is the abundance of species i in sample k. Each replicate panel's mean similarity to all other within or between site replicates was taken to be the datum.

Results

Experiment 1

A total of 57 species of invertebrates were observed during the assembly of the encrusting communities between April 1988 and June 1989 (Tables 9, 10, and 11). The composition and relative numbers of species found in the three mobile fauna exclusion treatments differed within sites. At the North Jetty (the native site) 41 encrusting species were observed in the closed treatments, while 31 and 26 encrusting species were found in

Table 9. Native Species Presence/Absence in Community Assembly Experiment 1 at the North Jetty Between April 1989 and August 1990

			NORTH JETTY											
			Closed					Partial				Open		
PHYLUM	Species	Days:	30	60	221	429	584	30	60	221	429	30	60	221	429
Crustacea															
	Balanus glandula				☑	☑	☑			☑	☑			☑	☑
Cnidaria															
	Hydroid (Phialella?)						☑							☑	
	Metridium senile														☑
	Obelia sp				☑	☑	☑		☑	☑	☑		☑	☑	
	Sarsia sp														☑
Ectoprocta															
	Alcyonidium polyoum?		☑	☑	☑	☑	☑		☑	☑	☑		☑	☑	☑
	Bugula californica						☑							☑	
	Bugula pacifica		☑			☑			☑		☑	☑	☑	☑	
	Callopora armata													☑	
	Callopora horrida		☑			☑	☑	☑			☑	☑		☑	☑
	Callopora inconspicua					☑	☑							☑	
	Caulibugula ciliata			☑		☑					☑			☑	
	Cheilopora praelonga				☑	☑	☑			☑	☑			☑	☑
	Coleopora gigantea		☑						☑			☑	☑	☑	
	Conopeum reticulum		☑		☑					☑				☑	
	Costazia costazii					☑								☑	
	Cribrilina annulata		☑		☑	☑	☑		☑		☑			☑	☑
	Crisia occidentalis		☑		☑	☑	☑		☑	☑	☑			☑	☑
	Dendrobeania lichenoides				☑	☑	☑							☑	
	Electra crustulenta					☑			☑				☑	☑	
	Fenestrulina malusii			☑	☑	☑								☑	
	Filicrisia fransiscana			☑	☑	☑	☑				☑			☑	
	Hippothoa divaricata			☑			☑							☑	
	Hippothoa hyalina		☑		☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑
	Lichenopora verrucaria				☑	☑								☑	☑
	Microporella californica				☑	☑	☑			☑	☑			☑	☑
	Microporella ciliata		☑		☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑
	Oncousoecia ovoidea		☑		☑	☑	☑				☑			☑	
	Porella columbiana				☑	☑								☑	☑
	Rhamphostomella costata					☑					☑			☑	
	Tricellaria erecta			☑							☑				☑
	Triticella sp										☑				
Entoprocta															
	Loxosomella nordgaardi					☑					☑			☑	
	Pedicellina cernua														
Mollusca															
	Mytilus trossulus			☑				☑							
	Pododesmus cepio						☑							☑	
Annelida															
	Serpulids				☑	☑	☑			☑	☑			☑	☑
	Spirorbids					☑	☑	☑	☑	☑				☑	
	Terebellids										☑				☑
Porifera															
	Halichondria panicea														
	Haliclona sp.				☑		☑				☑			☑	
	Leucosolenia sp				☑									☑	
Urochordata															
	Ascidia ceratoides			☑	☑	☑	☑		☑		☑		☑	☑	
	Boltenia echinata			☑	☑					☑	☑			☑	
	Cnemidocarpa finmarkiensis					☑					☑			☑	☑
	Distaplia occidentalis														
	Perophora annectans														
	Pyura haustor						☑							☑	
	Styela gibbsi		☑										☑	☑	

Table 10. Native Species Presence/Absence in Community Assembly Experiment 1 at the Point Adams Jetty Between April 1989 and August 1990

		POINT ADAMS JETTY												
		Closed					Partial				Open			
PHYLUM	Species Days:	30	60	221	416	597	30	60	221	416	30	60	221	416
Crustacea														
	Balanus glandula			☑	☑	☑			☑			☑	☑	☑
Cnidaria														
	Hydroid (Phialella?)		☑											
	Metridium senile													
	Obelia sp		☑	☑	☑	☑		☑	☑	☑			☑	☑
	Sarsia sp													
Ectoprocta														
	Alcyonidium polyoum?		☑					☑	☑			☑		☑
	Bugula californica													
	Bugula pacifica		☑	☑		☑	☑	☑	☑	☑	☑	☑	☑	☑
	Callopora armata													
	Callopora horrida			☑	☑			☑	☑	☑				☑
	Callopora inconspicua													
	Caulibugula ciliata		☑											☑
	Cheilopora praelonga				☑			☑	☑	☑			☑	☑
	Coleopora gigantea		☑					☑				☑		
	Conopeum reticulum			☑								☑		
	Costazia costazii													
	Cribrilina annulata	☑		☑			☑	☑	☑	☑		☑		☑
	Crisia occidentalis				☑				☑	☑			☑	☑
	Dendrobeania lichenoides													
	Electra crustulenta		☑									☑		☑
	Fenestrulina malusii		☑						☑					
	Filicrisia fransiscana													
	Hippothoa divaricata													
	Hippothoa hyalina	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑
	Lichenopora verrucaria													☑
	Microporella californica		☑											☑
	Microporella ciliata		☑	☑	☑			☑	☑	☑		☑	☑	☑
	Oncousoecia ovoidea													
	Porella columbiana													
	Rhamphostomella costata				☑									☑
	Tricellaria erecta												☑	☑
	Triticella sp													
Entoprocta														
	Loxosomella nordgaardi													
	Pedicellina cernua													☑
Mollusca														
	Mytilus trossulus											☑		
	Pododesmus cepio													
Annelida														
	Serpulids		☑	☑	☑	☑			☑			☑	☑	☑
	Spirorbids	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑
	Terebellids				☑					☑				☑
Porifera														
	Halichondria panicea					☑								
	Haliclona sp.		☑											☑
	Leucosolenia sp					☑			☑			☑	☑	☑
Urochordata														
	Ascidia ceratoides		☑					☑	☑			☑	☑	☑
	Boltenia echinata													
	Cnemidocarpa finmarkiensis													
	Distaplia occidentalis					☑								
	Perophora annectans													☑
	Pyura haustor													
	Styela gibbsi					☑			☑	☑				☑

Table 11. Introduced Species Presence/Absence in Community Assembly Experiment 1 at Both Sites Between April 1989 and August 1990

INTRODUCED SPECIES	NORTH JETTY													POINT ADAMS JETTY												
	Closed					Partial				Open				Closed					Partial				Open			
PHYLUM Species Days:	30	60	221	429	584	30	60	221	429	30	60	221	429	30	60	221	416	597	30	60	221	416	30	60	221	416
Ectoprocta																										
Bugula neritina																										☑
Conopeum tenuissimum		☑													☑					☑						
Schizoporella unicornis														☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑
Watersipora edmonsonii?																		☑								
Urochordata																										
Botrylloides violaceus															☑		☑	☑		☑	☑	☑		☑	☑	☑
Botryllus schlosseri															☑			☑		☑						
CRYPTOGENIC SPECIES																										
Ectoprocta																										
Bowerbankia gracilis?					☑				☑			☑	☑		☑			☑				☑				☑
Cryptosula pallasiana					☑	☑				☑		☑		☑				☑	☑				☑			

partial and open treatments (Figure 44). The closed (mobile fauna exclusion) treatment panels accumulated species in linear fashion for the initial seven months attaining an average richness of 17.3 species per panel (s.d. = 2.89). After sixteen months exposure the species richness had dropped to a mean of 16.0 species per panel (s.d.=3.60). Partial and open treatments accumulated species at a much lower rate (Figure 44) reaching 16 (partial) and 12 (open) species by month sixteen (August 1990).

The panels at the Point Adams Jetty accumulated species at a higher rate, attaining mean richness of 7, 9, and 11 species (partial, open and closed treatments, respectively) within the first two months of exposure (Figure 45). In contrast to the North Jetty, the closed treatment panels lost species richness by the next sample period. Similarly partial treatment panels increased and declined by month 13.

During this experiment a number of mobile species were removed from the treatment blocks. Most of these species do not primarily prey upon the sessile encrusting community but are the mechanisms of disturbance events. These included the asteroids, *Evasterias troschelii, Henricia leviuscula, Pisaster ochraceus, P. brevispinus,* and *Pycnopodia helianthoides*, the brachyuran crabs, *Cancer antennarius, C. gracilis, C. magister, C. productus, Pugettia gracilis* and *P. producta*, and cottid (sculpins) and pholidid (gunnels) fish (*Clinocottus* spp. and *Apodichthys* spp.) (Table 12). Single individuals of juvenile *Cancer gracilis, C. magister, C. productus, Pisaster brevispinus,* and *Pycnopodia helianthoides*, were occasionally found in closed treatments. These had apparently recruited from the plankton as crab megalopae or asteroid brachiolariae into the blocks, or the asteroids may have migrated into the blocks following initial metamorphosis. Partial and open treatments had an average of 2.3 mobile species•half block^{-1}•mo^{-1} (s.d. = 1.5). Partial treatments had higher densities of mobile fauna than open treatments, possibly due to the nature of the mesh arrangement.

Table 12. Mobile Fauna Species List

PHYLUM	Species
Crustacea	
	Cancer antennarius
	Cancer gracilis
	Cancer magister
	Cancer productus
	Pugettia gracilis
	Pugettia producta
Echinodermata	
	Evasterias troschelii
	Henricia leviuscula
	Pistaster brevispinus
	Pisaster ochraceus
	Pycnopodia helianthoides
Pisces	
	Apodichthys spp.
	Clinocottus spp.

Crevice dwellers or nestlers may have preferred the narrow opening on one side in the partial treatments, whereas the open treatment had no mesh obstruction on either side of the block.

The accumulation of sediment in the concrete blocks did not appear to vary between treatments, but was associated with seasonal differences. Between May and September a large accumulation of drift algae, woody debris and fine silt filled in around the blocks at both sites. Inside and below the settlement panels silt built up to depths of 1 - 2cm, and although this was not generally sufficient to crowd or smother the community, the frequency of summer cleanings was increased. Increased water movement at the North Jetty during the winter caused pockets of sand to build up in amidst the jetty rocks but did not interfere with water circulation in the concrete blocks.

Experiment 2

A total of thirty-one species from seven phyla were observed during the encrusting community assembly on panels deployed September 1990 until February 1992. Twenty species settled at the native site (North Jetty; Table 13) and twenty-five species at the invaded site (Point Adams Jetty; Table 14), with fourteen native species shared between the two sites. As in the closed treatment of the first experiment, the density of predators was low (<1 species•half block^{-1}•mo^{-1}) and restricted primarily to juveniles. In some instances, however, larger predators were able to obtain entry, primarily when VELCRO fasteners on the blocks were in need of repair.

The accumulation of sediment followed similar patterns to those seen in experiment 1, with high siltation and organic debris build-up in mid-summer. During experiment 2 however, two differences were noted. First, the fine silt and sand that built up beneath the blocks became itself the settlement substrate for hundreds of *Tresus capax* juveniles

Table 13. Mean Percent Cover for All Species at the North Jetty During Experiment 2 Between September 1990 and February 1992

		Sample Period:	1	2	4	5	6	9	10	11	13	14	15	16	17
		Month:	N	D	J	F	A	J	A	S	O	N	D	J	F
PHYLUM	Species	Days:	28	55	114	141	193	264	307	340	383	410	438	470	500
Cirripedia															
	Balanus glandula		0.04	0.01	0	0	0.59	36.7	41.8	32	31.6	32	24.9	16.3	6.73
Cnidaria															
	Metridium senile		0	0	0	0	0	0	0	0	0	0	0	0	0
	Obelia spp.		0.5	0.03	0.01	2.51	11.3	0.03	0	0.01	0.28	0.28	0.28	0.58	3.5
	Scyphistomae (Aurelia spp.)		0	0	0	0	0	0	0	0	0	0	0	0	0
Ectoprocta															
	Alcyonidium polyoum		0	0	0	0	0	0	0	0	0	0	0	0	0
	Bowerbankia gracilis		0	0	0	0	0	0	0	0	0	0	0	0	0
	Bugula pacifica		0	0	0	0	0	0.07	0.1	0.01	0	0	0	0	0
	Cheilopora praelonga		0	0	0	0	0	2.46	3.59	4.79	6.22	3.92	4.39	4.09	3.15
	Conopeum tenuissimum		0	0	0	0	0	0	0	0	0	0	0	0	0
	Cribrilina annulata		0	0	0	0	0	0	0	0	0	0	0.14	0.05	0
	Crisia occidentalis		0	0	0	0	0	0	0	0	0	0	0	0	0.08
	Cryptosula pallasiana		0	0	0	0	0	0	0	0	0	0	0	0	0
	Dendrobeania lichenoides		0	0	0	0	0	0.25	0	0	0	0	0	0	0
	Hippothoa hyalina		0	0	0.04	0.1	1.98	23.9	15.3	9.23	6.61	4.37	4.54	9.37	14.7
	Microporella californica		0	0	0	0	0	0.55	0.56	0.83	0.97	0.24	1	0.5	0.68
	Microporella ciliata		0	0	0	0	0.14	0.16	0.21	0	0.33	0.53	0.42	0.38	0.68
	Oncousoecia ovoidea		0	0	0	0	0	0	0	0	0.06	0.02	0	0	0
	Rhamphostomella costata		0	0	0	0	0	0	0	0	0	0	0	0	0.26
	Schizoporella unicornis		0	0	0	0	0	0	0	0	0	0	0	0	0
	Tricellaria erecta		0	0	0	0	0	0	0	0.11	0.05	0	0	0	0
Mollusca															
	Mytilus trossulus		0	0	0	0	0	0	0.15	0	0	0	0	0	0
Annelida															
	Eudistylia vancouverensis		0	0	0	0	0	0	0	0	0.43	0.66	0.89	1.02	0.67
	Serpulids		0	0	0	0	0	0.04	0.08	0.1	0.2	0	0:01	0.24	0.23
	Spirorbids		0	0	0	0	0	0	0	0	0	0	0	0	0
	Terebellids spM.		0	0	0	0	0.26	0	0	0	0	2.41	0.44	0	0
	Terebellids spS.		0	0.02	0.08	0.08	0	0	0	0	0	0	0	0	0
Porifera															
	Haliclona sp.		0	0	0	0	0	0	0	0	0	0	0	0	0
	Leucosolenia sp.		0	0	0	0	0	0	0	0	0	0	0	0	0
Urochordata															
	Botrylloides violaceus		0.02	0	0	0	0	0	0	0	0	0	0	0	0
	Cnemidocarpa finmarkiensis		0	0	0	0	0	0	0	0.14	0	0	0	0	0
	Distaplia occidentalis		0	0	0	0	0	0.13	0	0	0.63	0.79	0	0	0
	Styela gibbsii		0	0	0	0	0	0	0	0	0	0	0	0	0
	BARE SPACE		99.4	99.9	99.9	97.3	85.8	35.8	38.2	52.8	52.6	54.7	63	67.4	69.3

Table 14. Mean Percent Cover for All Species at the Point Adams Jetty During Experiment 2 Between September 1990 and February 1992

