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Kachemak Bay Experimental and Monitoring Studies: Recruitment, Succession, and Recovery in Seasonally Disturbed Rocky-Intertidal Habitat

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Final Report

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Executive Summary

The purpose of this study was to establish a multi-year sampling program in rocky-intertidal assemblages of outer Kachemak Bay and to assess recruitment and successional patterns leading to recovery of selected intertidal species and the intertidal community after seasonal disturbances. The specific objectives were to:

1. Determine whether the season in which a disturbance takes place affects recovery rates or succession processes.
2. Quantify inter- and intra-annual abundance patterns for major species.
3. Determine the effect of wave exposure on community structure and response to seasonal disturbances.

The study was initiated in response to questions raised during injury assessment studies following the *Exxon Valdez* oil spill [Highsmith et al. 1994]. Several organisms showed increased numbers or percent cover in oiled compared to unoiled rocky-intertidal habitat. Data were not available to determine if these increases were correlated with the time of year that space had become available, due either to the oil or to subsequent clean-up activities, and thus reflecting timing of reproduction or recruitment for some species but not others. The responses of the various invertebrates and algae to the oil spill differed by species, tidal height, region, habitat, and wave exposure as reflected by increases, decreases, or no change to abundance, biomass, or percent cover. Rates of recovery, or convergence with control sites, also differed among the numerous taxa and depended upon the above variables. Another question raised was whether there were inherent differences between oiled and control sites, based on the prevailing currents that carried oil to the impacted sites. A lack of pre-spill intertidal data necessitated the comparison of oiled shorelines to unoiled control beaches for all of the intertidal injury and restoration studies [Gilfillan et al. 1995; Houghton et al. 1993; Highsmith et al. 1994]. With data for the major space-occupying species, Highsmith et al. [1994] used the multi-dimensional scaling (MDS) method to evaluate recovery of invertebrate and algal communities on rocky substrates. Their results showed that site exposure to waves explained the ordinations and oiling category did not. Kachemak Bay rocky-intertidal communities have been generally surveyed and have some similarities to lower-latitude west coast communities that have been more intensively studied. However, extrapolation of the lower-latitude results to southcentral Alaska is not appropriate as certain key intertidal species are not present or occur in very low abundances in Kachemak Bay. In Alaska, physical extremes, such as temperature and photoperiod, are greater and many species are at their northern geographical limit. In fact, some of the major community-structuring species in the Pacific Northwest do not occur in the Kachemak Bay intertidal zone, e.g., *Mytilus californianus,* or are in such low densities, e.g., Pisaster ochraceus, that they have little role in community dynamics. Studies in lower-latitude west coast areas have shown effects of season on population dynamics and recovery rates after disturbances in rocky-intertidal habitat [Kinnetic Laboratories, Inc. 1992; Minerals Management Service 1996; Kim and DeWreede 1996]. In Alaska, seasonal effects may be a primary factor in determining recovery rates. Generally, information on inter- and intra-annual variability in Alaskan intertidal communities is lacking. This report contains results from a study in outer Kachemak Bay to provide multi-year data on rocky-intertidal assemblages and to assess recovery and successional patterns after seasonal disturbances.

In this study, experimental disturbances in different seasons and over a range of wave exposures were used to assess recruitment and succession patterns during recovery in rocky-intertidal habitat sites. To simulate seasonal environmental disturbances, quadrats at three tidal heights at eight sites were cleared of all invertebrates and algae during March, July and October 1994, and March 1995. These dates were selected to provide potential settlement sites (bare rock) for organisms that recruit in different seasons. Undisturbed control quadrats were also established to provide data on inter- and intra-annual variability of dominant invertebrates and algae and for comparative statistical analyses of degree of recovery of disturbed plots. The eight study sites were selected to represent a range of wave exposures from highly-sheltered to frequently-impacted by storm waves. Sites were surveyed, and quadrats were established, cleared, and subsequently monitored for organism abundance and/or percent cover. Sampling dates were July 1995, October 1995, June 1996, and September 1996. Data were analyzed using two main approaches. First, dominant or key invertebrates and algae were analyzed across time using repeated-measure ANOVAs (rmANOVA) to assess the effects of site and disturbance date. To assess recovery of the intertidal community, a multivariate technique, multi-dimensional scaling, was used. This method plots multi-species, multi-sample data sets on a two-dimensional graph such that the rank ordering of the sample distances agrees with the rank order of distances from a dissimilarity matrix. The ordination gives a visual representation of the similarity or dissimilarity of species composition between samples [Clarke and Warwick 1994]. Ordination gradients were then used to evaluate the importance of environmental variables in recovery dynamics from the disturbance.

This study showed that time of disturbance relative to seasonal reproductive events of major space-occupying species affected the time required for recovery. Summer and fall disturbances took longer to recover from than spring disturbances because the latter occurred just prior to the peak of barnacle larval settlement. Therefore, early barnacle recruitment appears to be a critical element in recovery rates. Although this three-year study provides a data and knowledge base for continued work, this project was not long enough for all end-points to be reached. A primary recommendation is that long-term, i.e., 5–10 years, monitoring of experimentally disturbed sites is needed in Kachemak Bay in order to fully understand the specific events and time-course of recovery from seasonal disturbances.

In control quadrats, the community remained relatively stable throughout the study, although some intra-annual variability was detected due to life histories, such as in annual algae. The acorn barnacles, *Semibalanus balanoides* and *Balanus glandula*, were the first to colonize the disturbed quadrats in the high (1.5 meters of vertical drop below mean higher high water) and mid (2.5 MVD) intertidal zones, often with > 80% cover. Adult percent cover of these species remained above control quadrat levels at the end of the study, suggesting stability had not yet been achieved. The dominant alga in the mid to upper intertidal zone, *Fucus gardneri*, colonized disturbed plots only after the above barnacle species were established and had not returned to control levels at the end of the study except in quadrats that had 2.5 years to recover. A similar scenario occurred for the dominant algal and barnacle species in the low intertidal zone (3.5 MVD). Recruitment of the kelp *Alaria* spp. followed recruitment by the barnacle *S. cariosus*, and neither had recovered to control levels by the end of the study. The blue mussel *Mytilus trossulus* which also appears to recruit in large numbers only after barnacles have become established, had not recovered by the end of the study and the data indicate that much longer than 2.5 years may be required for recovery at wave-exposed sites. Generally, recovery rates within quadrats scraped on different dates were driven by the seasonal timing of barnacle recruitment relative to the date of scraping (bare rock substrate availability).

Multi-dimensional scaling showed that scraped quadrats had not fully converged with control quadrats by the last sampling date, 30 months after the first set of quadrats was scraped in March 1994. Recovery rates varied by the season that quadrats were scraped. Quadrats scraped in July and October 1994 showed slower recovery rates than quadrats scraped in March 1994 or 1995. The dissimilarities of scraped quadrats compared to control quadrats were reduced between July 1995 and September 1996, suggesting community recovery was in progress but just not complete after 2.5 years. Although there were recruitment differences for some species between protected and exposed sites, wave exposure as a matrix variable did not account for community-level differences in recovery.

Introduction

Purpose

The purpose of this study was to establish a multi-year sampling program in rocky-intertidal assemblages of outer Kachemak Bay and to assess the recovery and successional patterns of intertidal organisms after seasonal disturbances. The information obtained during this project will 1) support environmental assessment processes for Cook Inlet and Gulf of Alaska lease sales, 2) help in the decision-making process during shoreline response operations in the event of an oil spill, and 3) increase the ability to monitor recovery in the event of an oil spill in Cook Inlet.

Background and need

Cook Inlet shorelines include numerous habitats such as marshes, sheltered and exposed tidal flats, coarse textured beaches, and sheltered and exposed rocky habitats. The unique combination of tidal currents, upwelling, the Alaska Coastal Current, and freshwater inputs creates a well-mixed tidal estuary that supports high biological productivity, exemplified by the extremely productive rocky shorelines of outer Kachemak Bay [Rosenthal and Lees 1976; Lees and Houghton 1977; Lees et al. 1980; Carroll 1994; Highsmith et al. 1994]. These shorelines contain diverse and rich invertebrate and algal assemblages and include state park lands, a state critical habitat area, and a national estuarine research reserve. Although not immediately adjacent to the active lease sales and oil industry operations in Cook Inlet, these rocky shores are still at risk from accidental releases of oil from tankers transiting the inlet, pipeline fractures, or well blow-outs. Depending upon prevailing winds and currents, oil could be carried from remote release points to almost any shoreline within Cook Inlet, including Kachemak Bay. In fact, in February 1999, the oil tanker *Potomac Trader* was towed to outer Kachemak Bay after a hairline fracture of its hull was caused by ice in the inlet. Oil trajectory models indicated that if significant oil had leaked from the ship, the path would take the oil directly south onto the rocky shorelines included in this study. Extensive over-flights of the area detected no oil hitting the shorelines. This incident, however, highlights the potential value of the baseline data presented in this report.

Intertidal communities are especially vulnerable to spilled oil due to their location at the interface between marine waters and the shoreline where incoming tides and prevailing currents may strand floating oil. Once ashore, stranded oil can impact intertidal communities as a direct result of oiling or indirectly due to subsequent clean-up efforts. Intertidal impacts can include immediate death from oiling or response efforts; sub-lethal effects such as failure to molt, swim, feed, or reproduce; and reductions in fertility, recruitment success, or growth rates. Changes to one intertidal species can directly or indirectly affect other organisms [Menge 1995]. One indirect effect of an oil spill, reduced cover or shelter due to the loss of attached intertidal organisms, can be most dramatic at rocky shores compared to other habitats [Gilfillan et al. 1995]. Rocky shores act as buffers to upland habitat, provide habitat for a variety of plant and animal species that require hard substrate, and are important habitats for a diverse association of marine species [Dobroski and Bogardus 1990].

The intertidal community was the largest habitat category affected by the *Exxon Valdez* oil spill (EVOS), with damage from the oil and resultant cleanup activities occurring over several hundred kilometers of shoreline. Several EVOS studies conducted within rocky-intertidal habitat after the oil spill reported varying levels of injury and recovery in key organisms, including *Fucus gardneri* (the major structural component of rocky-intertidal communities in southcentral Alaska), limpets, littorines, and barnacles [Houghton et al. 1993, 1996; DeVogelaere and Foster 1994; Highsmith et al. 1994; Gilfillan et al. 1995; Highsmith et al. 2000]. In contrast, some organisms showed significantly increased numbers or percent cover on oiled sites compared to control sites, perhaps due to lack of competitors or predators. Recovery is occurring or has occurred in the low and mid intertidal zone for most organisms. The longest on-going intertidal study conducted after the EVOS describes the onset of recovery as occurring within the first several years after the spill [Coates et al. 1999], with most major intertidal assemblages having recovered within six years. However, a series of studies conducted in Herring Bay in Prince William Sound showed that *F. gardneri* and several grazing invertebrates continued to show reduced densities relative to control sites on oiled upper intertidal shorelines up to six years after the oil spill [Stekoll and Deysher 1996; van Tamelen and Stekoll 1996; Highsmith et al. 2000].

Pre-spill data did not exist for the intertidal studies conducted after the EVOS to estimate injury to invertebrates and algae and, thus, oil effects had to be estimated from a comparison of oiled and non-oiled areas. Information on intertidal community structure and patterns would have made damage and recovery studies much more time and cost efficient. The statistical advantage of collecting pre-spill data, as opposed to using a post-spill matched-pair design, is that inherent physical, geological and biological differences between paired sites would not be factors in the analyses. These examples illustrate the recommendations by intertidal researchers to establish reference sites in areas where the potential for oil spills exists [Hawkins and Hartnoll 1983; Hiscock 1985; Dobroski and Bogardus 1990]. In addition to pre-spill data collections, multi-year data collection is necessary to describe seasonal and inter-annual fluctuations and trends in community structure. This information can aid in determining whether changes in the community are due to pollution or natural disturbances. For example, a major die-off in the mid to upper intertidal zone due to freezing was reported in southcentral Alaska just weeks prior to the EVOS [Carroll 1994].