	Sample Period:	1	2	4	5	6	9	10	11	13	14	15	16	17
	Month:	N	D	J	F	A	J	A	S	O	N	D	J	F
PHYLUM	Species Days:	28	55	114	141	193	264	307	340	383	410	438	470	500
Cirripedia														
	Balanus glandula	0	0.01	0	0	0	0.49	1.71	1.51	2.82	3.02	2.95	2.81	2.71
Cnidaria														
	Metridium senile	0	0	0	0	0.06	0.02	0.28	0	0.31	0.43	0.89	0.76	1.13
	Obelia spp.	0	0.5	0.5	2	4	7	2.25	0.43	0	0	0	0	0
	Scyphistomae (Aurelia spp.)	0	0	0	0	0	0.07	0.06	0	0	0	0	0	0
Ectoprocta														
	Alcyonidium polyoum	0	1.01	1.12	2.96	6.91	6.19	3.15	0.34	0	0	0	0	0
	Bowerbankia gracilis	0	0	0	0	0	0	0	0	0.28	0.58	0	0.08	0
	Bugula pacifica	0	0.11	0.28	0.32	0.68	0	0.36	0.92	0.55	0.95	0.78	1.48	1.73
	Cheilopora praelonga	0	0.1	0.34	1.09	0.62	3.18	2.73	5.11	0.69	0	1.15	0	0.93
	Conopeum tenuissimum	0	0.02	0.01	0	0	0	0	0.14	0	0	0	0	0
	Cribrilina annulata	0.01	0.16	0.15	0.07	0	0	0	0	0	0	0	0	0
	Crisia occidentalis	0	0	0	0	0	0	0	0	0	0.01	0.07	0.07	0.08
	Cryptosula pallasiana	0	0	0	0	0	0.82	1.41	0.91	0.05	0	0	0	0
	Dendrobeania lichenoides	0	0	0	0	0	0	0	0	0	0	0	0	0
	Hippothoa hyalina	0.02	0.59	0.71	0.39	0.41	0.46	1.34	1.53	0.68	0.33	0.83	0.31	0
	Microporella californica	0	0.04	0.08	0.11	0.04	0	0	14.6	0	0	0	0	0
	Microporella ciliata	0	0	0	0	0	0	0	0	0	0	0	0	0
	Oncousoecia ovoidea	0	0	0	0	0	0	0	0	0	0	0	0	0
	Rhamphostomella costata	0	0	0	0	0	0	0	0	0	0	0	0	0
	Schizoporella unicornis	0	0.72	1.25	1.59	3.22	59.2	67.2	58.4	50.2	33.6	40.8	37.7	38
	Tricellaria erecta	0	0	0	0	0	0	0.62	0.44	0.22	0.17	0.5	0.08	0.25
Mollusca														
	Mytilus trossulus	0	0	0	0	0	0	0	0	0	0	0	0	0
Annelida														
	Eudistylia vancouverensis	0	0	0	0	0	0	0.07	0	0.07	0.17	0.08	0.41	0.2
	Serpulids	0	0.05	0.13	2.73	0.17	0.88	1.16	0.31	0	0	0	0.04	0.05
	Spirorbids	0	0	0	0	0	0.03	0	0	0	0	0	0	0
	Terebellids spM.	0	0	0	0	0	0	0	0	0	0	0.17	0.1	0
	Terebellids spS.	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera														
	Haliclona sp.	0	0	0	0	0	0	0	0.59	0.97	1.01	0.11	0.2	0
	Leucosolenia sp.	0	0	0	0	0	0	0	0	0	0.22	0	0	0.36
Urochordata														
	Botrylloides violaceus	0.39	1.17	7.41	43.2	52.4	1.77	10.8	5.06	4.63	10.3	9.7	14.2	17.5
	Cnemidocarpa finmarkiensis	0	0	0	0	0	0	0	0	0	0	0	0	0
	Distaplia occidentalis	0	0	0	0	0	0	0	7.14	36.7	43.4	22.3	14.3	13.3
	Styela gibbsii	0	0	0	0	0	0	0	0	0	0	0.29	0	0.3
	BARE SPACE	99.6	95.5	88	45.5	33.7	19.9	7.88	3.89	4.09	6.5	19.3	27.5	23.5

between June and September 1991 (mean = 243 individuals•half block^{-1}•sample period^{-1}, with a range between 24 and 750 individuals) . The siphons of these infaunal clams were <10 mm away from the settlement surface of the experimental plates, and thus may have drastically altered the larval supply during this period (*Tresus* were removed at each sample date). Second, during the August 1991 sample period, sediment accumulation was extremely high. In at least one instance a plate suffered anoxic conditions that may have reduced larval settlement or caused resident mortality (although none was observed).

Community Statistics

The North Jetty colonization curve shows an increase in species number; no asymptote or dynamic equilibrium is identifiable (Figure 46; Table 15). In contrast, species number at the invaded site increases rapidly and after the third sample period (December 1990) remains at about seven species per panel (Figure 47; Table 15).

Diversity (H') of the living cover increases gradually for the North Jetty community (Figure 48). Diversity at the invaded site increases initially to a mean of 1.25 but after 6 months drops to a mean below 0.7 (Figure 49). Evenness (J') exhibits similar patterns to the Shannon-Weaver diversity index. At the North Jetty the increase in mean evenness is consistent throughout the 17 mo sampling period (Figure 50). Similarly, the Point Adams Jetty evenness follows the same pattern as that for diversity. Evenness rises immediately to a high evenness which declines to a mean of less than 0.5 within the first five months and then increases to 0.6 during the last 4 months (Figure 51).

The two dominance measures, MD and the number of dominant species that comprise 75% of occupied space, exhibit very similar results. Both the North Jetty and Point Adams Jetty communities are dominated by a few species. McNaughton's index (MD) shows that at both sites the top two space occupiers on any given panel hold at least half

Table 15. Summary of Monthly Community Richness Statistics During Experiment 2 Between September 1990 and February 1992.

Site	Sample Period (mo)	TOTAL S	Mean S	S.D.	N	Maximum S	Minimum S
Native							
North Jetty	1	3	0.8	0.5	4	1	0
	2	3	2.8	1.0	4	4	2
	4	3	4.3	0.5	4	5	4
	5	3	1.3	2.5	4	5	0
	6	5	3.0	1.6	4	5	1
	9	10	6.0	0.8	4	7	5
	10	8	3.0	3.5	4	6	0
	11	9	3.3	2.6	4	7	1
	13	11	6.3	0.5	4	7	6
	14	10	6.0	2.9	4	9	2
	15	10	2.3	1.0	4	3	1
	16	9	3.8	0.5	4	4	3
	17	10	4.5	0.6	4	5	4
Invaded							
Point Adams	1	3	6.3	2.2	4	8	3
	2	12	6.8	3.0	4	10	3
	4	11	6.8	0.5	4	7	6
	5	10	4.0	2.6	4	6	1
	6	10	6.5	1.0	4	7	5
	9	12	7.8	0.5	4	8	7
	10	14	6.0	3.4	4	8	1
	11	15	5.5	2.5	4	8	2
	13	13	6.3	1.7	4	8	4
	14	13	8.5	2.4	4	10	5
	15	14	4.8	3.4	4	8	0
	16	14	5.5	0.6	4	6	5
	17	13	6.0	1.4	4	8	5

and generally more than 80% of the occupied space (Figures 52 and 53). Similarly Osman's method demonstrates that in no instance were more than three species co-dominant (Figures 54 and 55).

Introduced Species

The Point Adams community has several non-indigenous species that dominated the community (>50% cover) during much of the study (Figure 56). The three introduced species *Schizoporella unicornis*, *Botrylloides violaceus*, and *Botryllus schlosseri* are the most common non-indigenous members of the community. Here I treat the cryptogenic species (origin unknown *sensu* Carlton 1979b) as members of the introduced group; these species include *Bowerbankia gracilis,* and *Cryptosula pallasiana*. Introduced species contribute disproportionately to the community statistics of diversity (H') and dominance. The group (3 introduced and 2 cryptogenic species) comprises 20% of the total species seen during experiment 2 (5 of 25 species). The actual γ-diversity for Point Adams Jetty is 66 native encrusting species, 5 introduced and 3 cryptogenic species (Chapter 1), and thus the introduced group comprises less than 11% of the total species pool.

The information index may be partitioned such that the relative contribution (percent of H') of one species (or group of species in this case) can be compared with the expected distribution based on the species' (or group's) percentage of total species present (percent of S; Smith et al. 1979). Introduced species' contribution to the information index is significantly greater than expected based on their relative percentage of community richness in any given assemblage ($G_{[1]} = 5.44$, $p<.05$; Figure 57).

As noted above, the Point Adams Jetty assemblages tend to be dominated by less than three species at any one time (Figure 55). Through time the dominant species on any one panel at time *t* is more likely to maintain dominance until *t*+1; hence the results from a series of samples on the same panel are confounded with time. To avoid problems with temporal pseudo-replication (*sensu* Hurlbert 1984), the percent of dominant species (as defined by the 75% index) that are introduced was calculated for each time point and then averaged for the entire time series for a single panel. Thus a single datum was generated for each panel. The average was taken as the estimate of introduced species contribution to dominance and was equal to 69.2% (s.d.= 20.9, n = 4).

The effect of introduced species on native species percent cover was a result of overgrowth interactions (*pers. obs.*) and exploitative competition. The dominant introduced species, *Schizoporella unicornis* and *Botrylloides violaceus*, were highly resistant to larval recruitment (epibiosis), yet were able to recruit onto a variety of species substrates (Figure 58), resulting in the subsequent overgrowth of the substrate species. This is supported by the temporal shift from moderately to strongly negative correlation coefficients between the abundance of introduced and native species ($r^2 = 0.58$, n = 11, $p<.001$; Figure 59).

Community Dynamics

The immigration and extinction rates were linearly regressed against the number of species present for all panels at the two sites. For this analysis, only the closed (100% mesh cover) treatment in the first experiment (1989-1990) was used. Analysis of covariance (ANCOVA), using the number of species present as the covariate, showed highly significant differences in immigration rates between adjusted site means ($p<.001$), and within-site slopes ($p<.001$) and indicated that for both the first experiment (April 1989 to August 1990; Figure 60) and the second experiment (September 1990 to February 1992; Figure 61) a single line was not sufficient to explain all points (pooled regression $p>.05$). ANCOVA for extinction rates however, showed no significant difference in extinction rates between adjusted site means (between site $p > .05$), or within-site slopes ($p > .05$) and indicated that a single regression was sufficient to describe the extinction curve for all points (pooled regression $p < .001$).

As can be seen in Figure 61, immigration at the North Jetty during the second experiment is not signicantly different from zero ($r^2 = 4 \cdot 10^{-4}$, $n = 52$, $p > .05$). Thus one of the criteria of the equilibrium model has been violated. Both Simberloff (1969) and Schoener (1974a, b) have argued that the estimates of immigration and extinction may be biased due to unobserved immigration and extinction events between sample periods. For most taxa in this system, immigration is primarily from larval recruitment and once metamorphosed, the taxa are permanently attached. Similarly, an extinction event would generally be identifiable by the calcareous skeletal remains of most taxa. The following analysis must therefore be tempered by knowledge that this violation may underestimate the value of $\hat{S}$ for North Jetty communities.

From the theory of island biogeography, a prediction of the dynamic equilibrium ($\hat{S}$) can be generated from the intersection of the immigration and extinction curves. This provides an estimate for comparison with the colonization curves presented earlier (Figures 44 and 45 for experiment 1; Figures 46 and 47 for experiment 2). The predicted species equilibrium at the native site (North Jetty) is 15.9 species during experiment 1, but 7.2 species during experiment 2. As noted for the North Jetty, the curves for extinction during experiment 1 and immigration during experiment 2 are not significantly different from zero and consequently the predictions of dynamic equilibrium must be viewed with some degree of skepticism. At the invaded site (Point Adams Jetty) the predicted values of S are different between the two experiments with 10.9 species predicted in experiment 1 (Figure 60) and 7.1 species predicted in experiment 2 (Figure 61).

At the invaded site the immigration and extinction rates of the complete species pool were contrasted with those for the native species component of the pool in order to observe the change in the expected species equilibrium ($\hat{S}$) both with and without introduced species. The immigration regression lines for the total species pool and the native component show slight changes in slope (Figures 62 and 63). The extinction lines however, do not appear to differ. For the first experiment the total species pool predicts an equilibrium of 10.9 species while the species pool for natives only is 10.7. Similarly, in the second experiment the total species pool and the native pool both predict 7.1 species.

The boundedness of species richness was evaluated for experiment 1 (the entire duration) and experiment 2 (months 1 to 5 and 6 to 17). For each panel the mean S, coefficient of variation (CV), n (time periods) and calculated ω (Keough and Butler 1983) are presented in Table 16. The results of the one-tailed t-test with n-1 degrees of freedom are also presented (H_0: $CV_x \leq 15.3\%$; H_1: $CV > 15.3\%$). During experiment 1 neither the North Jetty and Point Adams Jetty closed treatment communities were found to be stochastically unbounded (Figures 44 and 45; Table 16).

With more extensive samples available for experiment 2, the data were analyzed for the two time periods previously described (months 1 to 5, October 1990 to February 1991; and months 6 to 17, April 1991 to February 1992). During the initial time period, none of the panels at either site satisfied the criteria for boundedness (Table 16, unable to calculate ω's due to high CV's). The North Jetty assemblages during the second time period were highly variable (H_0 rejected) with a single exception (ω = 0.27). At the invaded site three panels were bounded (ω's < 0.21) with one panel exhibiting high variability (ω = 0.41).

Through time the experiment 2 assemblages at the native site increase in Bray-Curtis similarity to one another, approaching a mean of 60% with a decreasing range of values (Figure 64). In contrast, on average the Point Adams communities are initially more similar to one another (Figure 65) although they are much more variable. By the end of the experiment, they too have approached a mean similarity of 60% and the range has

Table 16. Stochastic Boundedness of Species Richness for North Jetty and Point Adams Jetty Replicates During Experiments 1 and 2. Panel Replicates are Denoted by Letter, S is the Mean Species Richness, CV is the Coefficient of Variation, and N is the Number of Sample Periods. See Text for Description of Stochastic Boundedness.

Source	Panel	S	CV	N	ω	p value
Experiment 1						
North Jetty	A	12.0	48.87	6	0.27	ns
	B	11.5	48.80	6	0.27	ns
	C	10.0	43.82	6	0.26	ns
Point Adams Jetty	A	8.4	26.08	5	0.14	ns
	B	8.6	35.46	5	0.17	ns
	C	9.8	39.12	5	0.17	ns
	D	9.2	29.17	5	0.15	ns
Experiment 2						
North Jetty						
months 1 to 5	A	0.5	115.50	4		*
	B	0.0	-	4		*
	C	0.3	200.00	4		*
	D	1.8	71.90	4		*
months 6 to 17	A	3.5	36.26	10	0.38	*
	B	4.8	42.58	10	0.43	*
	C	5.8	37.95	10	0.40	*
	D	3.8	24.18	10	0.27	ns
Point Adams Jetty						
months 1 to 5	A	3.0	98.13	4		*
	B	3.8	102.99	4		*
	C	3.3	121.46	4		*
	D	4.5	82.15	4		*
months 6 to 17	A	7.6	6.79	10	0.08	ns
	B	6.7	39.20	10	0.41	*
	C	5.7	16.64	10	0.19	ns
	D	7.0	17.82	10	0.20	ns

* - $p<.05$

decreased. The two sites however have very different assemblages: the mean monthly similarity between sites (all panel comparisons between sites averaged), demonstrates that while within-site community structure is converging (60% similarity), the between-site similarity is less than 10% at any time (Figure 66).

As species temporally appear in the community they either remain within the assemblage or go extinct. The cumulative species distributions for the North Jetty and Point Adams Jetty communities exhibit large initial differences (Figure 67). Within the first 55 days the Point Adams Jetty communities have accumulated on average 7 species, as opposed to 1 species at the North Jetty. After five months the slopes of average accumulated species for the two sites are very similar.

The correlation between the realized diversity of a sample and the cumulative diversity the sample has experienced (the history of species in the assemblage) is a measure of the openness of community membership. The predicted correlation for assemblages with unlimited membership would be a slope of 1.0, that is all species will enter and remain in the community. The North Jetty site has a pooled slope of 0.63; that is roughly two-thirds of the species that have entered the community are still present. In contrast the invaded Point Adams site has a pooled slope of 0.42, and thus less than half of the species have successfully entered and remained in the community (Figure 68).

Community Composition

In order to assess the nature of compositional development (i.e., seasonal, successional, or random), the sequence of individual species appearance in experiment 2 is described below for each taxon.

Cirripedia

Balanus glandula was the only barnacle encountered during the assembly of communities at the North Jetty and Point Adams Jetty. At the North Jetty, *Balanus* settled on one panel at low densities between initial deployment and February 1991 (141 days). In the following sample period (April 1991) a small settlement had occurred on three panels (mean = 9 individuals•panel^{-1}, s.d. = 11.7, n = 4) constituting <2% cover on any panel. Beginning in June (day 264) and continuing until September, *Balanus* settlement (Figure 69) increased from an average 123.5 individuals•panel^{-1} (s.d. = 77.8, n = 4) to 266.7 individuals•panel^{-1} (s.d. = 306.9, n = 4). This increased *Balanus* contribution to the community from less than 1% in April to an average of 42.8% in August and 32.0% in September (Figure 70). Immediately following the peak recruitment events, there was significant mortality, evidenced by numerous basal plates and dead tests. Cohort survival showed a significant exponential decrease for *Balanus* following the peak recruitments (Figure 71). Although the cohort survival was low (p_{50} = 47.4 days), *Balanus* continued to hold an average of 30% space until December 1991 (day 438), after which time mortality continues to reduce the percent cover (Figure 70).

At the invaded site, Point Adams Jetty, *Balanus glandula* was conspicuous in its relative rarity. At no time did its contribution to living cover exceed 10.0% on any panel (maximum 8.2%) and the maximum mean was 3.0%. No significant recruitment events were observed at Point Adams Jetty.

Cnidaria

Three cnidarians settled on the panels during the course of community assembly, a hydrozoan, *Obelia* spp., scyphistomae presumably of *Aurelia* sp., and an anthozoan, *Metridium senile*. Neither scyphistomae nor *Metridium* were seen on the panels at the North Jetty. *Obelia* was present at the North Jetty during all but one sample period (August 1991) but never exceeded 5.0% cover (Figure 72). At the invaded site *Obelia* colonized after 55 days (December 1990) and remained present at some point on all four replicate panels until September 1991 (340 days).

Scyphistomae were present on one panel at Point Adams during two sample periods: June and August 1991. They covered less than 1.0% space at all times. *Metridium senile* can be relatively large and extremely mobile, in comparison to other members of this community. The presence of single individuals on three panels at Point Adams had no discernible temporal pattern.

Ectoprocta

Sixteen species of ectoprocts (bryozoans) were identified during community assembly. Eleven species were seen at the North Jetty (Table 13) and 12 at Point Adams (Table 14). Of the 11 bryozoans in the North Jetty communities seven species, *Bugula pacifica, Cribrilina annulata, Crisia occidentalis, Dendrobeania lichenoides, Oncousoecia ovoidea, Rhamphostomella costata,* and *Tricellaria erecta*, were minor components, never attaining more than 2.0% space. *Bugula* and *Dendrobeania* recruited during the June sample period; the remainder settled late in the assembly sequence during September, October and November.

Of the remaining species, the earliest recruits were *Hippothoa hyalina* and *Microporella ciliata* in February 1991 and April 1991 respectively. *Hippothoa* was ubiquitous, being found on all plates for the duration of the study. On three plates it controlled more than 20.0% of available space for short periods (57.1, 36.2, and 20.9%; Figure 73). By the June sample period (day 264), *Microporella californica* had settled on one plate and throughout the study continued to increase in area (maximum of 4%). *Cheilopora praelonga* was found on all plates at an average of 4.0% space occupancy, and reached a single plate maximum of 22.7% in September 1991 (Figure 74).

At Point Adams five species attained less than 2.0% space during the study; these were *Bowerbankia gracilis*? (cryptogenic), *Cribrilina annulata, Crisia occidentalis, Conopeum tenuissimum* (introduced), and *Tricellaria erecta*. *Cribrilina* and *Conopeum* were early recruiters, settling within the first two sample periods, whereas the other three species settled after August 1991. *Hippothoa hyalina* recruited during the initial 28 day period (as did *Cribrilina annulata*) reaching a maximum of 5.0% space on one panel (Figure 73). During the December 1990 sample period (day 55) *Alcyonidium polyoum*?, *Cheilopora praelonga, Microporella californica,* and *Schizoporella unicornis* (introduced) recruited. *Alcyonidium*, *Cheilopora*, and *M. californica* settled on a maximum of two plates, but all three attained maximum plate densities of >20.0%. *Alcyonidium* occupied a maximum 27.1% (average of 6.91%), and *Cheilopora* reached 20.4% (maximum average of 5.1%; Figure 74).

The introduced Japanese bryozoan, *Schizoporella unicornis*, settled on all four Point Adams Jetty plates by day 55, and attained no less than 39.0% cover on all plates (plate maxima: 39.6, 82.2, 89.9, and 93.9%; Figure 75). *Schizoporella* did not go extinct from a plate once it recruited. Individual colonies had the ability to survive long periods of overgrowth (generally by compound ascidians) of up to 180 days (Figure 76). *Cryptosula pallasiana*, a cryptogenic species, settled on one panel in June 1991 and reached a maximum density of 5.6%.

Mollusca

The native mussel, *Mytilus trossulus*, was the only mollusk observed during community assembly and was a minor component. A single individual settled on one plate at the North Jetty during the August sample period (day 307) at 0.6% cover. No mussels were observed on the plates at Point Adams Jetty.

Annelida

Four identifiable taxa of polychaetous annelids were found at the two sites during this study. Spirorbids were not found on the panels at the native site. Terebellids were patchily distributed between panels at the North Jetty between December 1990 and May 1991. During any one sample period one panel had terebellids present at low (<2.0%) densities. In November 1991 terebellids on one panel reached densities of 9.6% declining to 1.8% in the following month. Serpulids settled on one panel in June and August 1991 but never achieved densities higher than 1.0%. *Eudistylia* spp. (*E. polymorpha* and *E. vancouveri*) were found on one panel between October 1991 and February 1992, at densities up to 4.1% (Figure 77).

Spirorbids at the invaded site were found at less than 1% during one sample (June 1991) on a single panel. Similarly terebellids were found on a single panel at densities less than 1% during December 1991 and January 1992. Serpulids were found to settle early (December 1990) on three of the four panels. This group achieved mean densities of 2.7% (a panel maximum of 7.7%; Figure 78) in February 1991 through growth of individuals settled in December (one individual per panel). *Eudistylia* spp. settled on three panels during the later half of the study (August and October 1991 and February 1992) but never achieved densities greater than 2.0%.

Porifera

No sponges were observed at the native site during the assembly of communities. At the invaded site however, two sponges were present. *Halichondrea panicea* was present on a single panel and achieved densities of 4.0% by November 1991. *Leucosolenia* spp. was observed during separate sample periods on two different panels and reached densities of 1.4% in February 1992.

Tunicata

Three native tunicates, *Cnemidocarpa finmarkiensis, Distaplia occidentalis,* and *Styela gibbsi*, and one introduced tunicate, *Botrylloides violaceus*, were observed during the assembly process. At the North Jetty a single *Cnemidocarpa* recruit was seen during the September 1991 sample, but was not found at the subsequent sample date (October 1991). Single individuals of *Distaplia occidentalis* recruited at two different times (June 1991 and October 1991) to two panels. One colony reached densities of 3.2% after two sample periods. A single, newly settled botryllid recruit (single zooid) was found during the first sample period at the native site but did not survive to the next sample period.

Invaded site tunicates included *Distaplia occidentalis, Styela gibbsi*, and *Botrylloides violaceus*. The solitary ascidian, *Styela,* settled on three panels but never achieved densities greater than 2.0%. *Distaplia*, a native colonial, settled on three panels during the September sample period and on the fourth panel in the following month and remained in the assemblages until the last sample date (February 1992; Figure 79). This species reached mean densities of 43.4% in November, and had panel maxima of 27.0, 31.1, 50.5, and 85.4%. *Botrylloides* first settled on three panels during the first sample period and on the fourth panel in June 1991and continued to have larval immigration throughout the study. Maximum mean densities of 52.4% were reached in April 1991 with panel maxima of 17.1, 93.8, and 98.6% in April and 39.8% in August (Figure 80).

Discussion

The non-interactive model of island biogeography (Wilson 1969) appears to apply to the native communities of the North Jetty. The experiment 1 assemblages had achieved a level of constancy ("stability") in species number after 16 months but had values of S lower than predicted. The species extinction events however were not correlated with the resident species richness (non-significant regression). Similarly the immigration rates in experiment 2 were not correlated with resident species richness resulting in wide variations (CV > 30%) in species richness which violated the tests of stochastic boundedness (Keough and Butler 1983).

Schoener (1974a, b) demonstrated that in several sites around the world the encrusting communities slowly accumulated species and that no biogeographic pattern in S could be discerned. In her studies the communities often failed to achieve a stable species number, which she attributed to seasonal variations in larval supply (immigration rates).

The invaded communities in experiments 1 and 2 achieve stable species numbers after the initial faunal buildup. These communities are also adequately described by the non-interactive model of island biogeography since the observed extinction rate was not exponentially correlated with resident species richness. The communities that developed at the invaded site however, became increasingly closed to species addition, that is the membership became limited as space became dominated by the introduced species.

Sutherland (1974, 1977a, b 1978) and Sutherland and Karlson (1977) found that certain species assemblages were persistent (stable), resisting larval recruitment (immigration) of all other species (*Styela*-dominated assemblages) or most other species (*Schizoporella*-dominated assemblages). In these systems, mortality (senescence) was the predominant means of vacating space and altering community structure. The resultant multiplicity of assemblage types were deemed "alternate stable states" (Sutherland 1974, 1981).

Is $\hat{S}$ a good estimator for these communities? At the invaded site the estimated $\hat{S}$ for the first experiment for closed treatment assemblages was determined to be 10.9 species (Figure 60). The actual species richness attained by the assemblages varied between 12 and 7 species, although during the last three sample periods the closed treatment assemblages averaged at 10 species (Figure 45). For the second experiment an $\hat{S}$ of 7.09 species was predicted from the immigration/extinction equilibrium (Figure 61). The mean species number across the four assemblages varied around 7 species (Figure 47). As has been demonstrated statistically, the apparent boundedness of these communities suggests that there is no trend away from the state in which they are presently found. This is not to say that the species composition will not change, but that the species richness (number) is sufficiently described as a dynamic equilibrium.

The differences between $\hat{S}$ in experiments 1 and 2 for both sites may be due to the seasonal changes in larval availability. Osman (1977, 1978) has shown that the larval availability varies seasonally and directly alters the colonization (immigration) curves for encrusting species which alter $\hat{S}$ accordingly. In the Woods Hole, Massachussetts communities, he demonstrated that the season of exposure may alter not only the rate of species accumulation but also the recovery period to a dynamic equilibrium. The study conducted in Coos Bay did not attempt to assess the seasonal component of community assembly, and with two initial time points cannot demonstrate any effect.

Osman and Whitlach (1978) have provided a series of predictions for the effects of an increase in the regional species richness, R (γ-diversity of Whittaker 1960, 1972) on $\hat{S}$ and the extinction/immigration ratio *e/m* (where *e* is the specific extinction rate and *m* is the basal immigration rate with 0 species present in the patch). They found that for R to increase $\hat{S}$ may either increase, stay the same or decrease depending on the value of *e/m*, but in all instances the value of *e/m* must change. For $\hat{S}$ to increase, the value of *e/m* must decrease either through a substantial increase in immigration or a reduction in extinction. If $\hat{S}$ stays the same, *e/m* must change very little either by a decrease in immigration or a slight increase in extinction. For $\hat{S}$ to decrease a substantial increase in the extinction rate is necessary in a sufficient number of patches to alter the regional *e/m* ratio.

The regional diversity in the encrusting communities of the lower Coos Bay (within the Point Adams Jetty "region") has been increased by at least 9 species in ecological time. Examination of the difference in $\hat{S}$ (derived from the immigration and extinction rates) between the total species pool and the native component of the species pool suggests that no change in equilibrial state (realized S) has occurred. Yet the *e/m* ratio has decreased due to the high immigration rate of the new members of the community and no apparent reduction in extinction rates (Figures 62 and 63). Osman and Whitlach (1978) provide a *caveat*; there exist many circumstances in which a species addition may result in the replacement of species such that R does not increase.

A species addition can be described as a community perturbation away from equilibrium (Ritte and Safriel 1977; Sutherland 1981; Pimm 1984). In the face of dominant invaders this perturbation may be sufficient to force the community from one community state (or trajectory) to a separate "basin of attraction" (Lewonton 1969; Sutherland 1974, 1981). These community level alterations have been documented in several invaded systems (Pimm 1984, 1987, 1991; Pimm and Hyman 1987). The Great Lakes of North America have been recently invaded by the zebra mussel, *Dreissenia* *polymorpha*, which is altering planktonic and benthic community structure (Mills et al. 1993). Similarly the soft substrate communities of San Francisco Bay have recently been invaded and replaced by the asian clam, *Potamocorbula amurensis* (Nichols and Thompson 1985; Carlton et al. 1990; Nichols et al. 1990). In this system, the communities that develop in the presence of the introduced species have altered patterns of species accumulation on highly disturbed patches (clean settlement panels). The native communities develop slowly with seasonal recruitment events that stochastically alter community composition (e.g., barnacle settlement and mortality). In contrast the introduced species dominate the communities at the invaded site and shift the community composition.

The results for the native communities in this study do not indicate a successional pattern (directional change) in species composition but point to an open system in which species composition is largely controlled by immigration (Figure 68). These communities are similar to Schoener's (1974a, b) findings that throughout the assembly process species continue to accumulate with no apparent equilibrium. Comparisons of community composition at the endpoints of experiments 1 (August 1990) and 2 (February 1992) as well as the August 1991 sample of experiment 2, demonstrate the lack of a "climax" community at this site (Figure 81). The three taxa, *Balanus, Cheilopora,* and *Hippothoa* were consistently present but in varying densities and ratios. The lack of significant immigration at the North Jetty until *Hippothoa* recruits in February 1991, leaves more than 80% of the space available for settlement. Even after the high settlement of *Balanus* (August to September 1990) the amount of free space remains at an average of 40%. Thus the competitive interference and exploitative effects of primary space occupancy are not seen during the 17 months of community development at this site.

The Point Adams Jetty communities in contrast are quickly colonized by several species, including the introduced species, *Schizoporella unicornis* and *Botrylloides* *violaceus*. Here, the unoccupied space is quickly reduced (less than 5% in three panels by April 1991). If one examines the *fundamental species* (Sutherland 1977a, b, 1978; Sutherland and Karlson 1977), species which occupy at least 10% of living space at any time during the assembly, the sequence of appearance is highly ordered. *Botrylloides* and *Schizoporella* recruit in the first two sample periods. *Botrylloides* reaches a peak abundance in April 1991and the colonies senesce by June. This exposes the *Schizoporella* colonies that have survived overgrowth and by August *Schizoporella* reaches peak abundance. *Distaplia* recruitment and subsequent growth reduces the cover of *Schizoporella* again by direct overgrowth. *Distaplia* senesces shortly after it peaks (November - December) and re-exposes the overgrowth resistant *Schizoporella* colonies. At this point the space is divided between *Schizoporella*, *Distaplia,* and new *Botrylloides* recruits (on two panels). Occasionally this sequence is altered by the early recruitment and space occupation by a species that is resistant to fouling by other species (e.g., *Alcyonidium* in one panel and early *Schizoporella* recruitment in a second). This "successional" pattern manifests itself to some extent in all four panels as demonstrated by comparisons of community composition at the endpoints of experiments 1 (August 1990) and 2 (February 1992) as well as the August 1991 sample of experiment 2 (Figure 82).

Sutherland (1974, 1977a, b, 1978) demonstrated that two alternate stable states exist in the encrusting communities of Beaufort, North Carolina. The solitary ascidian, *Styela plicata*, and the bryozoan, *Schizoporella errata* develop dense monocultures which resist the settlement of other species and thus have the propensity to hold space and persist for long periods of time, shifting states only with the massive die-off of the entire assemblage. The adults of both species were good competitors, able to gain and hold space. In this system however, the larvae of *Schizoporella errata* were poor interference competitors, i.e., they were unable to recruit onto occupied substrate.

The Japanese fauna from which *Schizoporella unicornis* and *Botrylloides violaceus* were introduced is a diverse assemblage of encrusting species with a large number of tunicates and bryozoans (Hirata 1986, 1987, 1991; Nandakumar et al. 1993). Within these communities the competitive abilities of *Schizoporella* and *Botrylloides* relative to the other bryozoans and tunicates are low. Hirata (1987) considers both species to be transitional in that they settled on fouling panels after 4 months of initial immersion and were replaced after 13 months. *Schizoporella* never achieved densities greater than 3% and *Botrylloides* reached maximum densities of 20% space. Yet in the invaded communities of Coos Bay these two species are competitive dominants for space with the ability to overgrow a majority (90%) of the native species, generally reaching maxima of greater than 90% space coverage.

Both introduced species recruit year-round (Powell 1970; Ross and McCain 1976; Chapter 1) at moderate densities with peak recruitment in mid to late summer at levels of 20 to 45 recruits•panel^{-1}•mo^{-1}. The majority of native encrusting species recruit during limited periods of the year (Chapter 1: Figure 20) at moderate densities. *Schizoporella* and *Botrylloides* both have the ability to settle on a wide variety of other species as substrates; that is few native species resist epizooism by *Schizoporella* and *Botrylloides*. From the opposite perspective, the introduced species are highly resistant to being settled upon by most species (Figure 58). Two native species have comparable resistance to epizooism, *Cheilopora praelonga* and *Distaplia occidentalis*. While *Distaplia* recruits at similar densities, it recruits during a short period in September (Chapter 1).

In Coos Bay the competitive hierarchy of the invaded site demonstrates that, with few exceptions, the introduced species are dominant. *Botrylloides* and the native tunicate *Distaplia* tie; both outcompete *Schizoporella unicornis*; but the ability of the bryozoan to resist the lethal effects of overgrowth prevents competitive exclusion and local extinction. Thus *Schizoporella*, the inferior competitor, is the most persistent of the three. Todd and

Turner (1988) documented a variety of bryozoans with the ability to undergo long periods of non-lethal overgrowth. *Schizoporella unicornis* is a member of the Scottish encrusting community and they documented its ability to withstand overgrowth by a variety of colonial tunicates, including *Botryllus schlosseri* and *Botrylloides leachii,* for 50 to 165 days. They speculated that the alterations in the competitive hierarchy by these examples of incomplete interactions may add an additional stochastic component to community diversity. I have documented similar periods of overgrowth survival in Coos Bay for *Schizoporella unicornis* (Figure 76).