Pacific coast studies south of Alaska have assessed various aspects of disturbances on recruitment, recovery, and successional patterns on rocky-intertidal shorelines. Foster et al. [1986] reviewed disturbances in rocky-intertidal communities in the northeastern Pacific and the processes that might affect impacts at various spatial and temporal scales. Much of the variation in patterns of distribution and abundance of intertidal organisms was attributed to disturbances that removed portions or entire assemblages of epibenthic communities. A subsequent series of studies was conducted that looked at disturbances to, and recovery of, rocky-intertidal sites during different times of the year along a latitudinal gradient from central to northern California [Kinnetic Laboratories, Inc. 1992; Minerals Management Service 1996]. The disturbances were created by removing intertidal organisms and the researchers found that recovery rates varied by tidal height or assemblage, with upper intertidal zone recovery occurring in as little as one year while lower intertidal mussel beds were estimated to take at least ten years to recover. Recovery rates were slower for assemblages that were disturbed in the fall compared to those disturbed in the spring. Recovery rates were not significantly correlated with latitude.

Kachemak Bay rocky-intertidal communities are biologically productive and, in many ways, are similar to those of California, Oregon, Washington, and British Columbia [Carroll 1994; Pentec Environmental, Inc. 1996]. Studies in these areas have shown effects of season on population dynamics and on recovery rates after disturbances in rocky-intertidal habitat [Kinnetic Laboratories, Inc. 1992; Minerals Management Service 1996; Kim and DeWreede 1996]. Physical extremes related to latitude, such as temperature and photoperiod, are greater in Alaska than further south, suggesting that seasonal effects would be even greater in determining recovery rates for rocky-intertidal communities in Alaska, especially because many species are at or near their northern geographical limit. For Alaska, there is a lack of post-disturbance data on inter- and intra-annual variability of recovery rates and patterns for intertidal invertebrates and algae. This study established a multi-year sampling program in rocky-intertidal assemblages and assessed their recovery and successional patterns after experimental seasonal disturbances.

Goals and objectives

The goals of this study were 1) to establish reference sampling sites that can provide baseline information, including inter- and intra-annual variability, for intertidal habitats in southcentral Alaska; and 2) to evaluate seasonal influences on recovery rates for a range of wave exposures. This information will aid in estimating expected recovery rates for disturbances that occur during different times of the year.

For rocky-intertidal habitats in outer Kachemak Bay, the specific objectives of the study were to:

1. Determine whether the season in which a disturbance takes place affects recovery or succession processes.
2. Quantify inter- and intra-annual abundance patterns for major species.
3. Determine the effect of wave exposure on community structure and response to seasonal disturbances.

Methods

Definitions

In this study, disturbance is defined as any discrete event that reduces the amount of living biomass in an area and opens up space for the establishment of new individuals or colonies [Kim and Dewreede 1996]. Recovery is the point when population- or community-level variables measured in disturbed areas are not significantly different from those of undisturbed or control areas. Succession is the sequence of changes in community structure that occurs after a site has been disturbed [Berlow 1997]. Recruitment includes both settlement and survival and, for a given species, includes the smallest recognizable individual [Carroll 1994].

Study area

The study area is located in outer Kachemak Bay on the eastern side of Cook Inlet, Alaska (Figure 1). The semi-diurnal tidal range in the area averages more than five meters, making spring tides some of the largest in the world. Field crews used lodging and laboratory facilities at the University of Alaska Fairbanks' Kasitsna Bay Laboratory. All of the sites were accessed by boat.

Kachemak Bay was selected for this study for several reasons: it has extreme seasonal variations in air temperature, wind-induced waves, and solar radiation; it is near or at the northern geographical limit of many intertidal species; it has high biological productivity in the intertidal zone; the beaches are accessible and close to the Kasitsna Bay Laboratory; and there is public and agency interest in the area due to its proximity to oil transportation routes and production sites.

The upper intertidal zone of rocky substrates in the area is dominated by the rockweed *Fucus gardneri* and the acorn barnacles *Semibalanus balanoides* and *Balanus glandula*. Grazing invertebrate populations are dominated by the periwinkle snail *Littorina sitkana*. The most common limpet in the area is *Lottia pelta*, although *L. digitalis* is also common among barnacle tests.

The diversity of the mid intertidal community is greater than that of the upper intertidal zone. The blue mussel *Mytilus trossulus* is more abundant, as is the thatched barnacle *Semibalanus cariosis*. *Fucus gardneri* is still abundant and red algae are more common, dominated by *Odonthalia floccosa*. The green algae, *Acrosiphonia* sp., *Ulva* sp. and *Monostroma* sp., are also abundant.

The brown algae *Alaria* spp. is the dominant overstory component in the low intertidal zone, especially at exposed sites. The dominant barnacle is *Semibalanus cariosus*. The most abundant herbivores are the limpets (Lottiidae), mainly *Lottia pelta* and *Tectura scutum*, but the black chiton *Katharina tunicata* dominates in some areas.

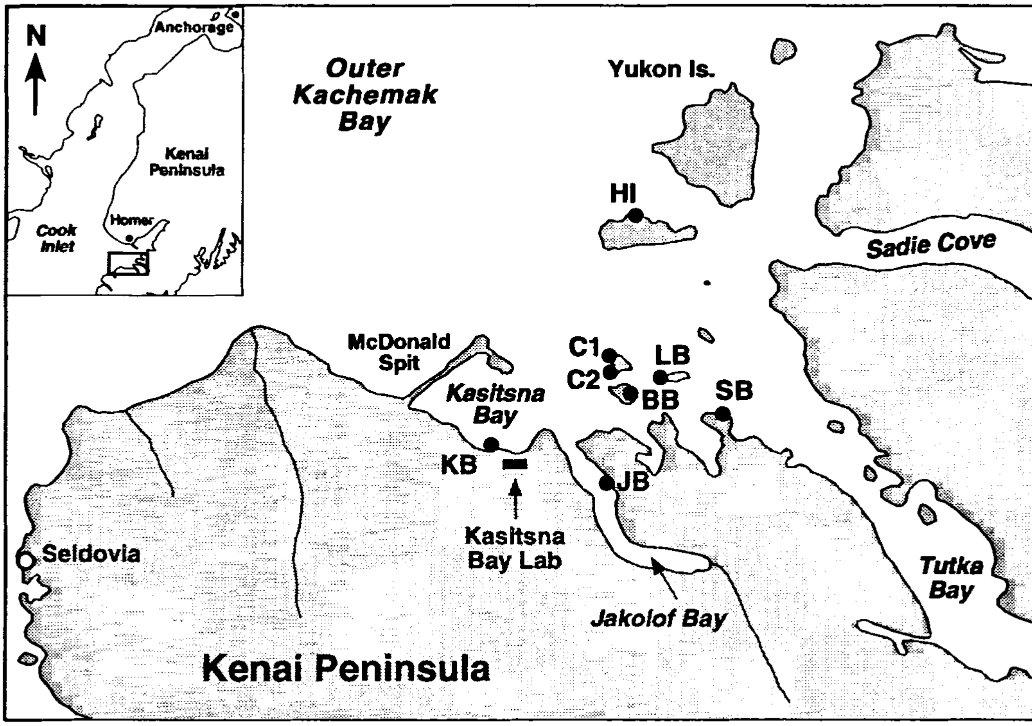


Figure 1. Study site locations for the Kachemak Bay intertidal experimental and monitoring study. Note that the sites BB, LB, C1, C2, and HI are located on islands, while sites KB, JB, and SB are located on the mainland of the Kenai Peninsula.

Site selection

Sites were selected to represent rocky substrates typical of the area and to include a range of wave exposures. The field team surveyed the shorelines around the mainland and islands in outer Kachemak Bay in an area bounded by McDonald Spit and the outermost islands to the west, Yukon Island to the north, the entrance to Tutka Bay to the east, and Kasitsna and Jakolof Bays to the south (Figure 1, Table 1). Much of the shoreline was too steep for safe field work or had coarse-textured beach below the mid intertidal zone, thus limiting the length of shoreline available for the study. The selected sites ranged from highly wave-exposed shorelines (Hesketh Island) to the most wave-sheltered sites (Jakolof and Kasitsna Bays). The relative ranking of wave exposure for the sites was defined by personal observations, the direction and length of the fetch for prevailing storm waves, and dissolution rates of calcium sulfate cylinders (see below). Wave exposure among the sites ranged from being subjected to waves several meters high during storms to total protection from waves. Sites were observed over the two and a half years of the study to verify the original subjective ranking by wave exposure.

Dissolution rates of calcium sulfate cylinders were used to estimate relative water movement at the eight sites spanning a range of wave exposures. Dissolution of the calcium sulfate cylinders is a function of the rate at which water moves past the cylinders, and thus is a function of wave, tide, and wind-driven currents. Dissolution cylinders were constructed from commercially available calcined gypsum (calcium sulfate). Gypsum powder was mixed with water, stirred, and poured into molds made from PVC pipe. A large screw was inserted through the center so that the head was flush with the surface of the calcium sulfate at one end of the mold and the pointed tip of the screw protruded at least one inch from the other end. The molds were removed after the mixture had set (1 to 1.5 hours), and rough seams were smoothed with a razor blade. The cylinders were dried overnight at 40°C. Waterproof epoxy was applied to both ends of each cylinder (without covering the screw head) to prevent dissolution from the ends and to allow for a radially symmetrical surface for dissolution. A numbered tag was embedded in the epoxy on the top of each cylinder. They were then re-dried for 48 hours at 40°C, placed in a desiccator to cool and weighed to the nearest 0.001g. Cylinders were deployed at the 2.5 m vertical drop (MVD) below mean higher high water (MHHW) at each transect on all eight sites. To deploy the cylinders, screw anchors were drilled into the rock substrate and the cylinders were screwed directly into the anchors, positioning them directly above the substrate. Cylinders remained deployed for several days, depending upon weather conditions. After collection, they were dried and weighed. The difference in weight of each cylinder is a relative measure of the rate of water movement past the cylinder [Muus 1968; Gerard 1982; Petticrew and Kalff 1991].

Table 1. Site codes, latitude, longitude, and general descriptive location of the eight recruitment and succession study sites.

Site	Latitude	Longitude	General Location
BB	59°29.883′	151°30.967′	North side on the southernmost of the Herring Islands
C1	59°29.033′	151°31.317′	Northwest corner on the northernmost of the Herring Islands
C2	59°29.017′	151°31.033′	Southwest corner on the northernmost of the Herring Islands
HI	59°30.617′	151°31.350′	North side of Hesketh Island
JB	59°28.017′	151°31.550′	East side of Jakolof Bay
KB	59°28.150′	151°33.600′	South side of Kasitsna Bay
LB	59°28.883′	151°30.000′	South side on the easternmost of the Herring Islands
SB	59°28.650′	151°29.133′	Just outside the mouth of Tutka Bay on the south side

Transect and quadrat locations

Stretches of rocky-intertidal habitat between 25 m and 100 m in length were measured at each of the eight selected sites. The shoreline was disjunct at several sites and a total of 100 m was attained by combining rocky shorelines encompassing coarse-textured pocket beaches. To establish transects perpendicular to the shore, the mean higher high water line was estimated based on a commercial tidal program, the location of the upper edge of the barnacle zone and the lower edge of the *Verrucaria* (a black lichen) zone above the barnacles. The interface between the *Verrucaria* and barnacle zones is a good indicator of MHHW [Highsmith et al. 1994]. To determine transect placement, the site length was divided by four and the resulting distance was multiplied by a random number less than 1.0. The first transect was located that distance from the left end of the defined beach. The other three transects at the site were placed one fourth of the total beach length apart to the right (facing shore) of the first transect, excluding any pocket beaches.