The communities at these two sites, a native, uninvaded site (North Jetty) and the invaded Point Adams Jetty, have very different patterns of community development. The North Jetty communities accumulate species throughout the study but with no discernible pattern. These communities have high quantities of bare space at all times, interspersed with periods of high species specific recruitment (e.g., *Balanus glandula*). Thus these communities appear to be alternately disturbance and recruitment driven systems. In contrast the invaded site exhibits a sequential addition and replacement of species that is identical in all replicate panels.

This directional change in species composition cannot be deemed "successional" because it appears to be driven by introduced species. These introduced species have however, drastically altered the pattern and trajectory of community development through the domination of primary space. As invaders the Japanese species have a unique array of life history traits which contribute to their position in the community. The availability of larval recruits year-round will increase the likelihood of available space being occupied by these species. This recruitment effect is increased by the recruitment abilities of *Schizoporella* and *Botrylloides.* The amount of space that is perceived to be available by *Schizoporella* and *Botrylloides* includes both the bare space on a panel but also the space occupied by species that are susceptible to being settled upon. Thus at any given time the larvae of these introduced species are more likely to recruit than their native counterparts. Once these species have established colonies, they have the competitive overgrowth abilities to expand and outcompete 90% of the native species. These colonies also resist the larval recruitment by native species, and thus maintain space through a combination of interference and exploitative mechanisms.

There is now evidence that the solitary tunicate of Sutherland (1974, 1977a, b, 1978) and Sutherland and Karlson (1977), *Styela plicata* has been introduced to the Atlantic coast of North America (J. Carlton *pers. comm.*). Thus Sutherland, without realizing it, elucidated a system in which an alternate stable state was established by an introduced species. The community at the Point Adams Jetty in this study has been invaded by several introduced species which together dominate the space and alter the community development. In comparison with the native, uninvaded communities at the North Jetty these introduced species have had drastic effects and are responsible for shifting the community into an alternate basin of attraction (Lewontin 1969). While this alternate state is not stable in the sense of being unchanging (Sutherland 1981; Pimm 1984), the community has experienced a compositional shift that was not previously accessible.

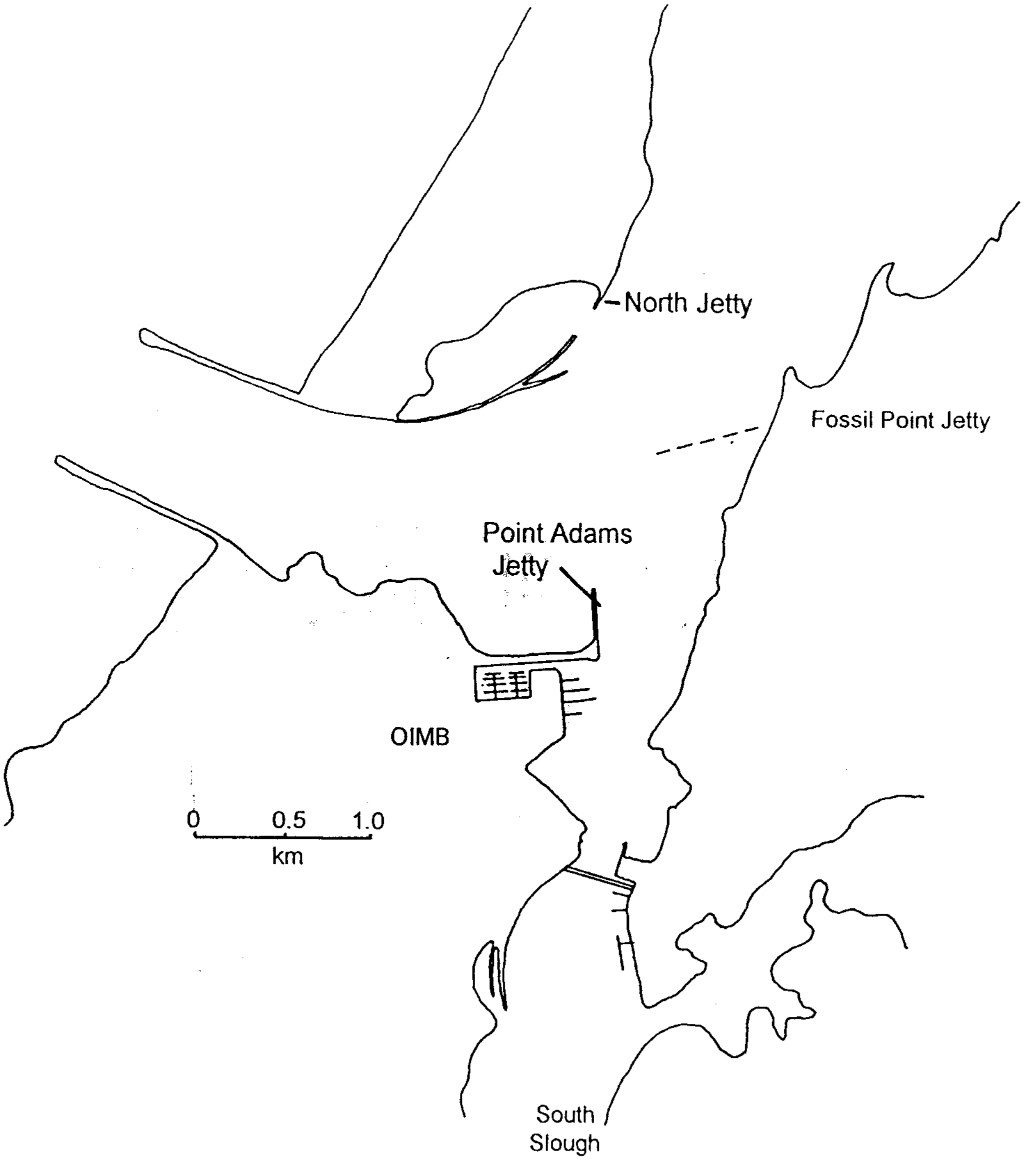


Figure 40. Map of the Lower Coos Bay Showing the North Jetty (Site 3) and Point Adams Jetty (Site 14). Scale Equals 1.0km.

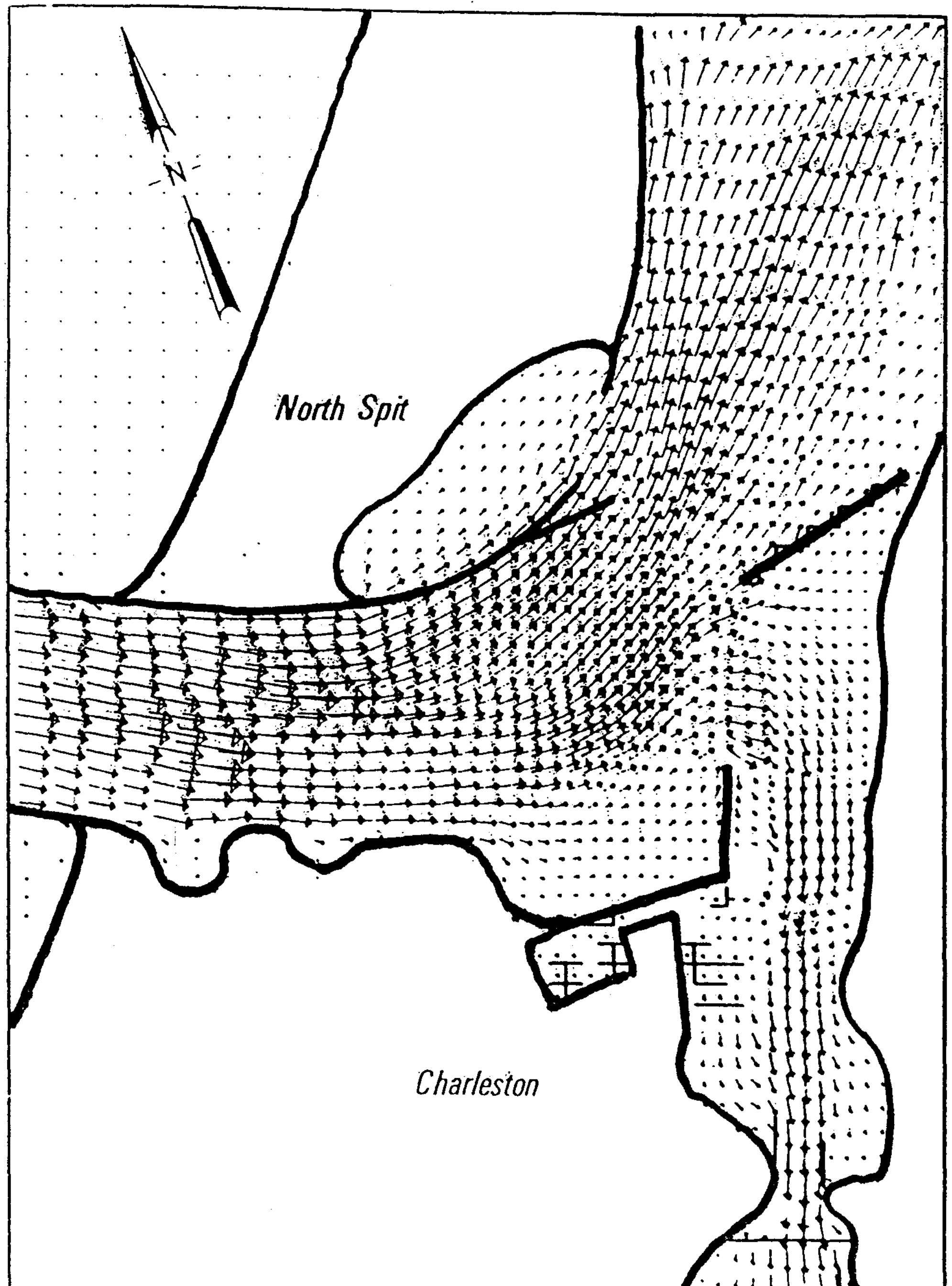


Figure 41. Army Corps of Engineers Flow Field Diagram for the Lower Coos Bay During Flood Tide (COE 1979).

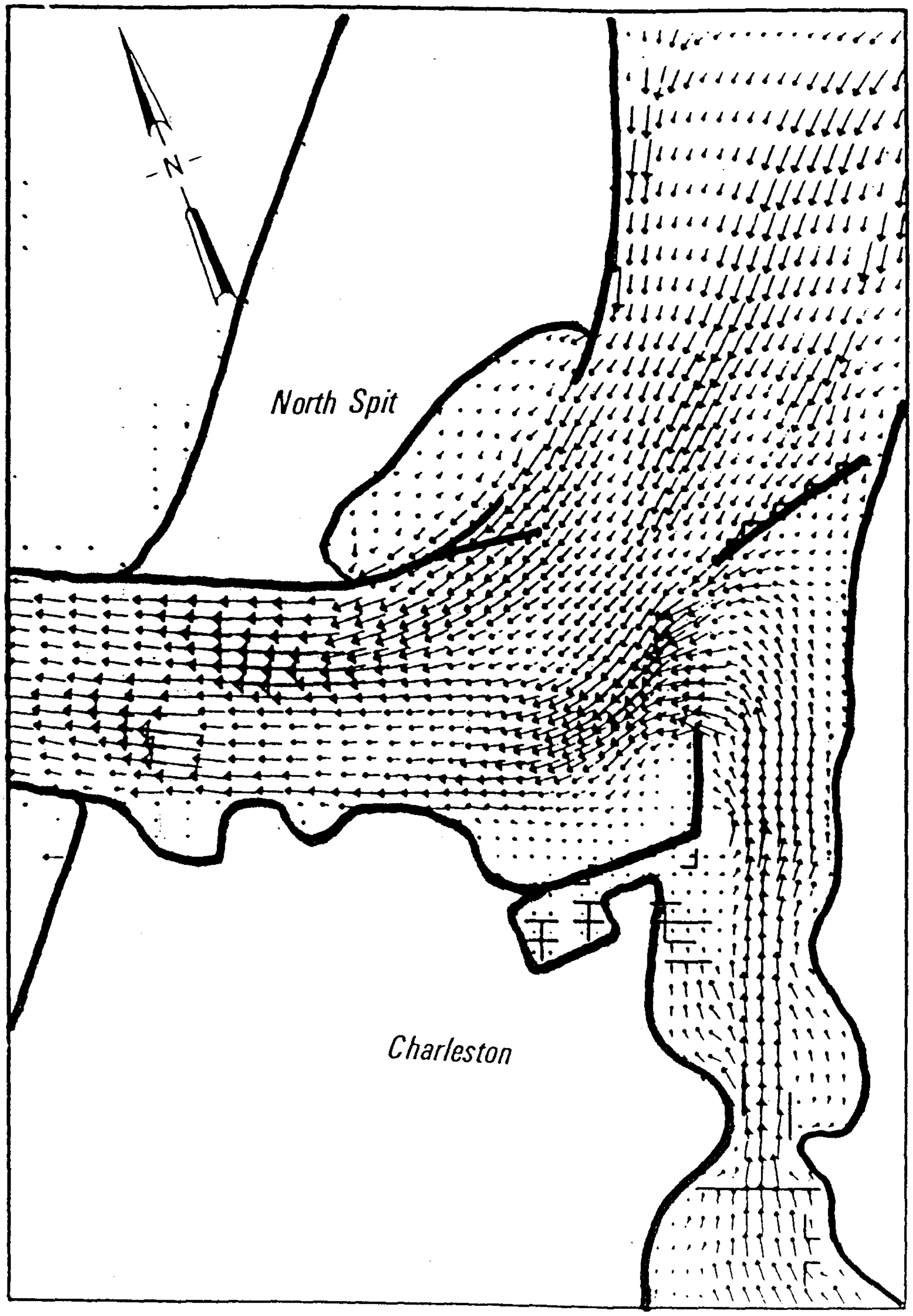


Figure 42. Army Corps of Engineers Flow Field Diagram for the Lower Coos Bay During Ebb Tide (COE 1979).

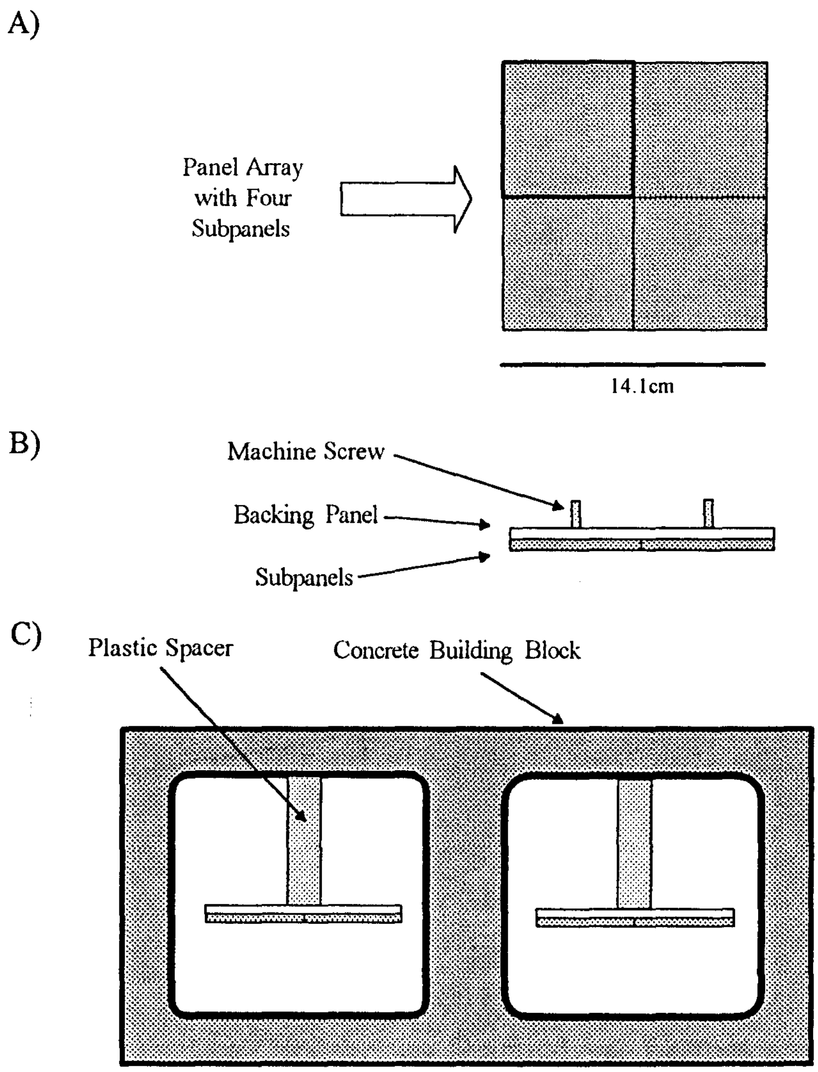


Figure 43. Diagram Illustrating the 2x2 Panel Array in Plan (A) and Side (B) Views and Concrete Block Design (C). See Text for Further Explanation of Design.

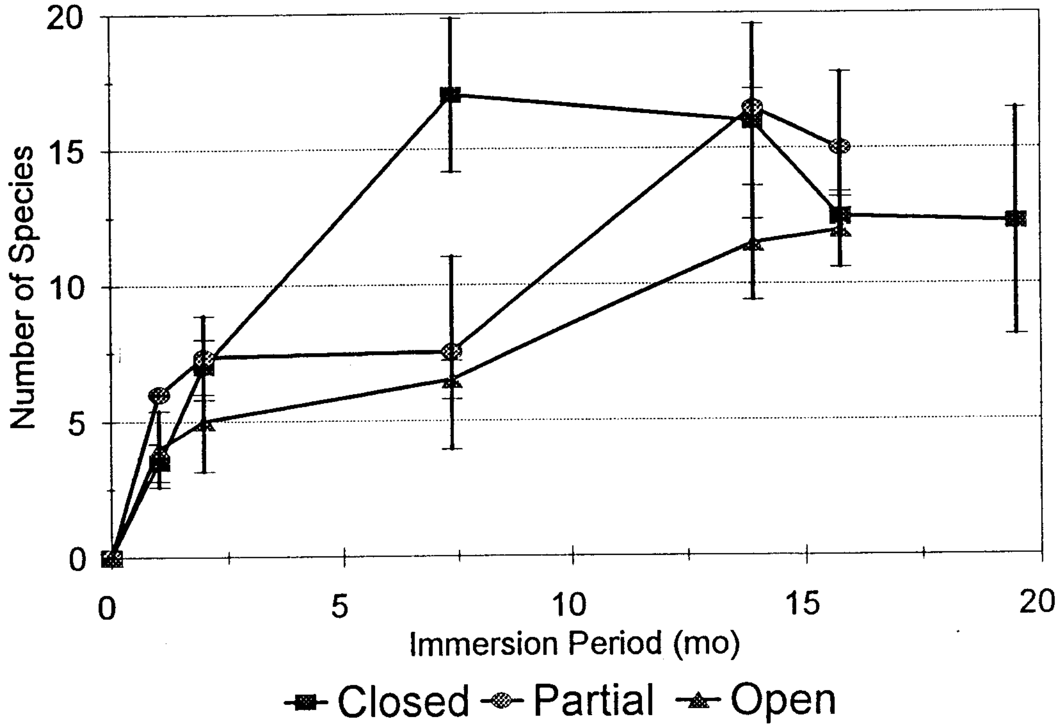


Figure 44. Species Accumulation at the North Jetty During Experiment 1 Between April 1989 and August 1990. Lines Represent Mean Species Richness (n = 4) with Standard Deviation Error Bars.

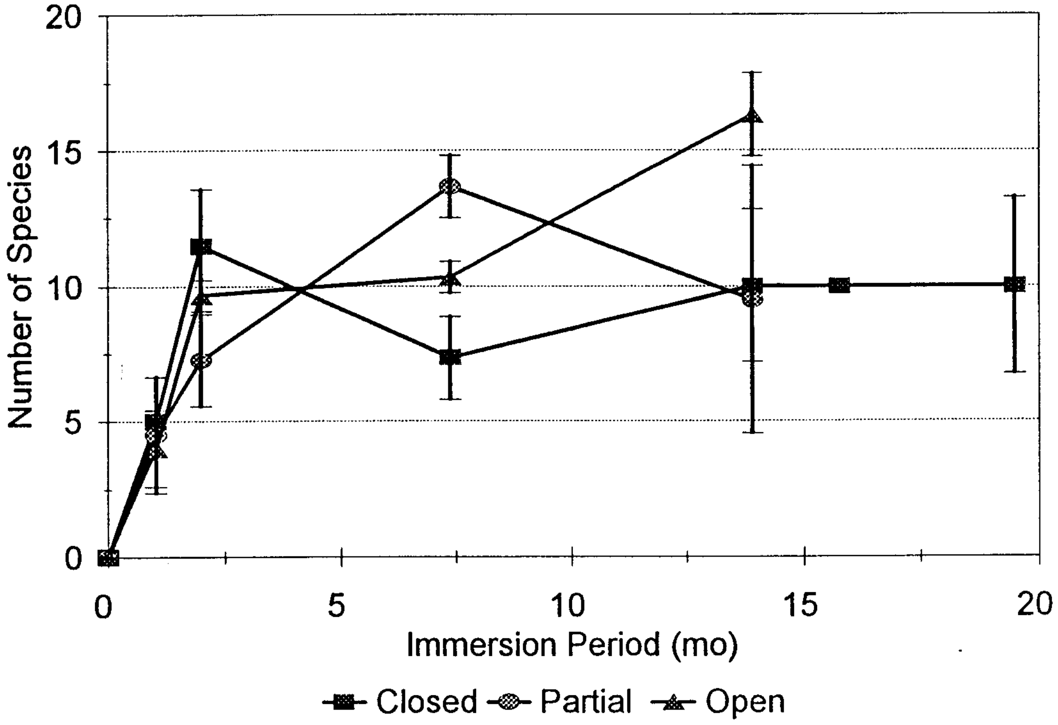


Figure 45. Species Accumulation at the Point Adams Jetty During Experiment 1 Between April 1989 and August 1990. Lines Represent Mean Species Richness (n = 4) with Standard Deviation Error Bars.

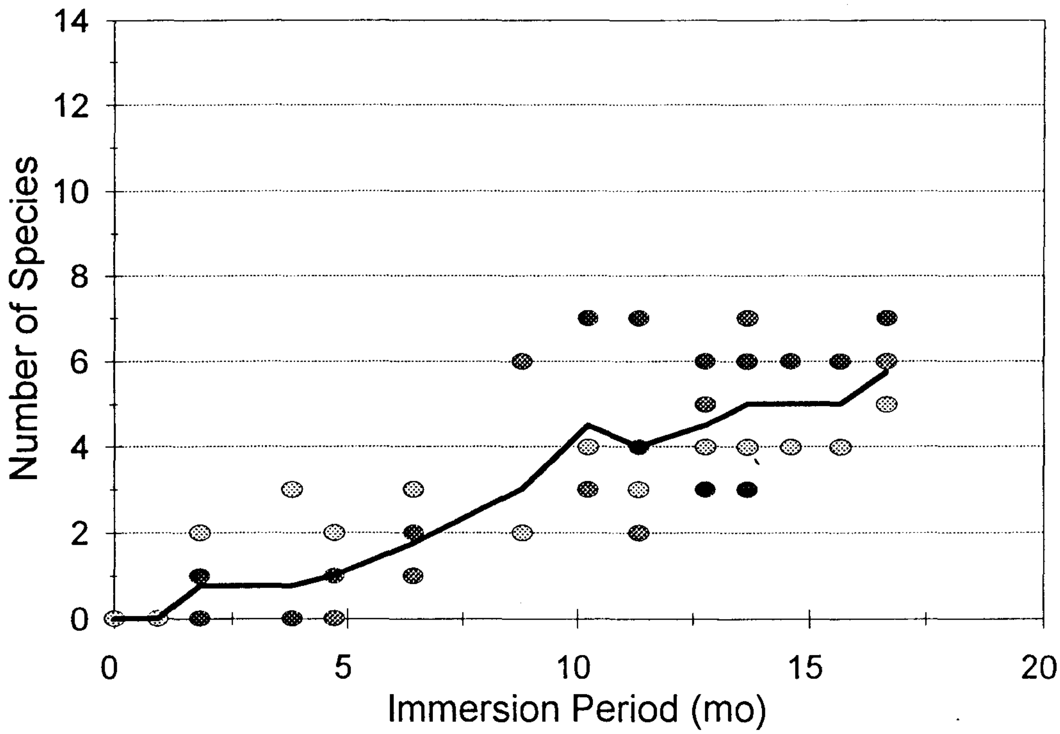


Figure 46. Species Accumulation at the North Jetty During Experiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

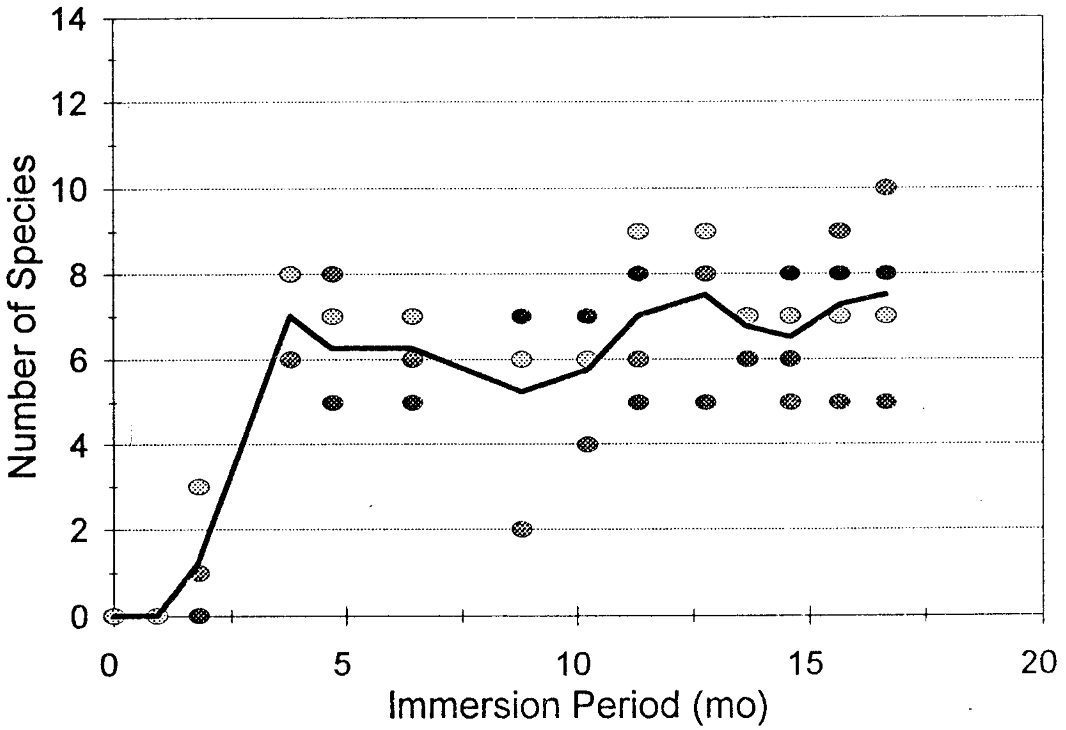


Figure 47. Species Accumulation at the Point Adams Jetty During Experiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

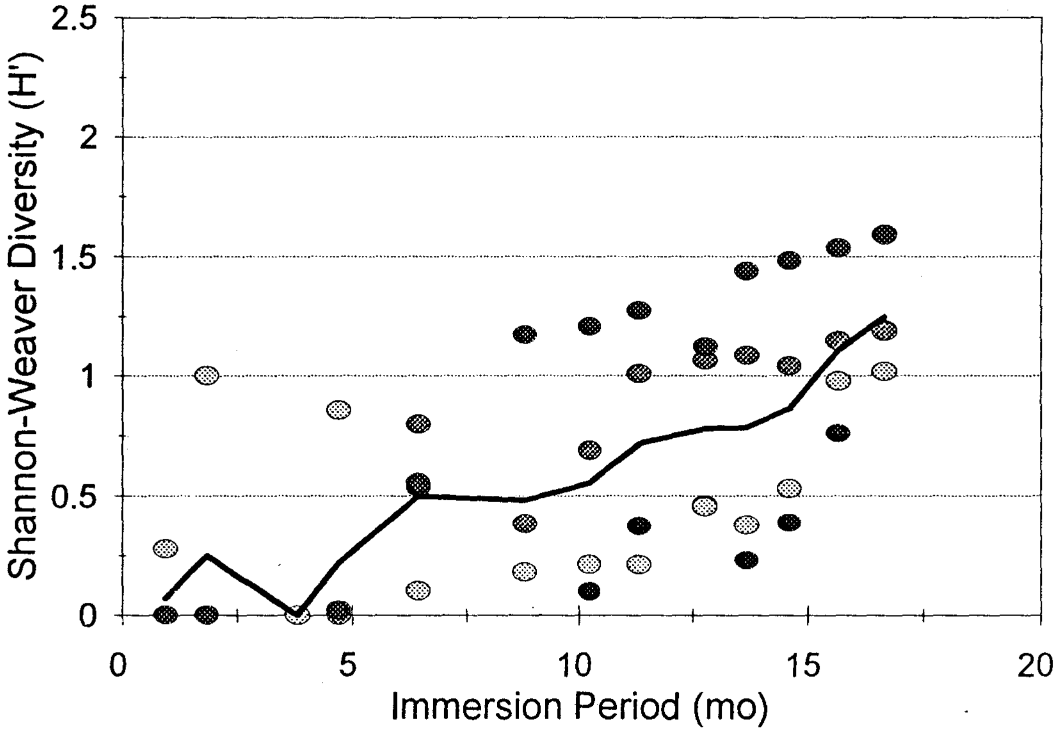


Figure 48. Shannon-Weaver Diversity (H') Change at the North Jetty During Experiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

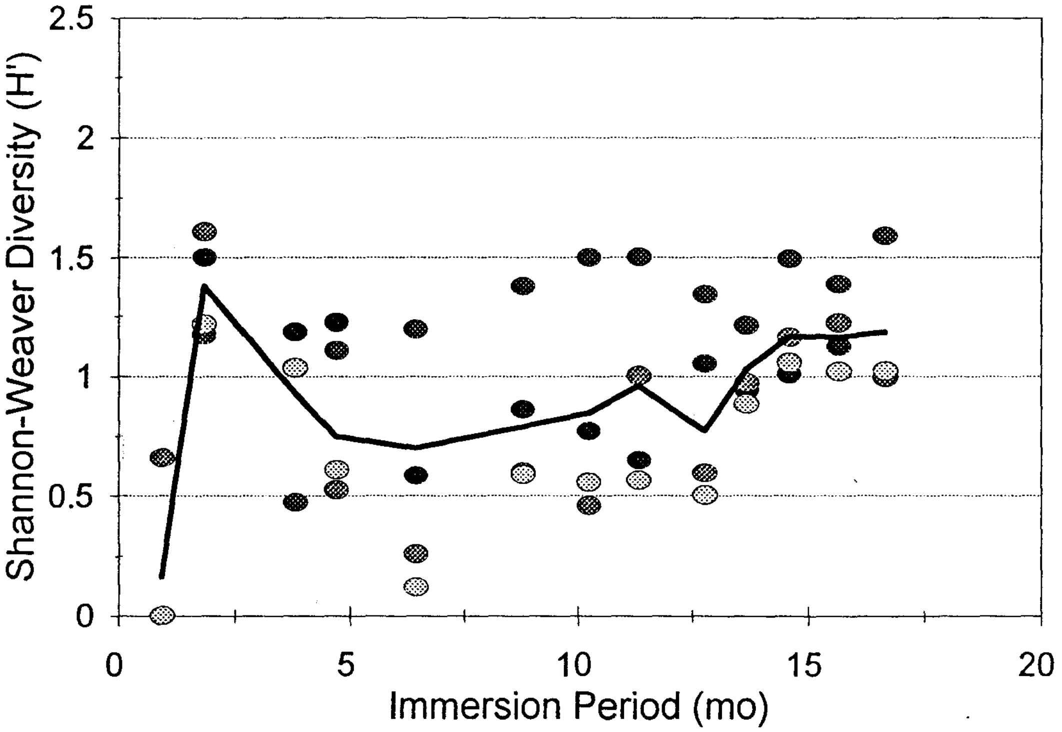


Figure 49. Shannon-Weaver Diversity (H') Change at the Point Adams Jetty During Experiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

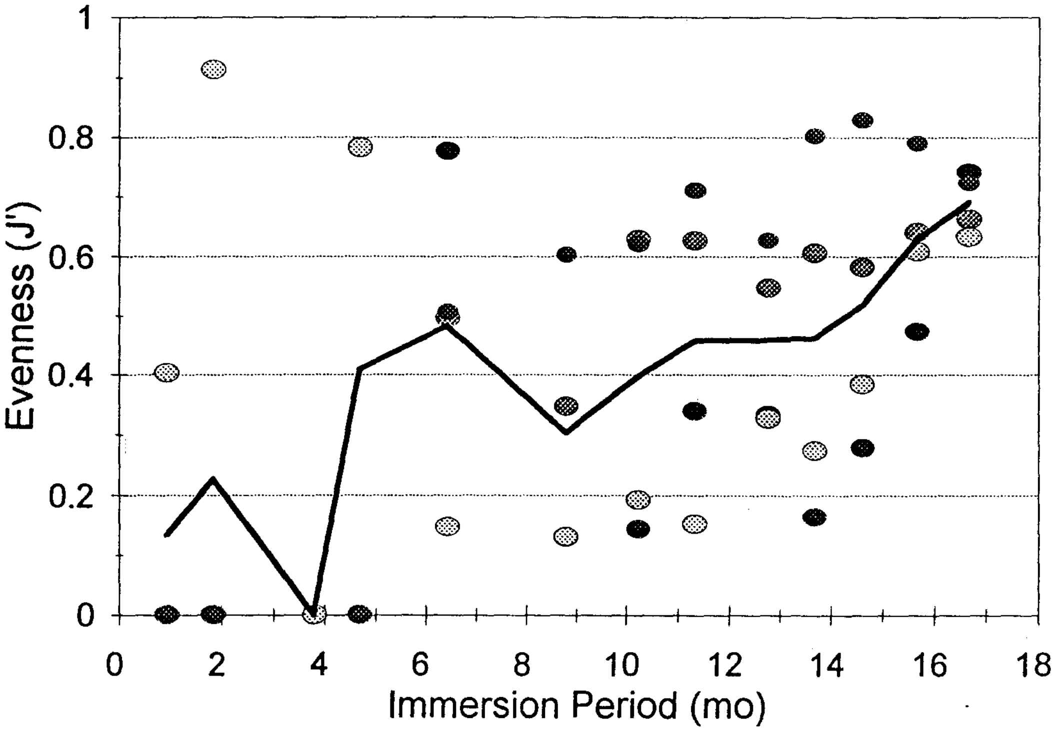


Figure 50. Evenness (J') Change at the North Jetty During Experiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