Three permanent 0.1 m^2 quadrats were established at 1.5, 2.5, and 3.5 MVD below the MHHW line (Figure 2). A surveyor's sight level was used to determine the MVD locations. To mark quadrat locations, stainless steel screws were secured in holes drilled in the rocks at the upper-right and lower-left corners of each quadrat. A numbered plastic tag was attached to one of the screws. Permanently marking the quadrats enabled exact positioning of the quadrat frame on return visits.

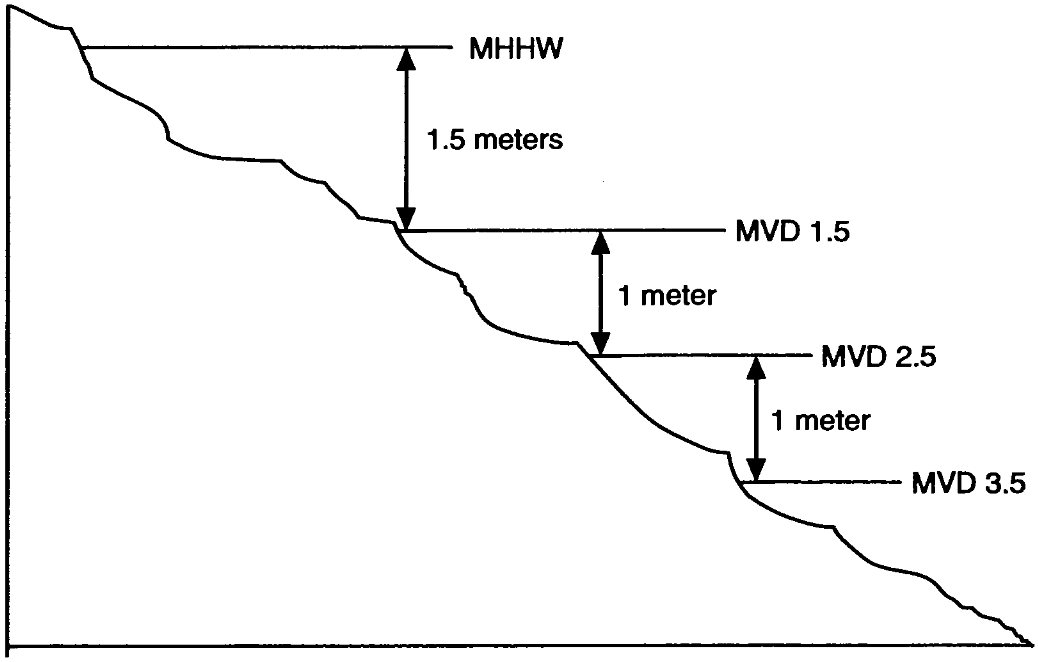


Figure 2. Schematic cross-section of a site showing the locations of meter vertical drops (MVDs) relative to each other and to mean higher high water (MHHW). The MVDs were determined with a surveyor's sight level.

Quadrat treatments

Experimental "disturbed" quadrats were created in March, July, and October 1994, and March 1995 by scraping away all invertebrates and algae, including tests and holdfasts of dead organisms. A 10-cm border was cleared around each quadrat to reduce migration problems. After physical removal of all organisms, the quadrats and border were burned with a propane torch to ensure removal of the smallest recruits or algal eggs. Finally, bleach was squirted into cracks to ensure that no *Fucus gardneri* eggs would survive. Control quadrats, in which no organisms were removed, were permanently established in March 1994. For control quadrats, the left edge of the quadrat frame was placed along the transect line centered at the 1.5, 2.5, and 3.5 MVDs (Figure 3). The March 1994 scraped quadrats were placed one meter to the left of the control quadrats. Subsequent scraped quadrats, made in July 1994, October 1994, and March 1995, were placed one meter to the left of the previously scraped quadrats. The dates for clearing quadrats were chosen to reflect different seasons: March 1994 was selected to provide space for spring-recruiting organisms; July 1994 was chosen to provide space for species that recruit in late summer or fall; October 1994 was selected to provide bare space for recruitment occurring during the winter or in early spring before the next March scrapes were made; and March 1995 was selected to provide a measure of inter-annual variability when compared to the March 1994 quadrats. By March 1995, there were 60 quadrats on each site (four transects × three MVDs × five treatments), with exceptions as noted below (Table 2).

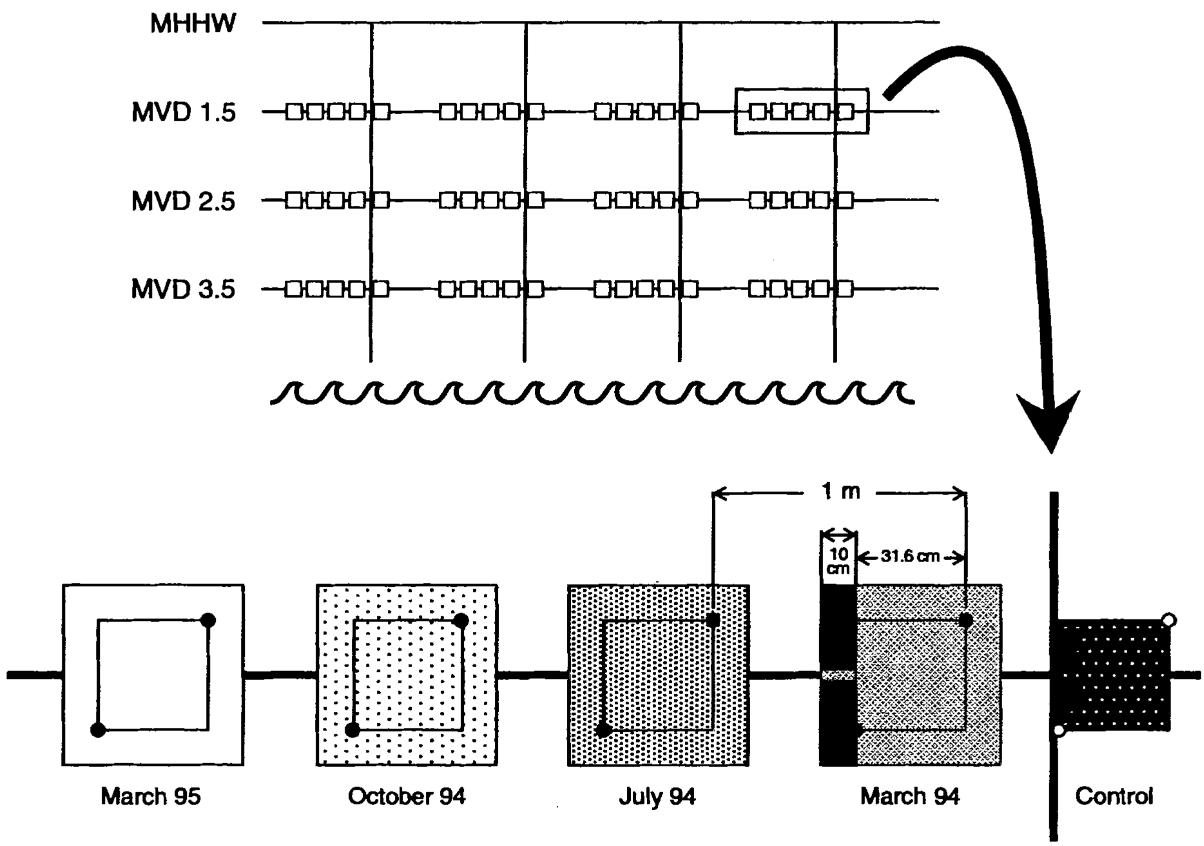


Figure 3. Schematic of study site layouts. Quadrats are one meter apart. MVD = meter vertical drop from mean higher high water (MHHW). The dates below each quadrat indicate when the quadrat was scraped. A 10-cm boundary was scraped outside of each 31.6 x 31.6 cm quadrat.

After the first visit to the Jakolof Bay (JB) site we removed its MVD 3.5 quadrats from the study because fine sediments collected on the rocky substrate and in crevices and precluded the recruitment of hard-substrate organisms. Sites JB and Kasitsna Bay (KB) were relatively narrower and lacked sufficient length to scrape quadrats in March 1995 without interfering with the established control quadrats. Thus, no March 1995 quadrats were scraped on these sites. After initially establishing four transects at the Tutka Bay site (SB), Transect 3 was dropped from the study because the substrate was generally cobble and too different from the rest of the site and other sites for comparative purposes. Table 2 lists total transects and quadrats at each of the eight sites.

Table 2. Dates and locations of control and scraped quadrats at the study sites. MVD = meter vertical drop. An X means that quadrats were established at that site and MVD for the number of transects listed.

Site	Number of Transects	MVD	Date Quadrats Scraped				
			Control	March 94	July 94	October 94	March 95
BB	4	1.5	X	X	X	X	X
	4	2.5	X	X	X	X	X
	4	3.5	X	X	X	X	X
C1	4	1.5	X	X	X	X	X
	4	2.5	X	X	X	X	X
	4	3.5	X	X	X	X	X
C2	4	1.5	X	X	X	X	X
	4	2.5	X	X	X	X	X
	4	3.5	X	X	X	X	X
HI	4	1.5	X	X	X	X	X
	4	2.5	X	X	X	X	X
	4	3.5	X	X	X	X	X
JB	4	1.5	X	X	X	X	
	4	2.5	X	X	X	X	
	4	3.5					
KB	3	1.5	X	X	X	X	
	3	2.5	X	X	X	X	
	3	3.5	X	X	X	X	
LB	4	1.5	X	X	X	X	X
	4	2.5	X	X	X	X	X
	4	3.5	X	X	X	X	X
SB	3	1.5	X	X	X	X	X
	3	2.5	X	X	X	X	X
	3	3.5	X	X	X	X	X

Quadrat data collections

Quadrats were revisited to collect recruitment and succession data after they were scraped, with the main data collection efforts made after the final scraped quadrats were created in March 1995. A non-destructive sampling procedure was necessary for monitoring quadrats through time. Two different point-contact methods were used for collecting percent cover data. The first method was used to perform rapid assessments in control and scraped quadrats. A 36-point, evenly spaced grid within the 31.6 cm x 31.6 cm quadrat frame was placed over each quadrat and aligned with the rock screws. The organisms directly beneath each of the 36 grid points were identified and recorded. Only overstory organisms, or bare rock, visible directly beneath the grid point without disturbing the substrate were recorded. Although this method misses understory organisms, it was used when the sampling team was establishing new scraped quadrats and did not have time for more detailed counting.

A more thorough, point-contact method was employed after the last quadrats were scraped in March 1995. A 36-point, evenly-spaced grid within a 31.6 cm x 31.6 cm frame was aligned over each quadrat. The organisms beneath each grid point were identified vertically through all layers. Overstory, midstory, and understory organisms were all sampled, providing a 3-dimensional view of the complex intertidal community [Foster et al. 1991]. Data were collected using this method in July 1995, October 1995, June 1996, and September 1996 (Table 3).

Table 3. Dates when invertebrate and algal data were collected from the study sites. An (X) signifies data collections made on a limited set of sites or using abbreviated methods. An X signifies data collected using the 3-D percent cover methods that sample vertically through the intertidal assemblages. The shaded area represents data that is presented in this report for the recruitment and successions study. Data represented by the non-shaded area were used for methods comparisons.