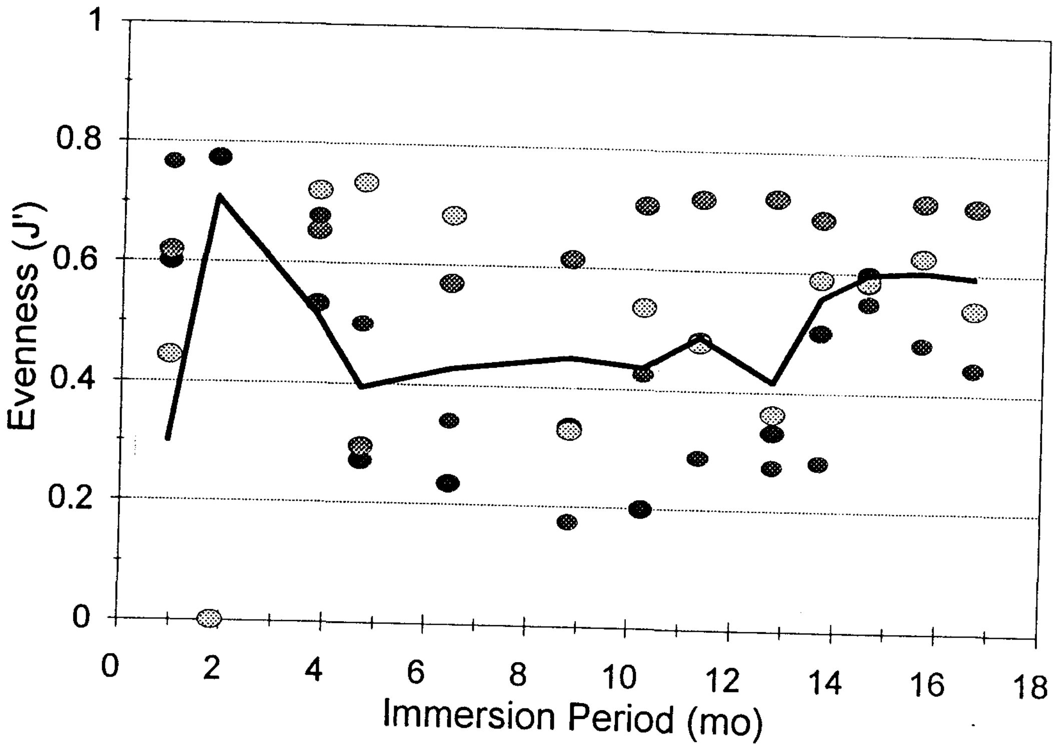


Figure 51. Evenness (J') Change at the Point Adams Jetty DuringExperiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

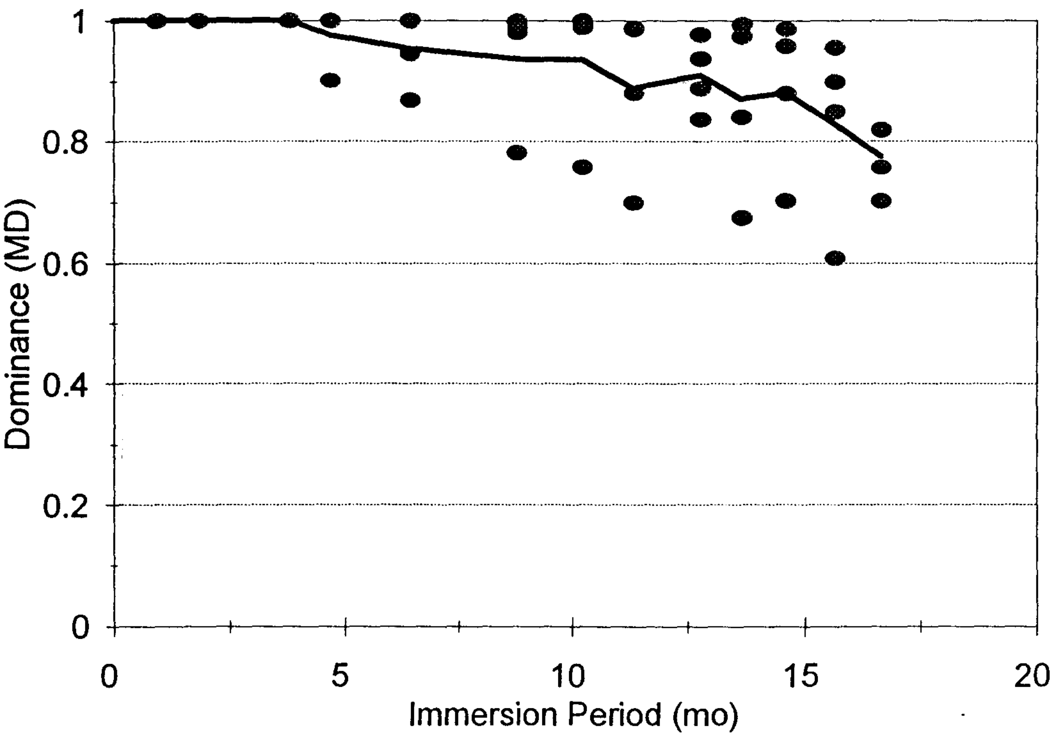


Figure 52. McNaughton's Dominance Index (MD) Change at the North Jetty During Experiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

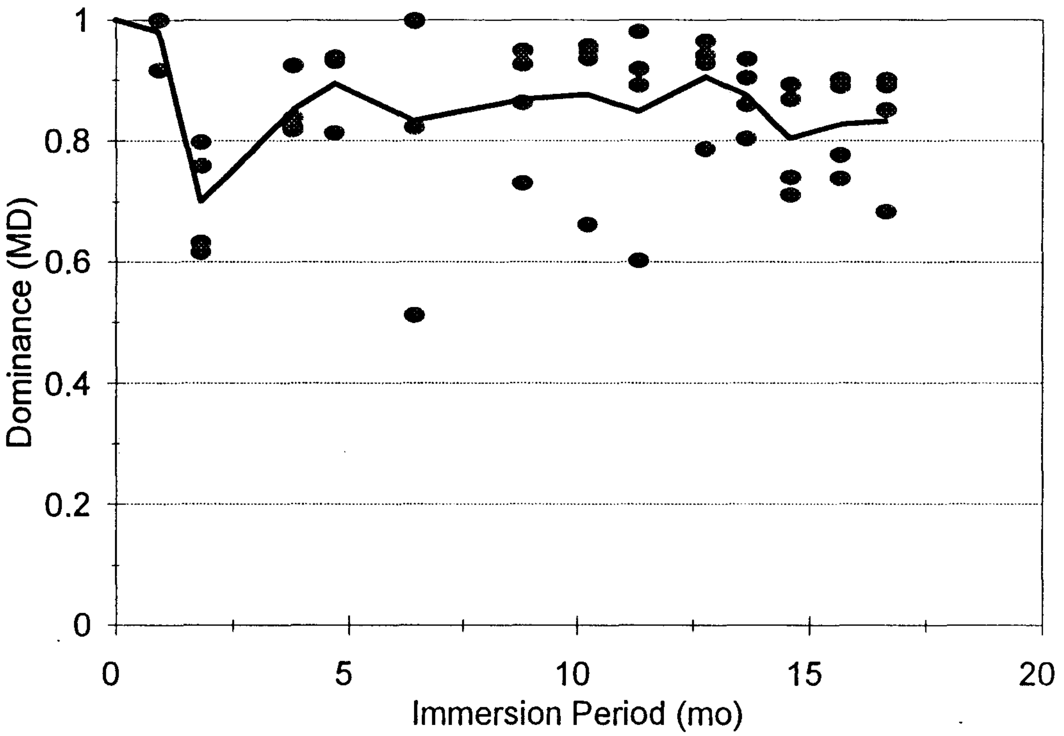


Figure 53. McNaughton's Dominance Index (MD) Change at the Point Adams Jetty During Experiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

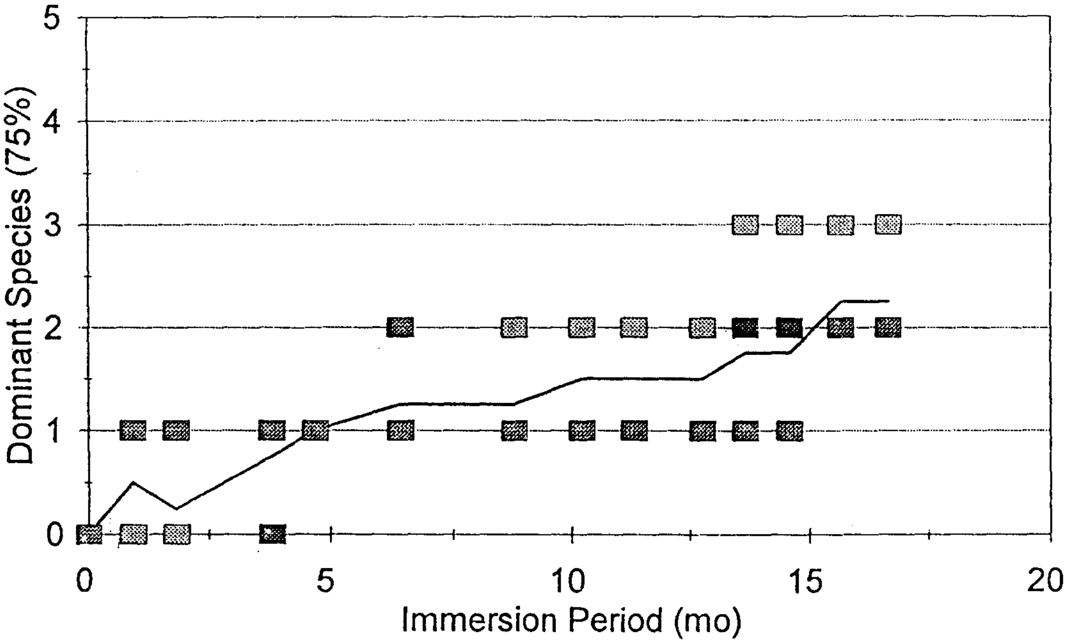


Figure 54. The Number of Species That Comprise 75% of the Living Cover at the North Jetty During Experiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

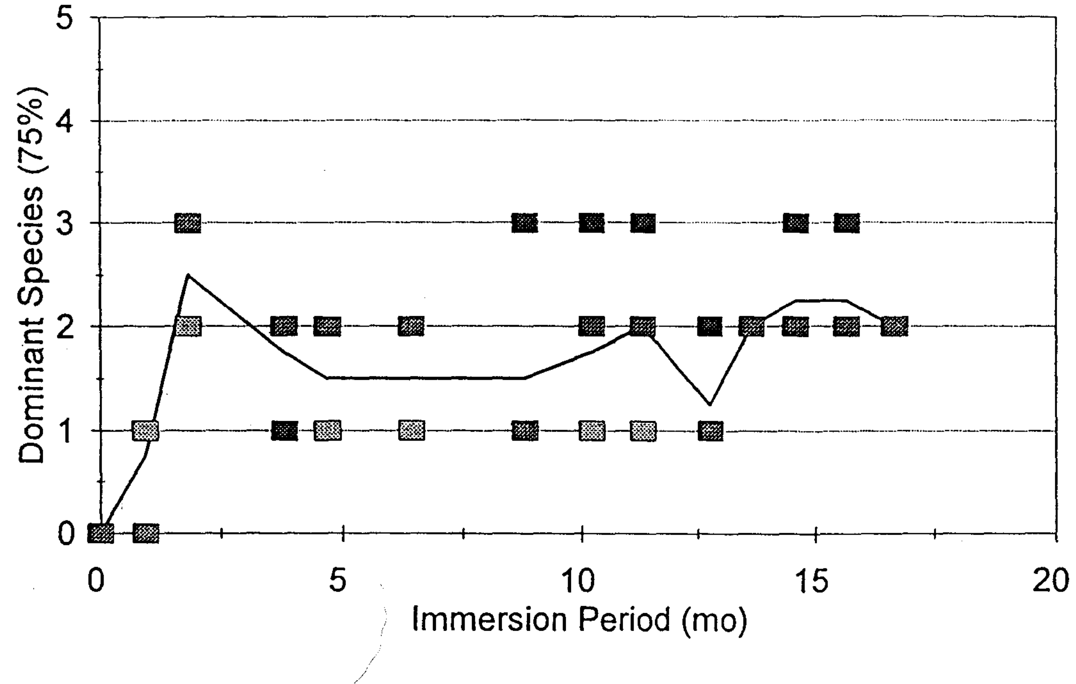


Figure 55. The Number of Species That Comprise 75% of the Living Cover at the Point Adams Jetty During Experiment 2 Between September 1990 and February 1992. The Line Represents the Mean of All Replicate Samples, Symbols Represent the Individual Panel Data.

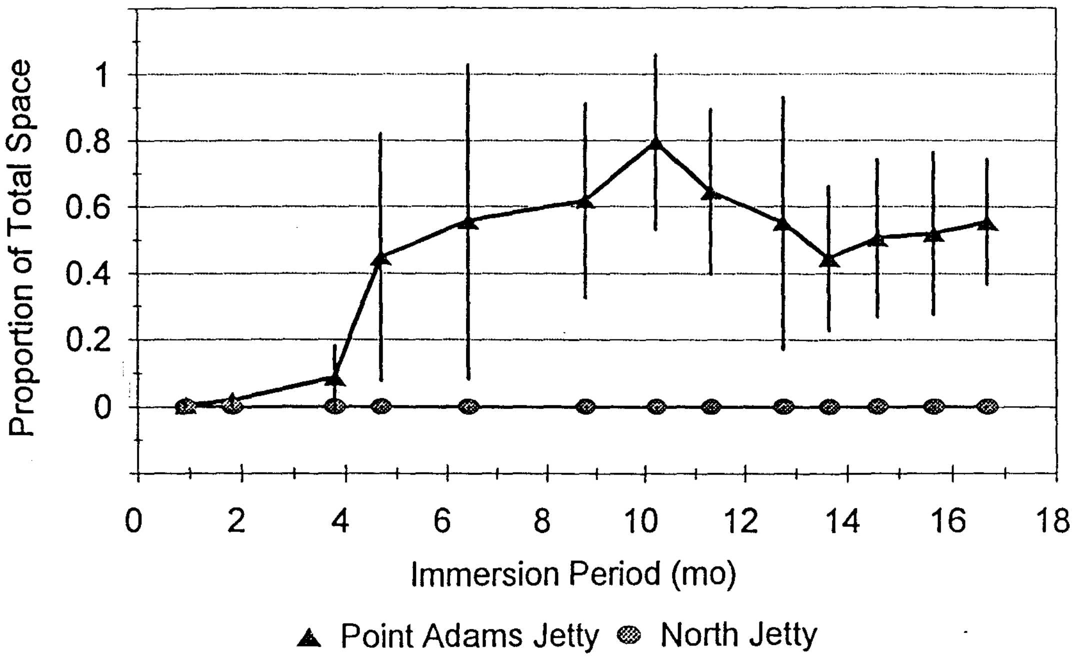


Figure 56. The Proportion of Total Space of Introduced Species at the North Jetty and Point Adams Jetty During Experiment 2 Between September 1990 and February 1992. Lines Represent the Mean with Standard Deviation Bars (n = 4).

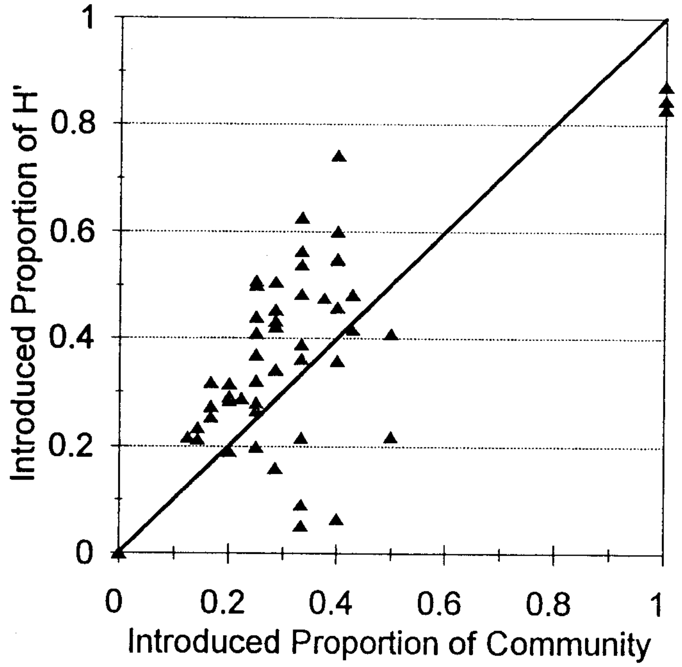


Figure 57. Introduced Species Proportion of Species Diversity (H') Correlated with the Introduced Species Proportion of Community Richness. Triangles Represent Individual Replicate Monthly Samples. The Line Represents a Direct Correlation.

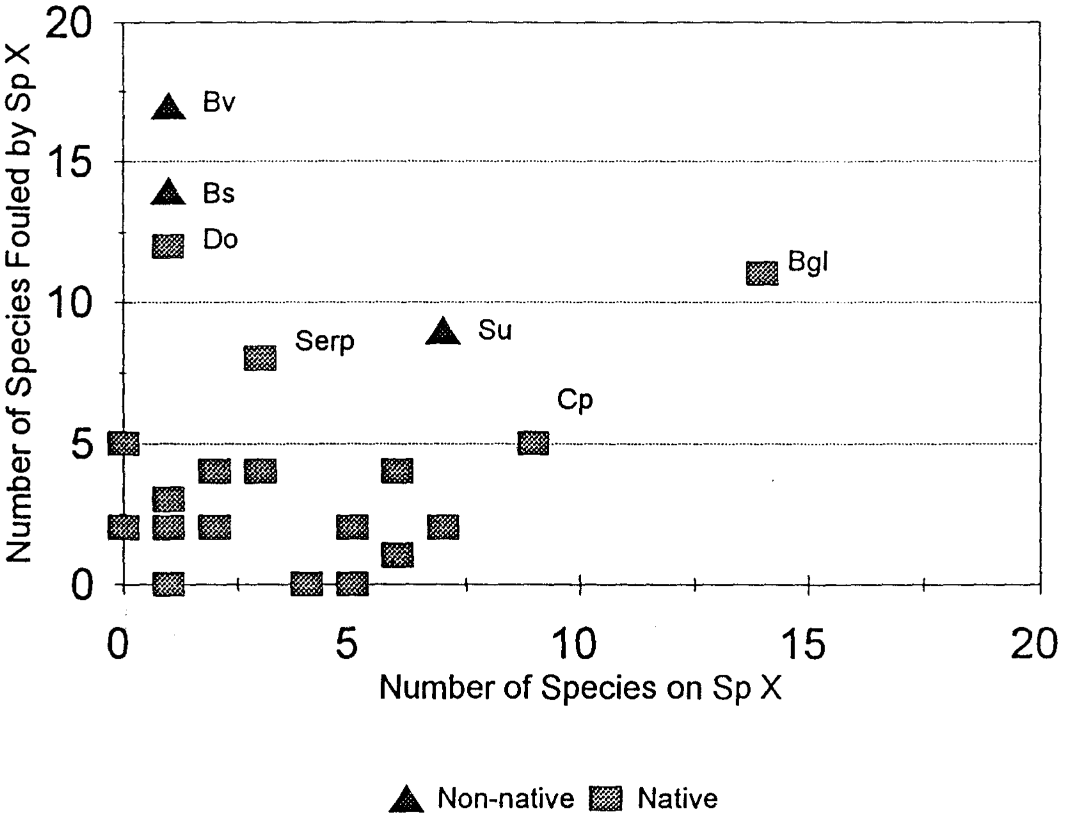


Figure 58. The Number of Species that are Settled Upon (Fouled) by Species X as a Function of the Number of Species that can Settle Upon (Be Fouled By) Species X. Species Identified are *Botrylloides violaceus*, Bv; *Botryllus schlosseri*, Bs; *Schizoporella unicornis*, Su; *Distaplia occidentalis*, Do; *Balanus glandula*, Bgl; Serpulid spp., Serp; and *Cheilopora praelonga*, Cp.

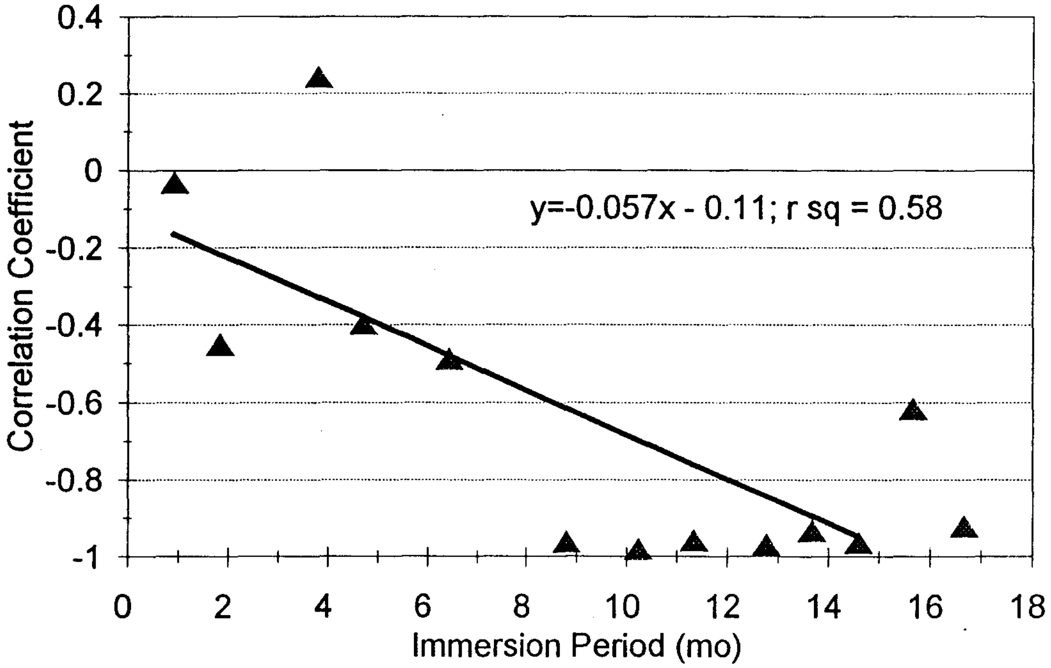


Figure 59. The Association Between Native and Introduced Species Cover on Replicate Panels at Point Adams Jetty as a Function of the Period of Immersion (see Text).

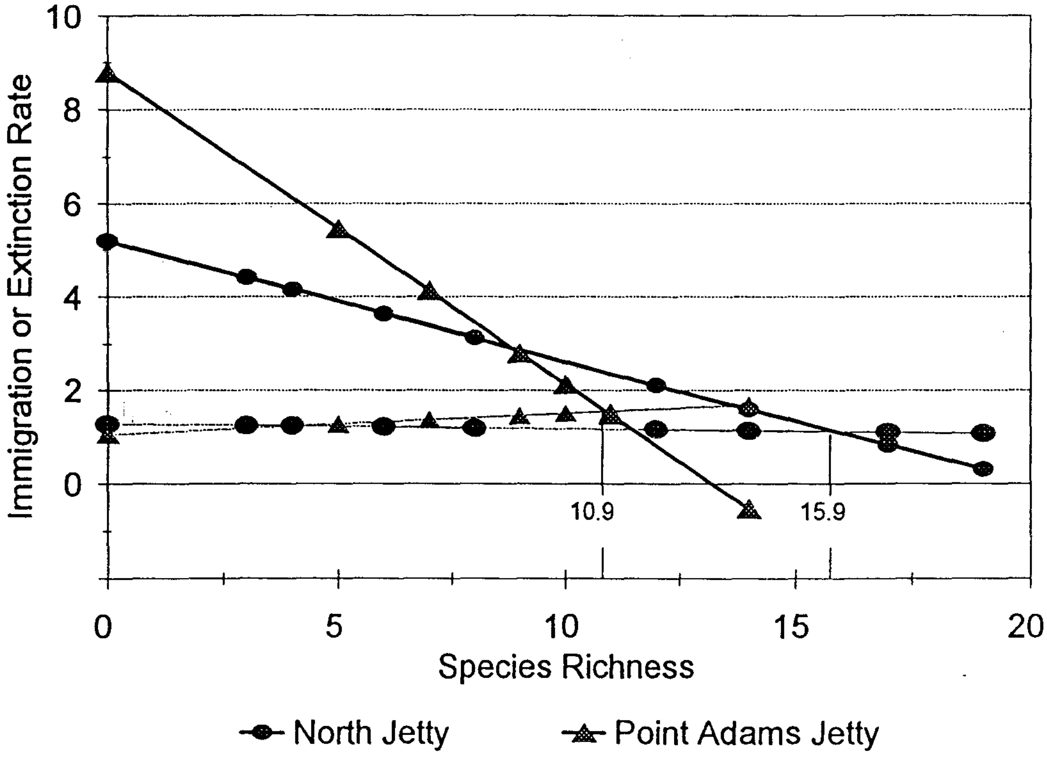


Figure 60. Experiment 1 Immigration and Extinction Rate Regression Lines as a Function of Resident Species Richness. Immigration Regressions are Represented by Thick Lines; Extinction Regressions are Represented by Thin Lines. Predicted Values of the Species Equilibrium (S) are Labelled with Vertical Lines from the Intersection of the Immigration and Extinction Regression Lines to the x-axis.

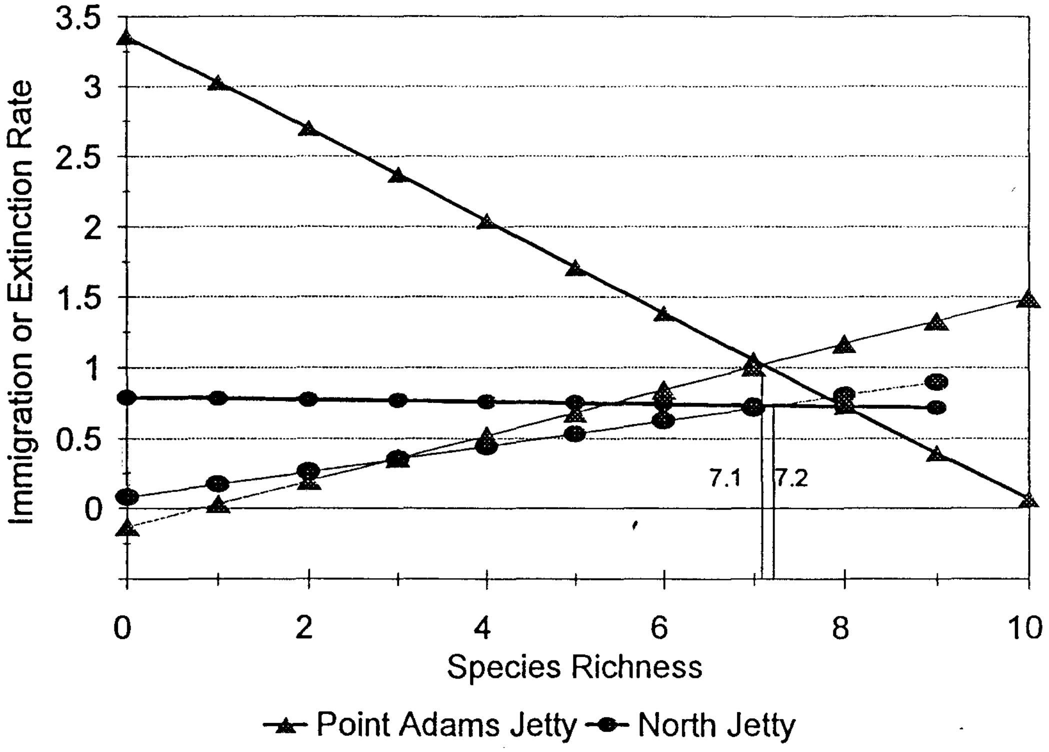


Figure 61. Experiment 2 Immigration and Extinction Rate Regression Lines as a Function of Resident Species Richness. Immigration Regressions are Represented by Thick Lines; Extinction Regressions are Represented by Thin Lines. Predicted Values of the Species Equilibrium (S) are Labelled with Vertical Lines from the Intersection of the Immigration and Extinction Regression Lines to the x-axis.

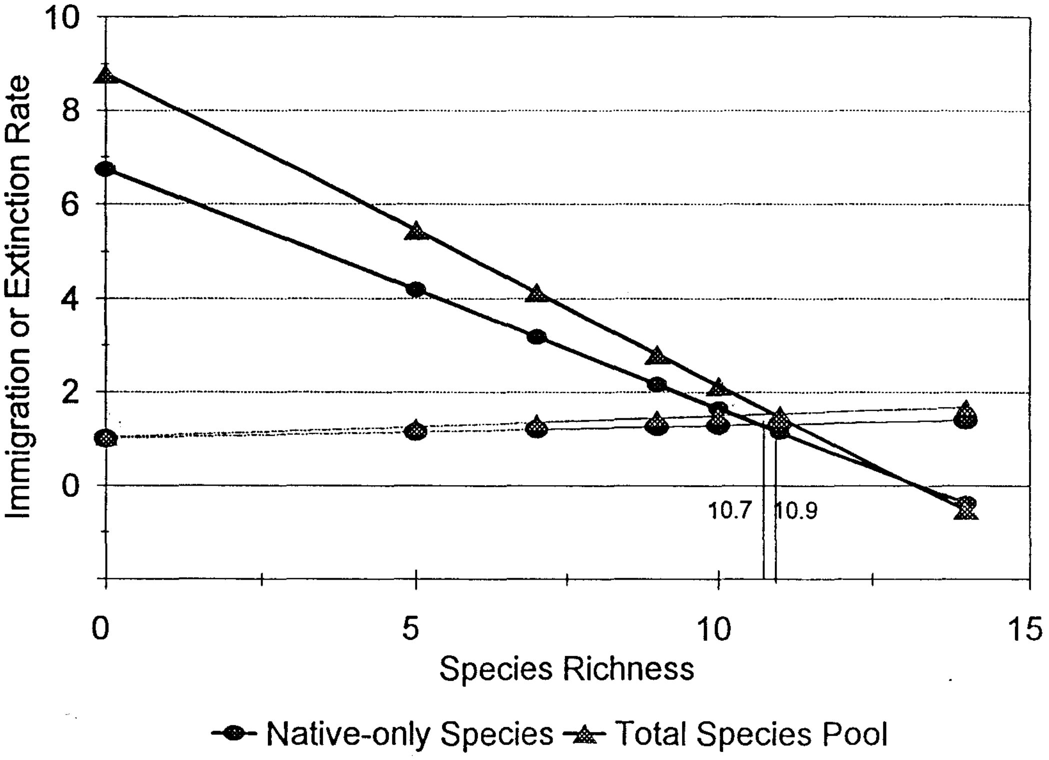


Figure 62. The Total Species Pool and Native-Only Species Pool Immigration and Extinction Rate Regression Lines as a Function of Resident Species Richness. Immigration Regressions are Represented by Thick Lines; Extinction Regressions are Represented by Thin Lines. Predicted Values of the Species Equilibrium (S) are Labelled with Vertical Lines from the Intersection of the Immigration and Extinction Regression Lines to the x-axis.