Date Data Collected	Control	March 94	July 94	October 94	March 95
March 1994	(X)				
July 1994	(X)	(X)			
October 1994	(X)	(X)	(X)		
March 1995					(X)
July 1995	X	X	X	X	X
October 1995	X	X	X	X	X
June 1996	X	X	X	X	X
September 1996	X	X	X	X	X

For data collected using the 3-D method, total percent cover greater than 100% can occur if all points are summed for all species. Organisms often occur in layers and each grid point could have more than one organism recorded as being directly beneath it. Therefore, we calculated total percent cover of all organisms based on percent of bare rock present. Percent bare rock is the percent of grid points under which no organisms occurred and is a measure of available, or unoccupied, space. Total organism percent cover was calculated by subtracting the number of grid points where bare rock occurred from 36, dividing the remainder by 36 then multiplying by 100. This value is referred to as "total percent cover".

Most invertebrates and algae were recorded at the species level in the field, with the following exceptions: The barnacles *Semibalanus balanoides* and *Balanus glandula* are difficult to differentiate in the field, especially when covered with algae. These two barnacles occupy similar ecological niches [O'Clair and Zimmerman 1987] and are treated together in this study. The green filamentous algae, *Acrosiphonia* sp. and *Cladophora* sp., are very similar morphologically and were combined as one taxonomic group. *Melanosiphon intestinalis* and *Scytosiphon lomentaria* were also treated as one taxonomic group. *Porphyra* spp. were identified to the genus level in the field. *Palmaria* species were combined for analyses, as were *Odonthalia* species.

Algal vouchers representing all species present in the quadrats were collected at each site. In addition, the general site areas were surveyed to collect species that may not have occurred in the quadrats. Examples of each alga were pressed on herbarium paper, dried, and mounted for archiving. Labels were attached to the final mounted specimens, documenting the collector and location of collection. Each specimen was inserted into a plastic sleeve and placed in a large binder, separated into rhodophytes, phaeophytes, and chlorophytes, and was used as a reference and review tool for the field data collection team. Table 4 lists the algal voucher specimens that were collected from the general study area in outer Kachemak Bay.

Table 4. Algal voucher specimens collected from intertidal zones in the general study area of outer Kachemak Bay.

Chlorophyta	Phaeophyta	Rhodophyta
Acrosiphonia sp. #1	*Agarum cribrosum*	*Antithamnionella pacifica*
Acrosiphonia sp. #2	*Alaria fistulosa*	*Bangia* sp.
Blidingia minima	*Alaria marginata*	*Bossiella* sp.
Chaetomorpha tortuosa	*Alaria praelonga*	*Callithamnion pikeanum*
Chaetomorpha melagonium	*Analipus japonicus*	*Callophyllis cristata*
Cladophora seriacea	*Chorda filum*	*Constantinea subulifera*
Codium ritteri	*Chordaria flagelliformis*	*Corallina* sp.
Derbesia marina (*Halicystis ovalis*)	*Coilodesme bulligera*	*Cryptosiphonia woodii*
	Colpomenia peregrina	*Devaleraea ramentacea*
Enteromorpha linza	*Costaria costata*	*Dumontia contorta*
Enteromorpha prolifera	*Cymathere triplicata*	*Endocladia muricata*
Kommannia leptoderma	*Desmarestia kurilensis*	*Gloiopeltis furcata*
Monostroma sp.	*Dictyosiphon sinicola*	*Halosaccion glandiforme*
Prasiola meridionalis (*Rhizoclonium* sp.)	*Eudesme virescens*	*Halosaccion (lepechini)*
	Fucus cottonii	*Mastocarpus papillatus*
Ulothrix sp.	*Fucus gardneri*	*Mazzaella* (Gigartinaceae)
	Hedophyllum sessile	*Membranoptera* sp.
	Laminaria groenlandica	*Mesophyllum* sp.
	Laminaria saccharina	*Mikamiella* sp.
	Laminaria (discoid holdfast)	*Neodilsea natashae*
	Leathesia difformis	*Neoptilota asplenioides*
	Melanosiphon intestinalis (*Myelophycus intestinalis*)	*Neorhodomela* sp.
		Odonthalia floccosa
	Nereocystis luetkeana	*Odonthalia kamtschatica*
	Petalonia fascia	*Opuntiella californica*
	Pilayella/Spongonema	*Palmaria callophylloides*
	Punctaria sp.	*Palmaria hecatensis*
	Ralfsia fungiformis	*Palmaria mollis*
	Saundersella sp.	*Phycodrys riggii*
	Scytosiphon lomentaria	*Polysiphonia* sp.
	Soranthera ulvoidea	*Porphyra abbottae*
		Porphyra cuneiformis
		Porphyra pseudolinearis
		Porphyra sp.
		Pterosiphonia sp.
		Ptilota serrata
		Rhodymenia pertusa
		Scagelia pylaisaei
		Tokidadendron kurilensis
		Turnerella mertensiana

Data analyses

Univariate methods (individual taxonomic group analyses)

Previous studies have shown that when rocky-intertidal assemblages differed significantly spatially and temporally, the differences were largely due to the relative importance of a few dominant species [Underwood and Chapman 1998; Chapman and Underwood 1998]. In addition, related studies have shown that recovery following disturbance to intertidal communities varied among sites and tidal heights [Kinnetic Laboratories, Inc. 1992; Carroll 1994; Minerals Management Service 1996]. Thus, repeated measures analysis of variance (rmANOVA) was performed only for several selected taxonomic groups, representing species that dominated in the nearby undisturbed rocky habitat. Two sites were selected to represent differences in wave exposure among the eight sites based on the relative ranking of sites by fetch and orientation, and the results of the calcium sulfate dissolution experiments (Figure 4). The Hesketh Island site (HI) represented highly wave-exposed sites and the Herring Island site (BB) represented protected sites. These were used in the "Site" effects comparison in the ANOVAs. Separate ANOVAs were performed for each MVD. The hypothesis tested for each species was that there was no difference in percent cover between sites, scrape dates (date when quadrats established), sampling periods (date when data were collected) or their interactions. Sampling date was selected as the repeated measures factor.

When a site has recovered from scraping, no significant differences in mean percent cover between control and the scraped quadrats at that site should be apparent. Therefore, a significant interaction between site or scrape date and sampling period indicates recovery when significant differences are observed for the July 1995 sampling period but not for the September 1996 period. Differences in the time to recovery will be affected by the unique environmental factors at each site, including wave exposure. Thus, significant differences between sites may represent the effect of wave exposure, and the suite of environmental factors for which exposure is a proxy, on recovery. Given a significant difference in an rmANOVA comparison, multiple comparisons were performed using the Tukey test. To summarize the matrices of multiple comparisons, key comparisons were extracted which depended on the particular effect. Primary interest was given to contrasts of the control means to the various scrape date means. Parameters analyzed included total percent cover (the percent of substrate that is not bare), *Semibalanus balanoides* and *Balanus glandula* (MVDs 1.5 and 2.5), *Semibalanus cariosus* (MVD 3.5), *Fucus gardneri* (MVDs 1.5 and 2.5), *Alaria* spp. (MVD 3.5), and *Mytilus trossulus* (MVDs 1.5 and 2.5). The significance level for all comparisons is 5%. All analyses were performed on percent cover data collected using the 3-dimensional method. The three null hypotheses tested by the univariate analyses are:

1. $H_0 1$: There are no significant differences in recovery for quadrats scraped during different seasons (Scrape Date).
2. $H_0 2$: There are no significant differences in recovery for quadrats scraped at sites with different wave exposures (Site).
3. $H_0 3$: There are no significant differences in quadrat data collected during different site visits (Time).

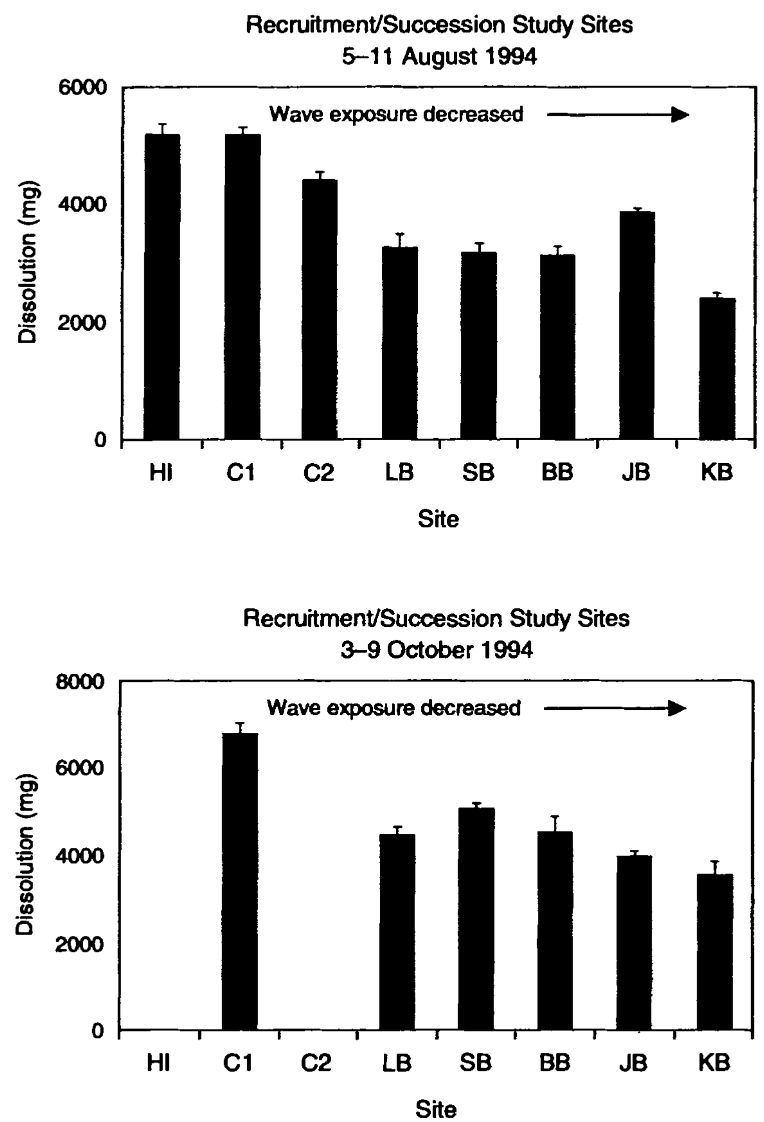


Figure 4. Mean dissolution of calcium sulfate cylinders deployed at the 2.5 meter vertical drop on study sites in August and October 1994. Sites are aligned from left to right in order of decreasing wave exposure. N = 4 for each site. Vertical bars are one standard error. Missing data indicate that cylinders were destroyed by waves or couldn't be retrieved in time due to weather.

Multivariate methods (community level analyses)

Nonparametric multi-dimensional scaling [MDS: Kruskal and Wish 1978; Field et al. 1982] was used to assess changes in the community-level composition of quadrats. Since the variability in percent cover of most organisms was very high, and the statistical power for most univariate analyses was low, these community level analyses provide an alternate method for assessing the convergence of scraped quadrats with control quadrats over time. Warwick and Clarke [1991] found that multivariate methods (e.g., MDS) were much more sensitive than the commonly used univariate methods at discriminating the response of marine communities to stress or environmental changes. Multivariate techniques incorporate population-level variation into community-level effects without the subsequent loss of species-specific information

[Whittle et al. 1998]. Among the applicable multivariate techniques (e.g., MDS, cluster analysis, principal coordinates analysis, detrended correspondence analysis), MDS was selected because of its robustness, applicability and ease of interpretation. The MDS algorithm attempts to plot samples on a two-dimensional graph such that the rank ordering of the sample distances agrees with the rank order of distances from a dissimilarity matrix. If successful, as measured by the "stress coefficient" (0.0–1.0), the ordination gives a visual representation of the similarity of the species composition between samples [Clarke and Warwick 1994]. That is, samples which are highly similar will be close together in the MDS plot while dissimilar samples should be widely separated. The stress coefficient reflects the extent to which the two sets of ranks do not agree and an accepted rule-of-thumb is that values <0.1 correspond to a good fit, values >0.1 and <0.2 give a useful 2-dimensional picture but too much reliance should not be placed on the details of the ordination, and values >0.3 indicate an almost arbitrary ordination [Clarke and Warwick 1994]. Thus, MDS is an indirect gradient analysis method, which is useful here because it provides a graphical means of revealing ecologically meaningful relationships among sets of multi-species data. Cluster analyses were also applied to the dissimilarity matrices and were conducted to corroborate MDS results. The combination of techniques is especially important when the stress value of the MDS ordination is high.