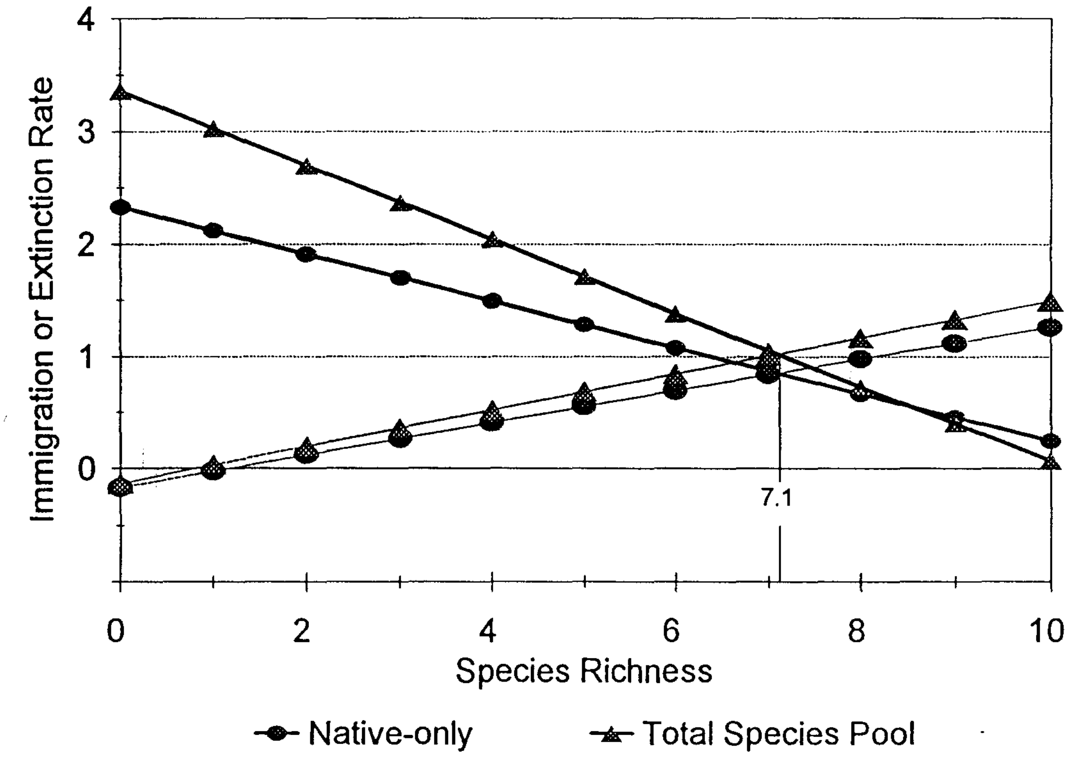


Figure 63. The Total Species Pool and Native-Only Species Pool Immigration and Extinction Rate Regression Lines as a Function of Resident Species Richness. Immigration Regressions are Represented by Thick Lines; Extinction Regressions are Represented by Thin Lines. Predicted Values of the Species Equilibrium (S) are Labelled with Vertical Lines from the Intersection of the Immigration and Extinction Regression Lines to the x-axis.

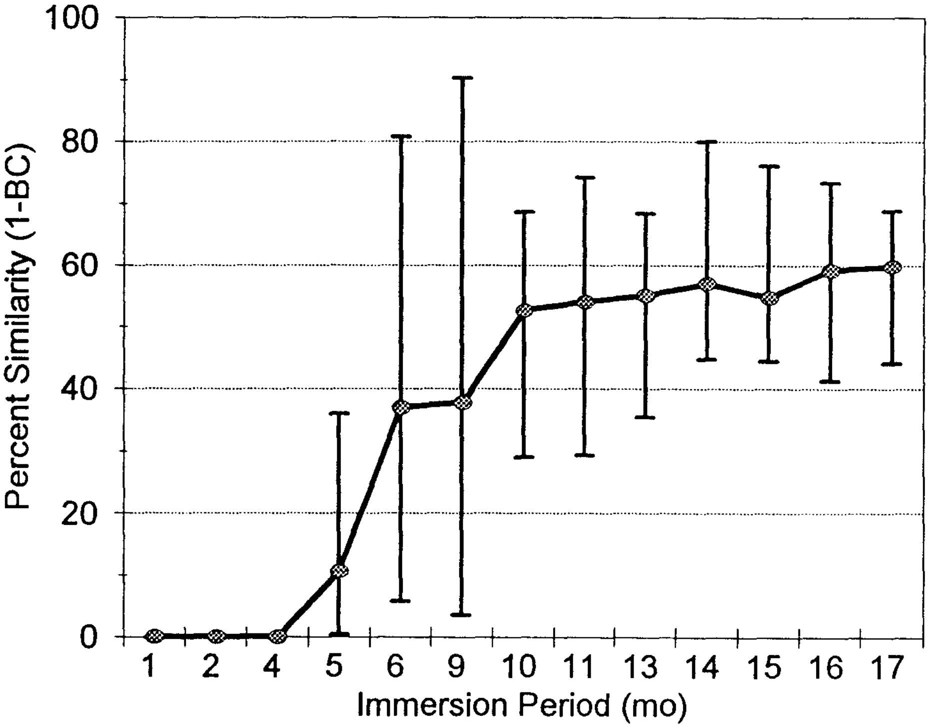


Figure 64. Bray Curtis Mean Similarity Between Replicate Panels at the North Jetty During Experiment 2 Between September 1990 and February 1992. Solid Line Represents the Mean with Range Bars (n = 4).

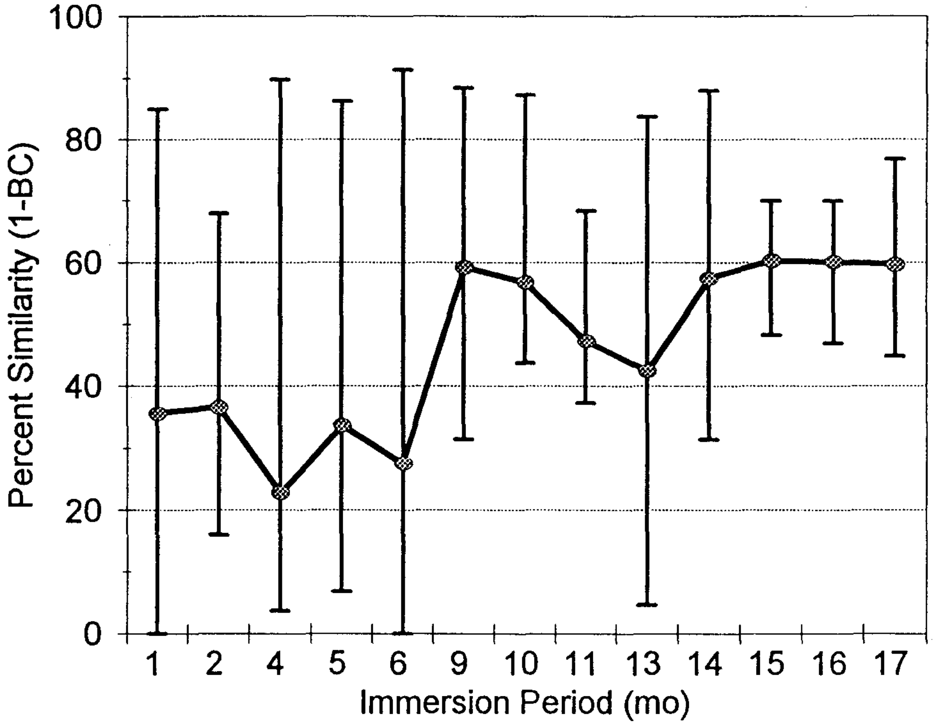


Figure 65. Bray Curtis Mean Similarity Between Replicate Panels at the Point Adams Jetty During Experiment 2 Between September 1990 and February 1992. Solid Line Represents the Mean with Range Bars (n = 4).

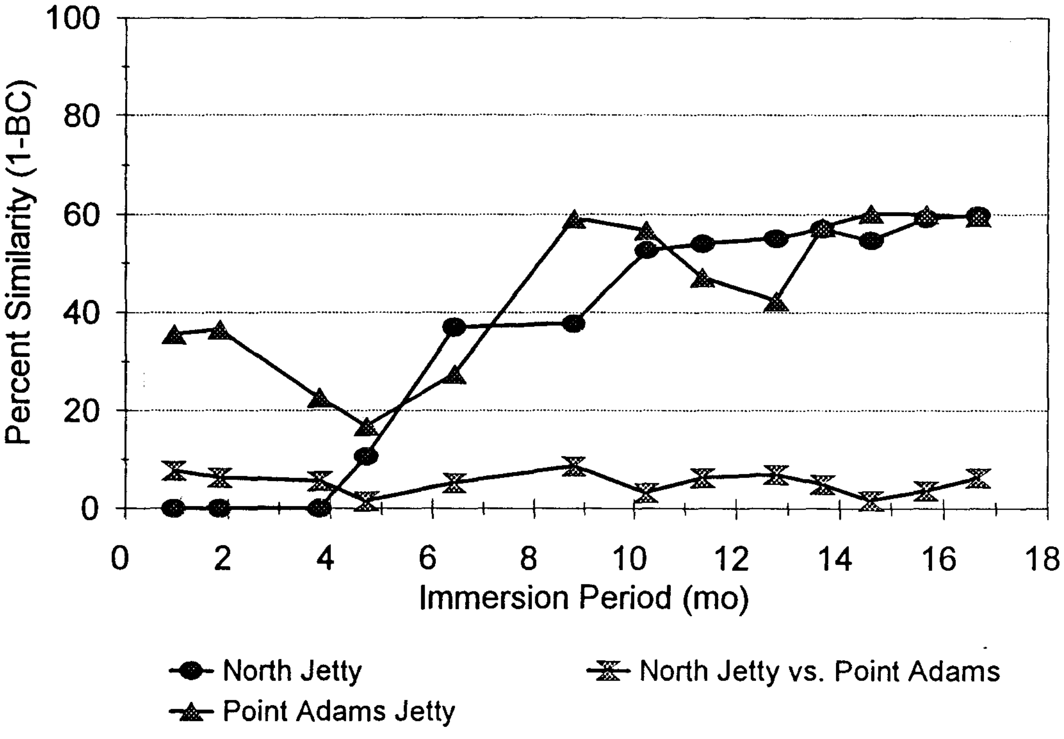


Figure 66. Bray Curtis Mean Similarity Between Replicate Panels Within and Between the North Jetty and Point Adams Jetty Sites During Experiment 2 Between September 1990 and February 1992. Solid Line Represents the Mean of Four Replicate Panels.

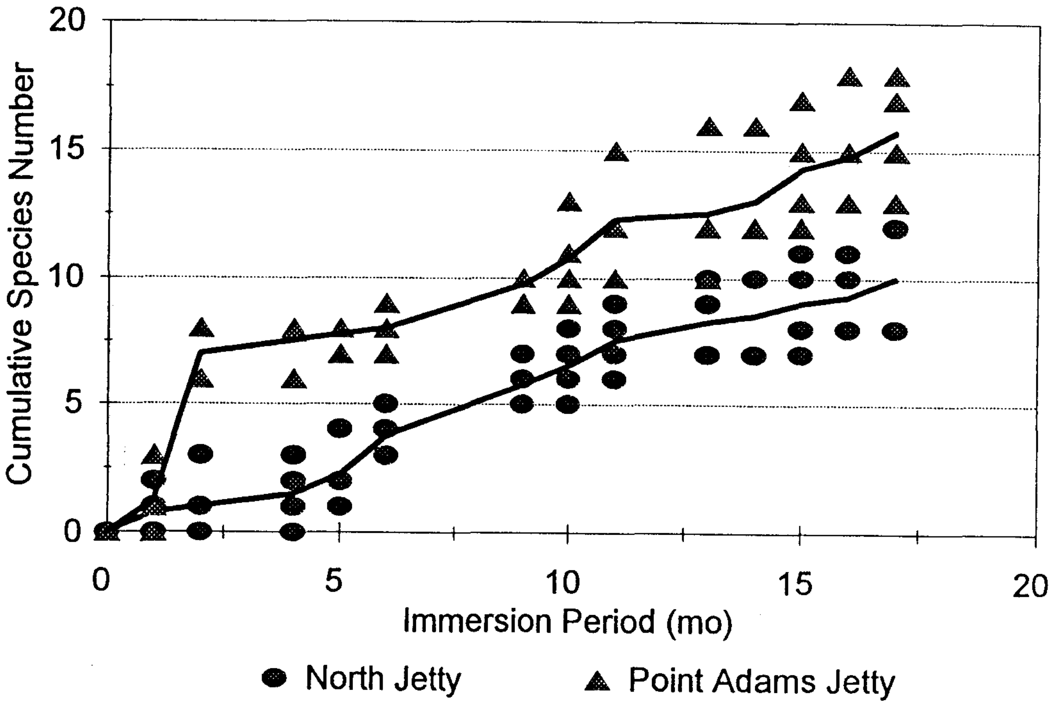


Figure 67. Mean Cumulative Number of Species at the North Jetty and Point Adams Jetty During Experiment 2 Between September 1990 and February 1992. Symbols Represent Replicate Panel Data, Lines Represent Means.

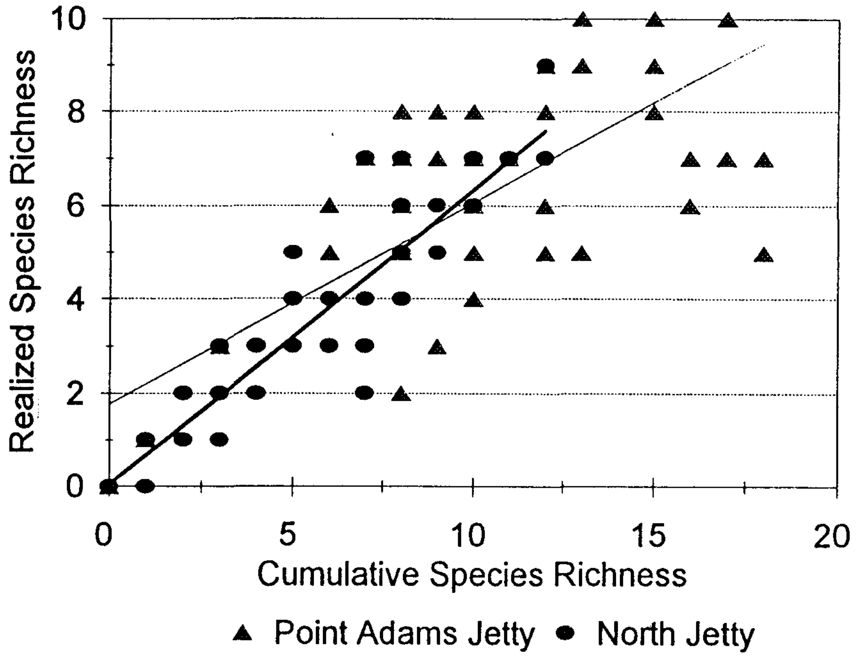


Figure 68. Realized Species Richness as a Function of Cumulative Species Richness for the North Jetty and Point Adams Jetty During Experiment 2. Symbols Represent Monthly Panel Data; Thick Line Represents the North Jetty Regression and the Thin Line Represents the Point Adams Jetty Regression.

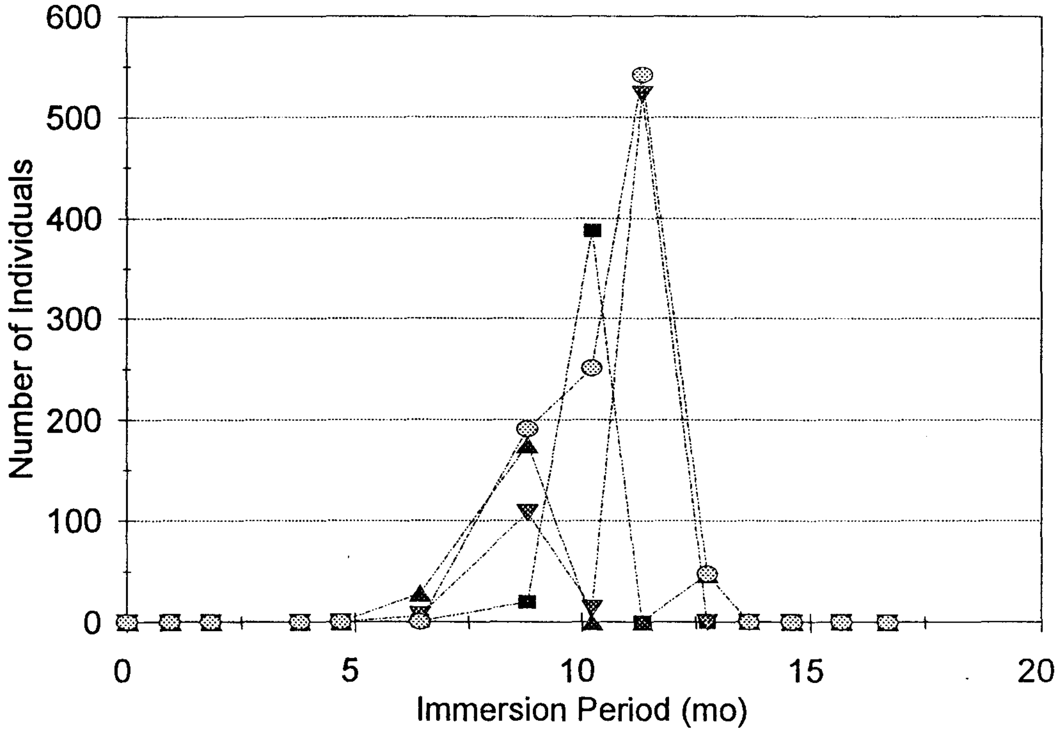


Figure 69. *Balanus glandula* Settlement Densities During Experiment 2 Between September 1990 and February 1992. Symbols Represent Four Replicate Panels.