Multivariate analyses were performed based on family level, or higher, percent cover estimates. It has been shown that very little information is lost analyzing data at higher taxonomic levels using MDS and in some instances it may better reflect the effects of some environmental variables [Clarke and Warwick 1994]. Advantages of lumping data to higher taxonomic levels include the reduction of redundancy in species that characterize the community composition, the ability to include data for those organisms that are difficult to identify to the species level in the field, and the reduction of the effects of rare species. The Bray–Curtis dissimilarity measure [Bray and Curtis 1957] was used to calculate distances between sites based on mean algal and invertebrate percent cover at each MVD. The statistical package STATISTICA for Windows (StatSoft, Inc., Tulsa, OK 74104) was used for MDS analyses. Results are reported for two-dimensional solutions. Dissimilarity matrices were constructed to compare data between scrape dates within a data collection date. Separate analyses were performed for each data collection date because the ordination plots contained too many variables when all of the data were combined, and were too difficult to interpret. Analyses were performed for the first and the last sampling dates to bracket the temporal range of data collection dates.

Results

General descriptive patterns

The study area contained a suite of green, red, and brown algae, as well as space-occupying, grazing, and predatory invertebrates on each site. The control quadrats at the eight sites showed some seasonal variability, but the dominant species were fairly constant across time. The dominants included the barnacles *Semibalanus balanoides* + *Balanus glandula* (Balanus) and *S. cariosus*, the perennial alga *Fucus gardneri*, the grazing snails *Littorina sitkana* and *L. scutulata*, the limpets *Lottia pelta, L. digitalis*, and *Tectura scutum*, and the blue mussel *Mytilus trossulus*. The abundance of the annual kelp *Alaria* spp. varied seasonally.

Balanus dominated in the high intertidal zone, about 1.5 m vertical drop below mean higher high water. Attached to or near the barnacle cover was *Fucus gardneri*, the dominant algal species at this tide height. Several other algal species commonly occurred, although at much lower percent cover than *F. gardneri*. They included the red algae *Endocladia muricata* and *Gloiopeltis furcata*. The most common grazers included *Littorina sitkana* and *L. scutulata*, with *L. sitkana* being more abundant, and the limpets *Lottia pelta* and *L. digitalis*, with *L. pelta* being more abundant.

At 2.5 MVD below MHHW, Balanus were the dominant barnacles, but at a lower percent cover than at MVD 1.5. *Fucus gardneri* still dominated the algal assemblage, but a more diverse algal community emerged. Other algae included the rhodophytes *Palmaria* spp., *Odonthalia* spp., *Polysiphonia* sp., *Pterosiphonia* sp. and the chlorophytes, *Ulva* sp., *Monostroma* sp. and *Acrosiphonia* spp. The blue mussel *Mytilus trossulus* was commonly attached to barnacle tests, among *F. gardneri* or *Odonthalia*, or in crevasses.

In the lowest intertidal zone studied, 3.5 m below MHHW, the dominant algae were the phaeophyte *Alaria* spp. The thatched barnacle *Semibalanus cariosus* was the dominant barnacle. The black chiton *Katharina tunicata* was most abundant at this tidal level compared to higher intertidal zones. Limpet and littorine snail densities were much lower, although the limpet *Tectura scutum* was common.

The temporal changes in the abundance of barnacles, *F. gardneri*, and *Alaria* spp. following the scraping disturbances are presented to illustrate patterns in recovery for all sites and scrape dates (Figures 5–8). Data are presented for the first sampling date that 3-dimensional percent cover data were collected, July 1995, and for the last data collection date in September 1996. The sites are ordered left to right, from the most wave-exposed sites to the most wave-protected sites.

In July 1995, barnacle spat had the highest percent cover (> 80% for some sites) in quadrats that were most recently scraped compared to control quadrats and quadrats scraped earlier. The latter had decreasing cover with time (Figure 5). The quadrats scraped in March 1994 were most similar to the controls. In September 1996, the percent cover values of spat in most quadrats were similar to the control quadrats. Figures 6–8 show that for Balanus, *Semibalanus cariosus*, *Alaria* spp. and *Fucus gardneri* the percent cover values observed in July 1995 were most similar between control quadrats and quadrats scraped in March 1994. Quadrats scraped after March 1994 were least similar to controls and had almost no coverage of these organisms in July 1995. By September 1996, the percent cover of Balanus in scraped quadrats was generally higher than in control quadrats (Figure 6). In contrast, *S. cariosus* had substantially lower percent cover in all scraped quadrats at MVD 3.5 compared to control quadrats, except for the most exposed site at Hesketh Island (Figure 7). This suggests that *S. cariosus* requires more than 2.5 years to fully recover from scraping. Also at MVD 3.5, *Alaria* spp. generally had higher percent cover on the more exposed sites, such as HI and C2, and had not recovered in most scraped quadrats by the last sampling date in September 1996 (Figure 7). *F. gardneri* is most abundant at MVDs 1.5 and 2.5, although sites LB and SB had relatively high percent cover at MVD 3.5 in quadrats scraped in March 1994 (Figure 8). For most quadrats, *F. gardneri* had recovered to levels similar to control quadrats by September 1996, although some scraped quadrats had higher percent cover than did the control quadrats.

Pie diagrams are presented in Figures 9 and 10 to show the relative contribution of major intertidal species to total cover in control and scraped quadrats. The pie diagrams include data from all MVDs and eight sites combined and are presented to illustrate general trends in species composition. The "slices" of each pie represent the relative contribution that the organisms make to total percent cover and should not be confused with actual percent cover on rocks. Data collected in July 1995 and September 1996 were chosen for presentation to illustrate species composition of intertidal cover on the earliest and latest sampling dates. Dominant or key intertidal taxa for the control and scraped quadrats are presented and are in the same order for each pie diagram to aid interpretation. Species that were not found in quadrats from a specific scrape date, or were found as a small contributor to total cover, are still named in the pie diagram to emphasize their absence in comparison to other quadrat categories.

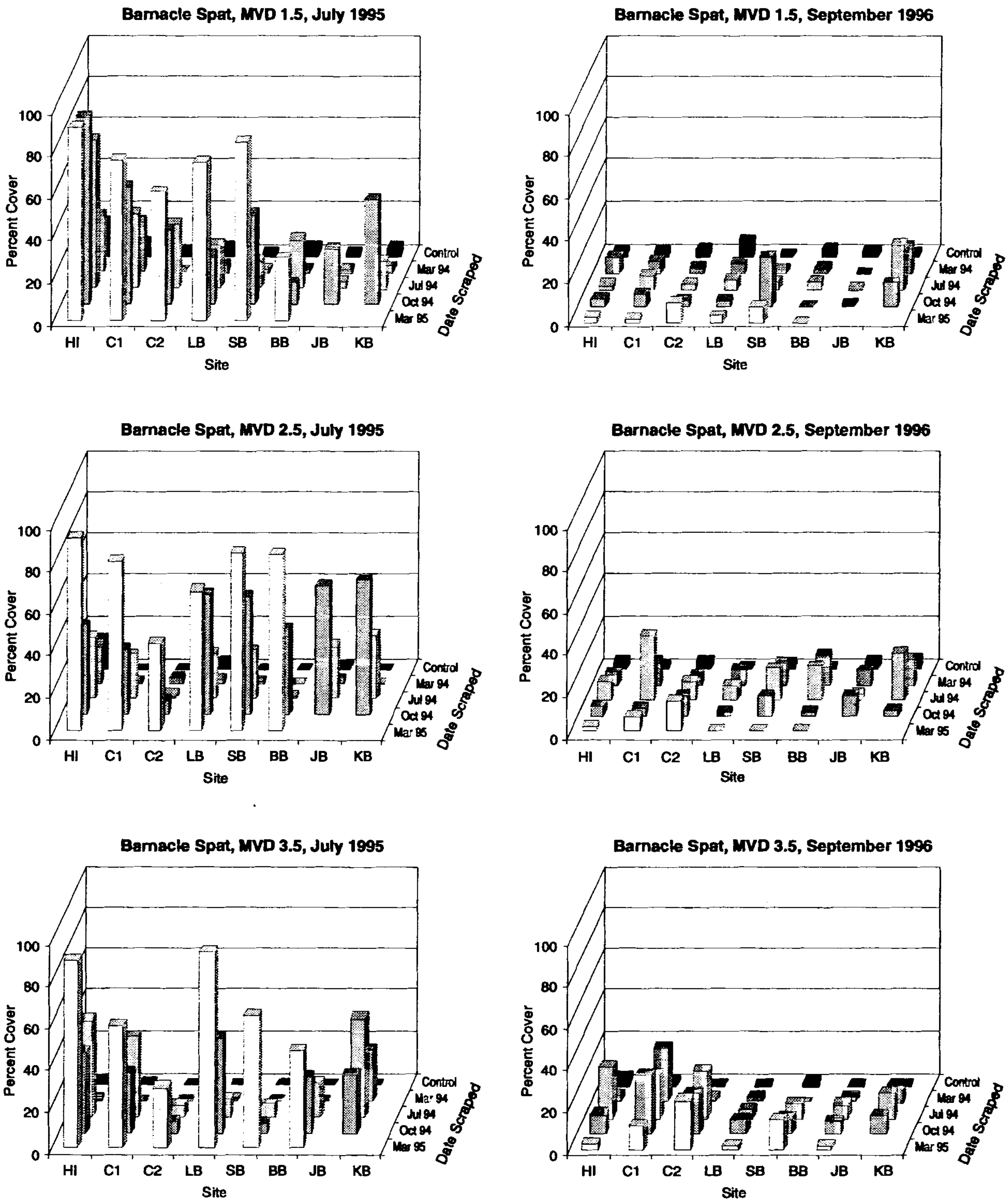


Figure 5. Mean percent cover of barnacle spat in scraped and control quadrats at each site measured in July 1995 and September 1996. Sites are ordered from left to right from most wave exposed to least exposed. MVD = meter vertical drop. Date Scraped = control quadrats or dates when quadrats were scraped. Quadrats were not scraped in March 1995 at site KB. Site JB was not sampled at MVD 3.5.

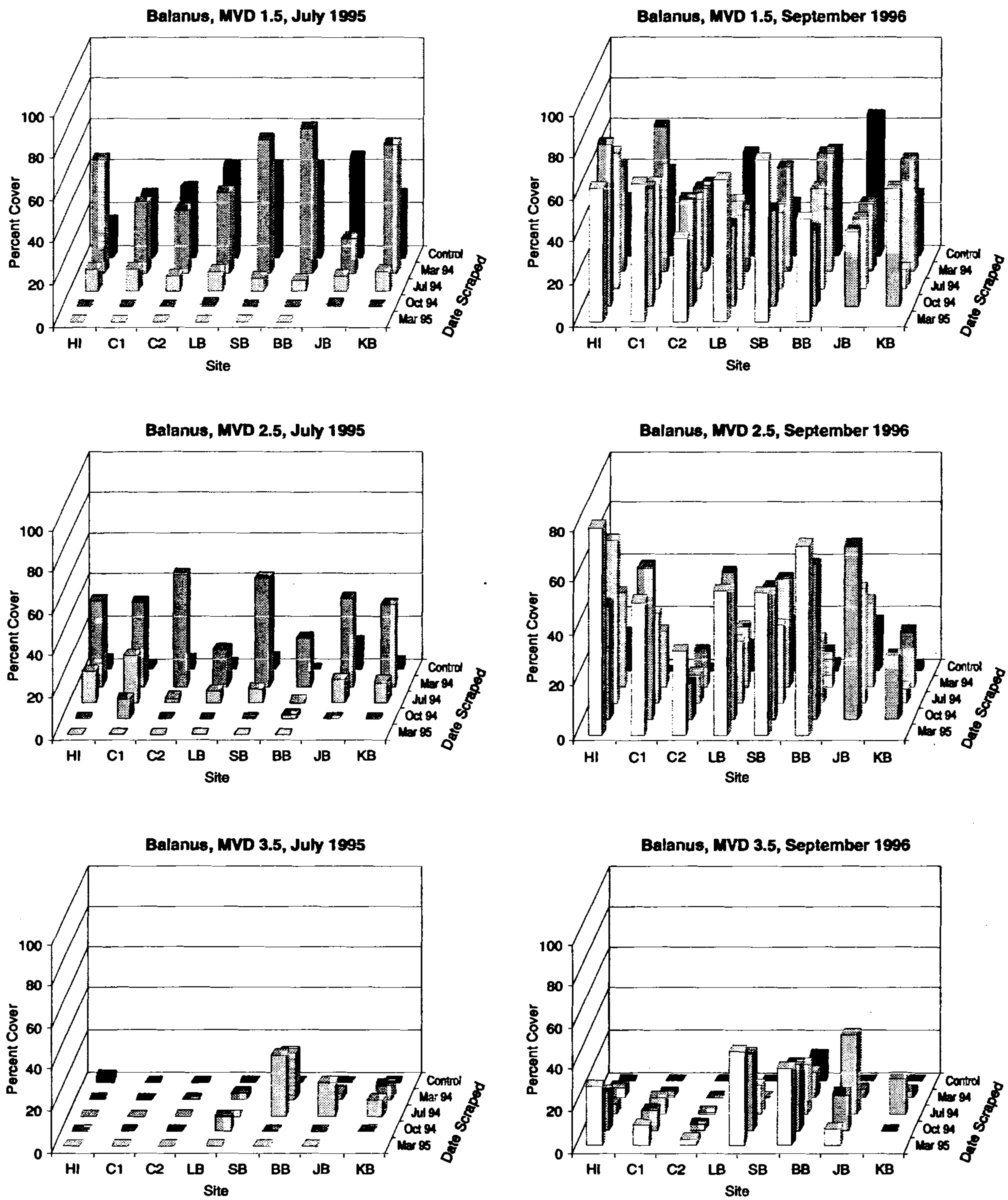


Figure 6. Mean percent cover of Balanus (*Balanus glandula* + *Semibalanus balanoides*) in scraped and control quadrats at each site measured in July 1995 and September 1996. Sites are ordered from left to right from most wave exposed to least exposed. MVD = meter vertical drop. Date Scraped = control quadrats or dates when quadrats were scraped. Note y-axis scale change for MVD 2.5, September 1996. Quadrats were not scraped in March 1995 at site KB. Site JB was not sampled at MVD 3.5.

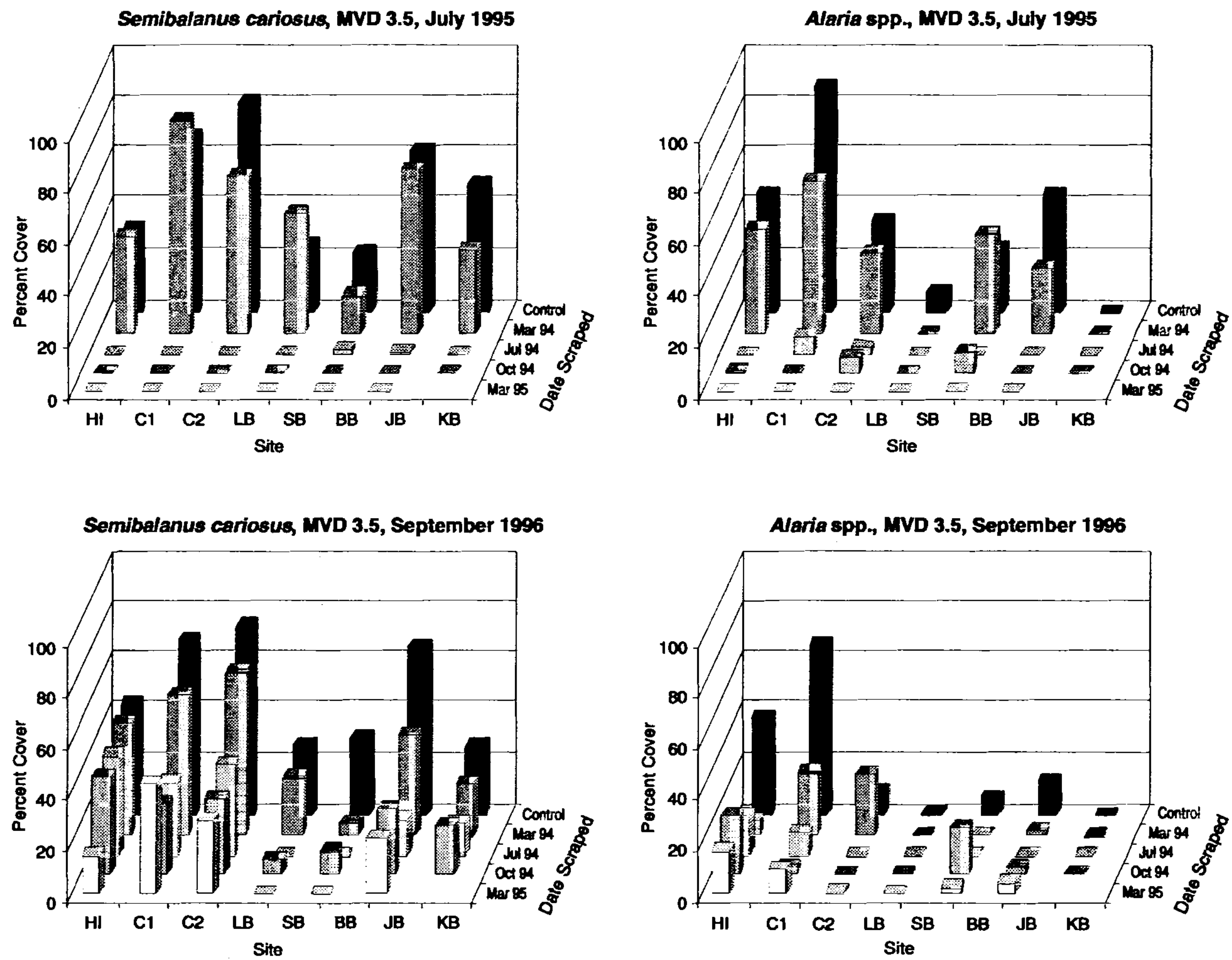


Figure 7. Mean percent cover of *Semibalanus cariosus* and *Alaria* spp. in scraped and control quadrats at each site measured in July 1995 and September 1996. Sites are ordered from left to right from most wave exposed to least exposed. MVD = meter vertical drop. Date Scraped = control quadrats or dates when quadrats were scraped. Quadrats were not scraped in March 1995 at site KB. Site JB was not sampled at MVD 3.5.

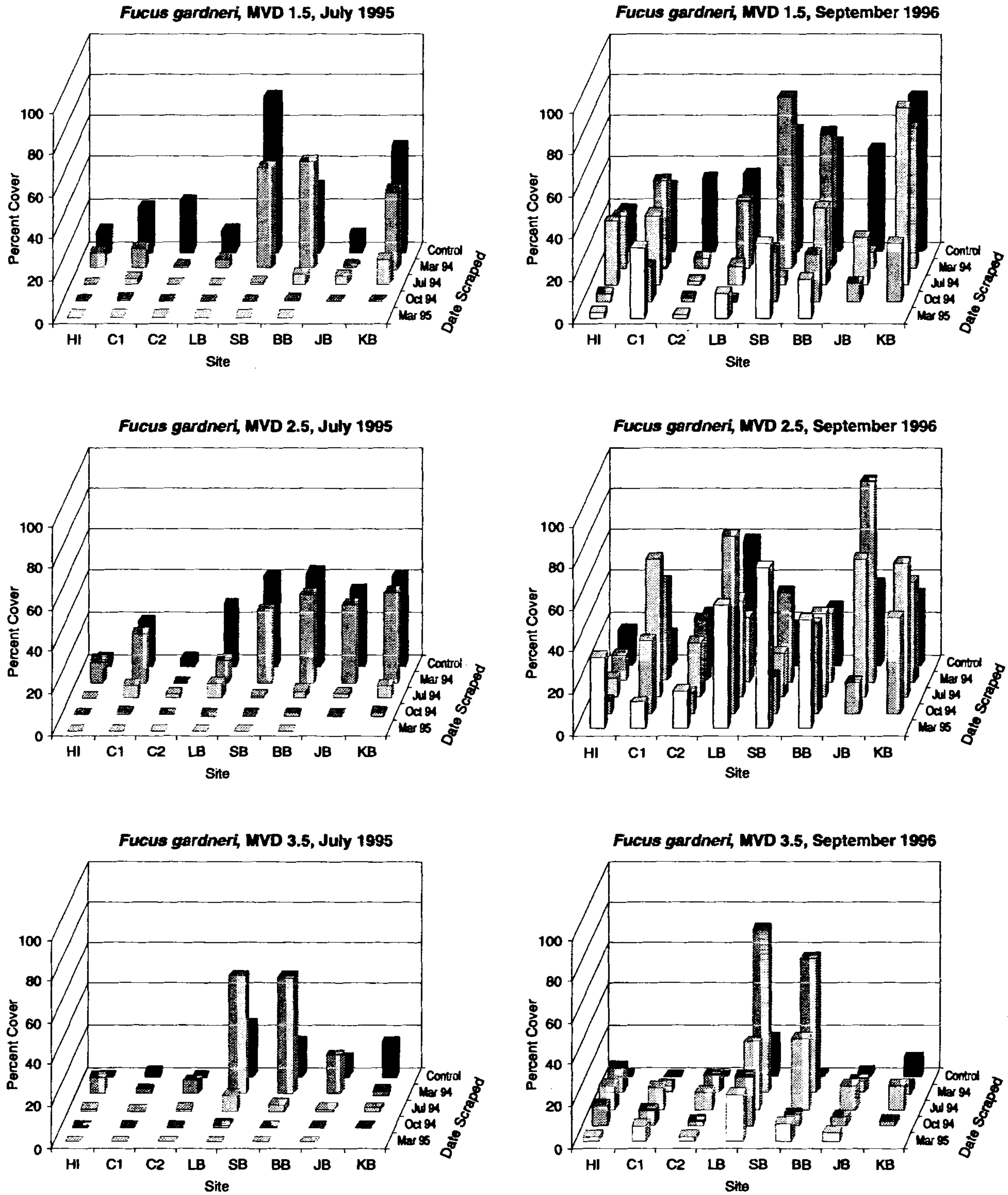


Figure 8. Mean percent cover of *Fucus gardneri* in scraped and control quadrats at each site measured in July 1995 and September 1996. Sites are ordered from left to right from most wave exposed to least exposed. MVD = meter vertical drop. Date Scraped = control quadrats or dates when quadrats were scraped. Quadrats were not scraped in March 1995 at site KB. Site JB was not sampled at MVD 3.5.

In July 1995, control quadrats had a diverse community, with no individual species dominating (Figure 9). Green algae (chlorophytes), red algae (rhodophytes), brown algae (phaeophytes), mussels, and barnacles are all major space occupiers. The relative contributions of the various intertidal organisms to total cover in scraped quadrats were very different from those in control quadrats. For most groups, total cover was lowest in those quadrats that had the least amount of time to recover since the scrape date. In contrast, barnacle spat cover was highest in the most recently scraped quadrats (Figure 9). Just four months after scraping, March 1995 quadrats showed a low distribution of most organisms and the highest cover of barnacle spat. Another exception is the red alga *Porphyra* spp., which had higher relative contributions to total cover in recently scraped quadrats (March 1995 and October 1994) compared to control quadrats. Note that the earliest scraped quadrats (March 1994) were very similar to control quadrats and had little contribution by barnacle spat. The blue mussel *Mytilus trossulus* did not contribute significantly to total cover in any of the scraped quadrats whereas in control quadrats it was a significant contributor, suggesting *M. trossulus* is not an early colonizer of bare space on rocks.

Figure 10 includes pie diagrams of the same organisms presented in Figure 9, for data collected in September 1996. The relative contribution of species in control quadrats was almost identical in July 1995 and September 1996. Scraped quadrats were more similar to control quadrats by September 1996 than they had been in July 1995. The major differences between scraped quadrats and control quadrats found in September 1996 include greater proportions of *Fucus gardneri* and Balanus in scraped quadrats. *M. trossulus* contribution to total cover, though greater than in July 1995, was still much lower in all scraped quadrats than control quadrats. Also, the relative contribution of *S. cariosus* was lower in most scraped quadrats than in control quadrats.

Total percent cover (percent substrate that is not bare rock) for all quadrats over time at sites BB and HI is plotted in Figures 11 and 12, respectively. These sites were selected to represent wave-protected (BB) and wave-exposed (HI) sites and are included in the univariate analyses presented in the next section. Site BB data (Figure 11) show that there is little intra- or inter-annual variability in total cover in control quadrats at all three MVDs. Scraped quadrats are at, or near, convergence with control quadrats by the last sampling date in September 1996. At site HI (Figure 12), total percent cover in scraped quadrats is higher than for similar treatments at Site BB. At HI, total percent cover is similar in scraped and control quadrats at all sampling dates at MVD 1.5 and during the last two sampling dates at MVDs 2.5 and 3.5. It should be noted that quadrats may have similar total percent cover but have very different species compositions. Percent cover data are more meaningful when trends are interpreted within the context of key species or groups of organisms as is done below.

Densities of grazers counted in July 1995 and June 1996 are shown in Figures 13–15. Direct counts of mobile organisms were only conducted twice due to time limitations. The periwinkles *Littorina scutulata* and *L. sitkana* were common grazers found in the quadrats. *L. scutulata* is commonly found at lower tidal heights than *L. sitkana*. However, both species occupy a similar grazing niche and are treated together in Figure 13. These snails are small, usually <5 mm, and their abundances are not accurately assessed using a 36-point sampling grid. The actual counts are plotted as numbers per square meter. These grazers tend to be found in conjunction with barnacles in the high intertidal zone and on or under *Fucus gardneri* when the alga is present [Highsmith et al. 2000]. The higher densities of these grazers in scraped quadrats than control quadrats may be a result of the higher percent cover of barnacles and *F. gardneri* in the scraped quadrats (Figure 10).

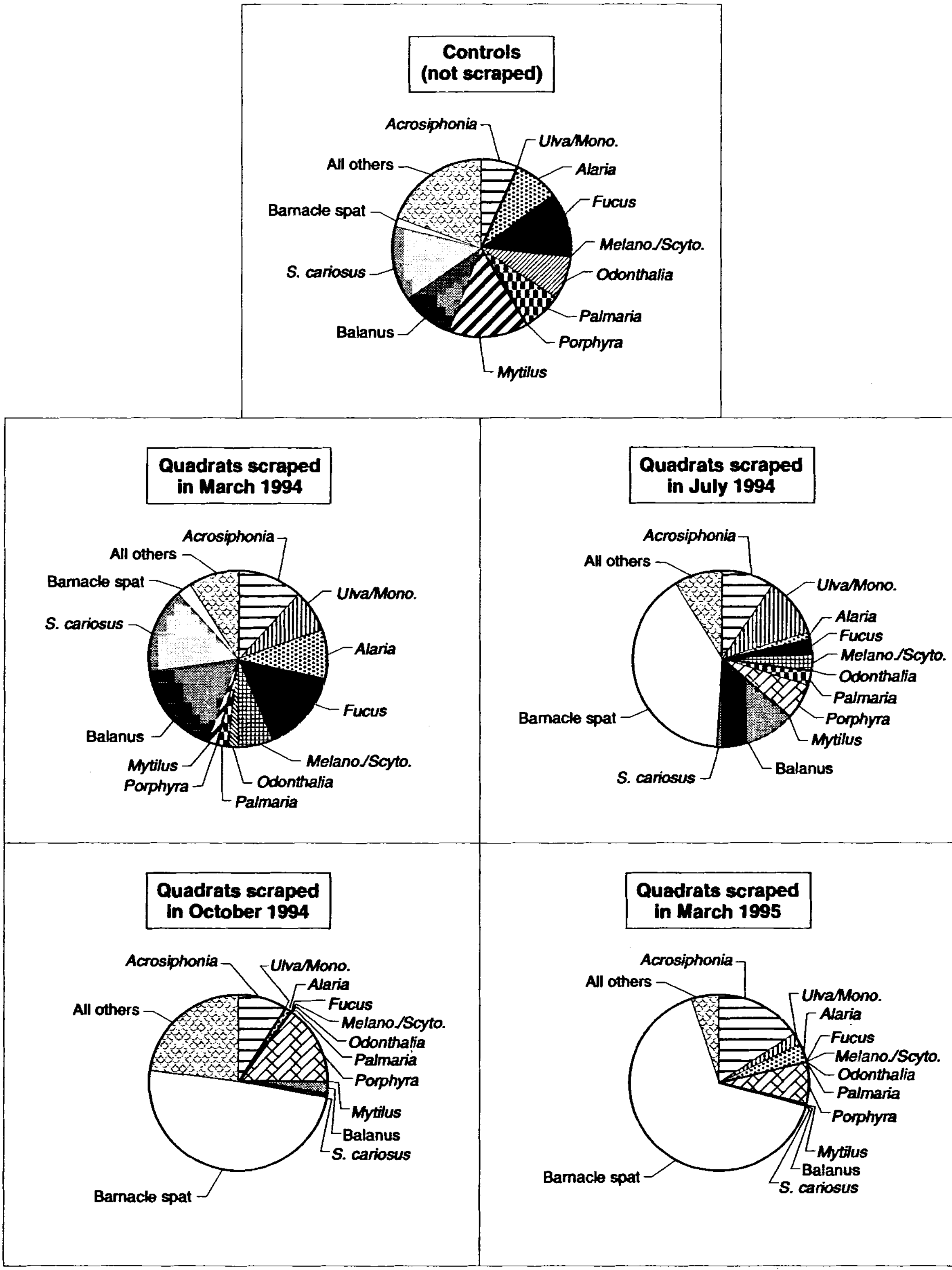


Figure 9. Contribution of major intertidal species to total cover within quadrats in July 1995. Species are presented in the same order for each pie diagram. Data represent all eight sites and MVDs combined and reflect the relative contributions to total cover.

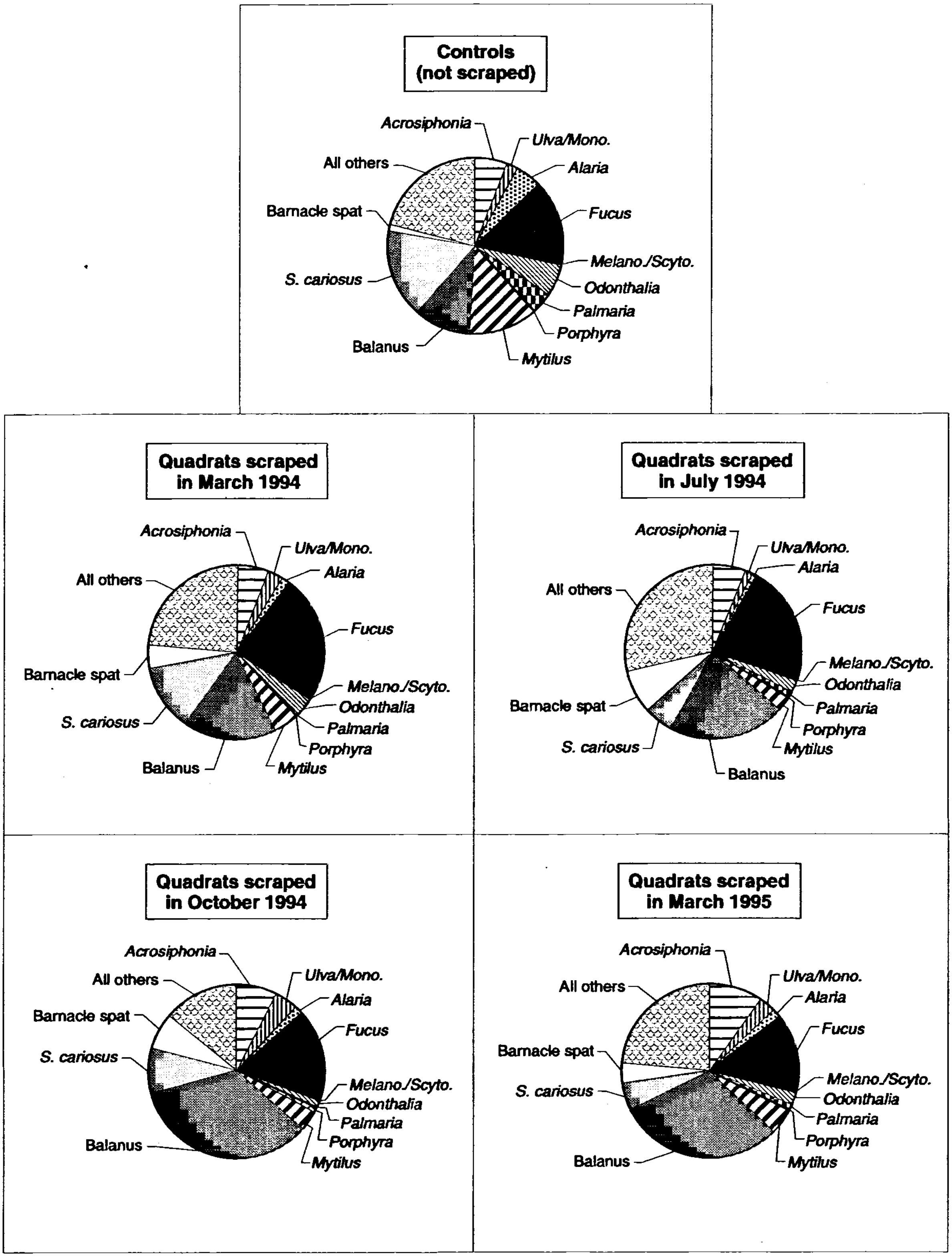


Figure 10. Contribution of major intertidal species to total cover within quadrats in September 1996. Species are presented in the same order for each pie diagram. Data represent all eight sites and MVDs combined and reflect the relative contributions to total cover.

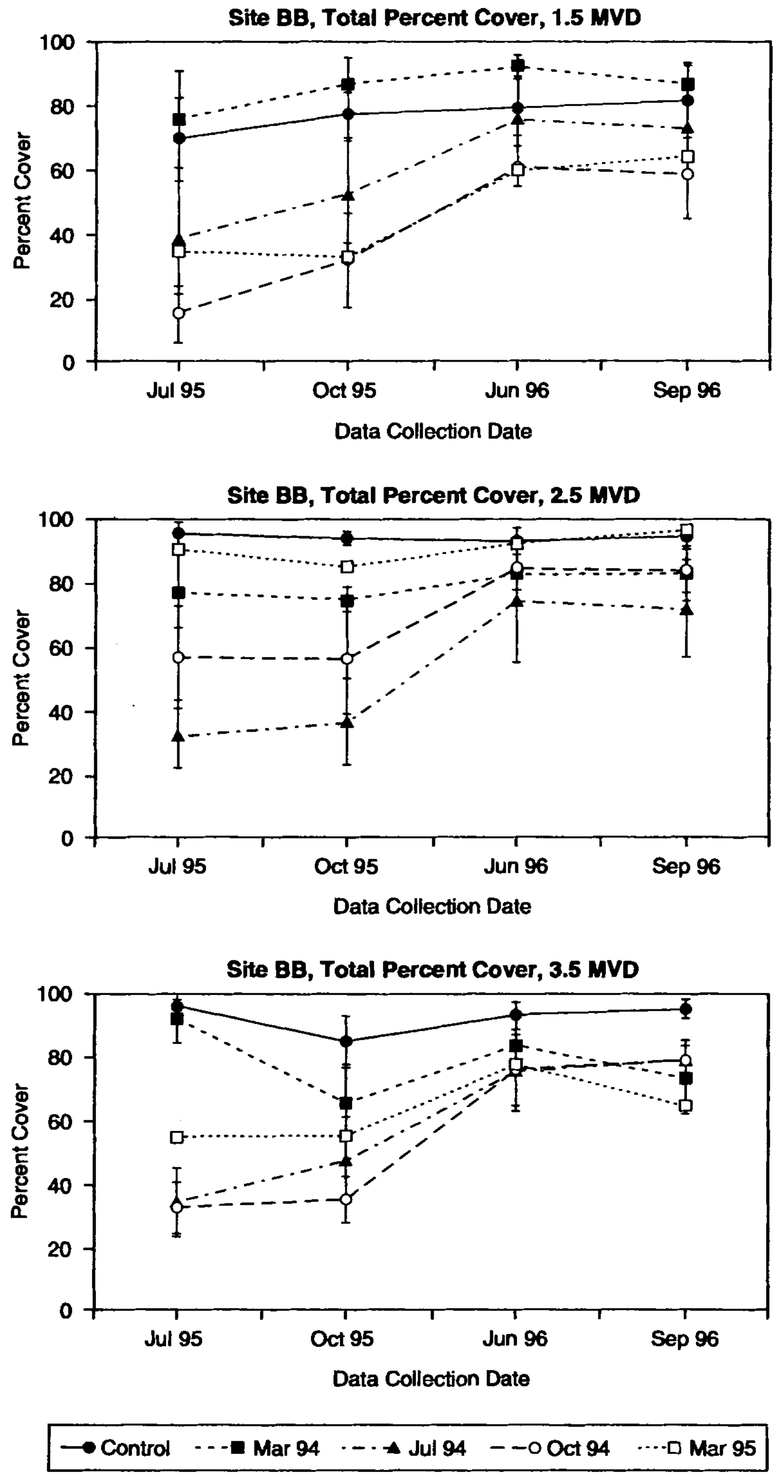


Figure 11. Mean total percent cover of all invertebrates and algae in scraped and control quadrats at sheltered site BB. Different symbols represent control quadrats or quadrats scraped on different dates, as shown in the legend. The x-axis represents the dates when percent cover data were collected. MVD = meter vertical drop. Error bars represent one standard error of the mean.

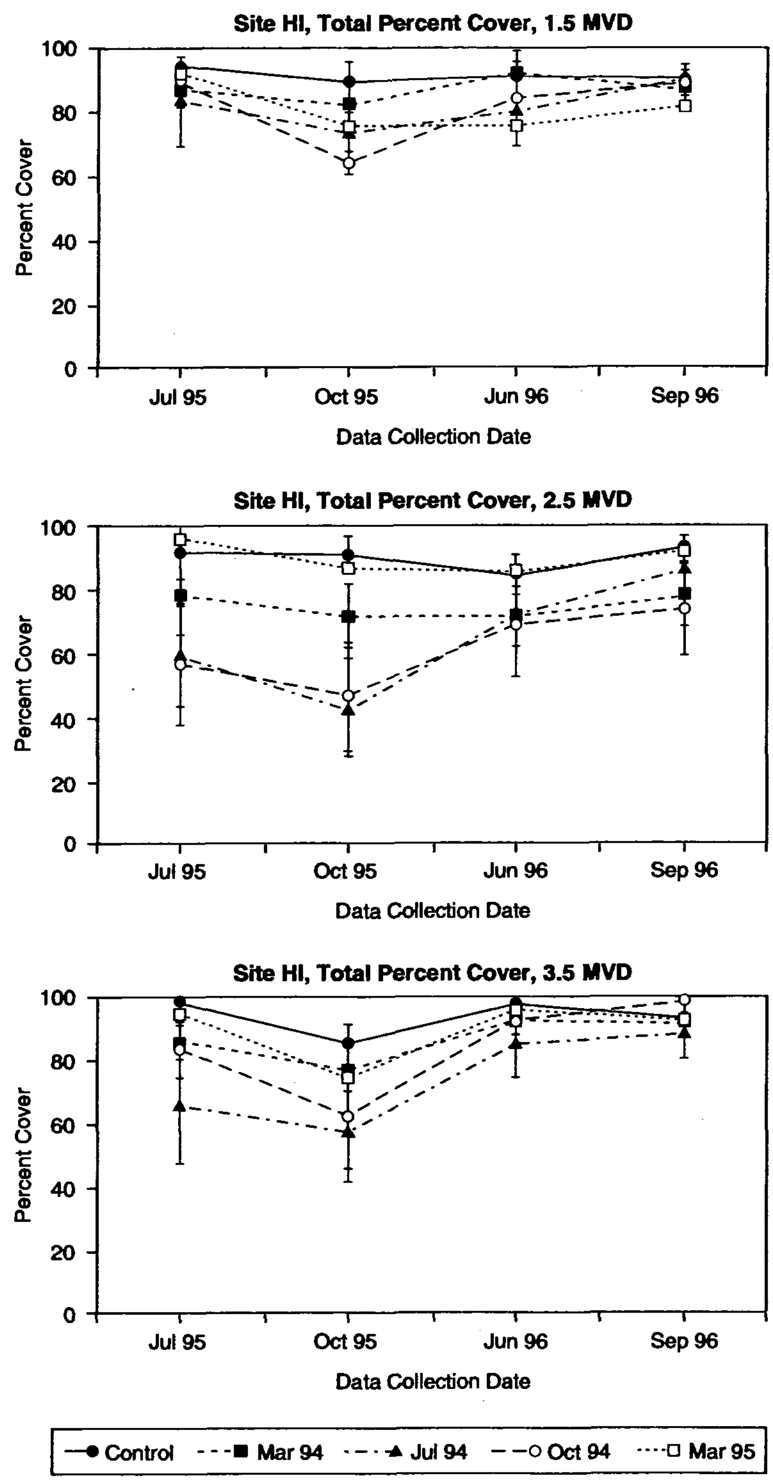


Figure 12. Mean total percent cover of all invertebrates and algae in scraped and control quadrats at wave exposed site HI. Different symbols represent control quadrats or quadrats scraped on different dates, as shown in the legend. The x-axis represents the dates when percent cover data were collected. MVD = meter vertical drop. Error bars represent one standard error of the mean.

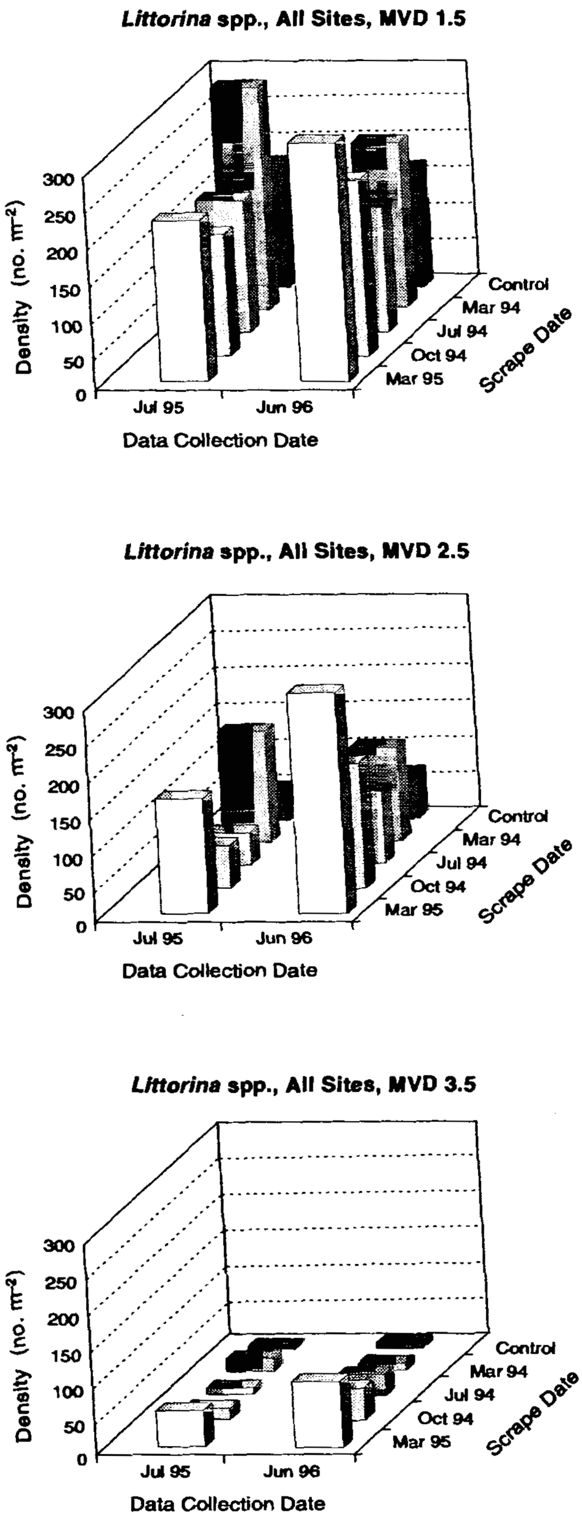
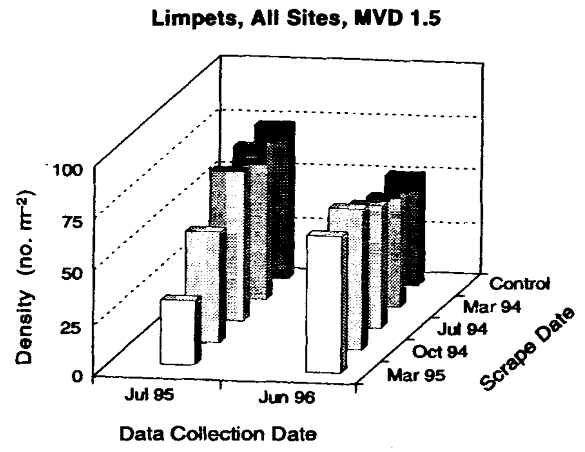
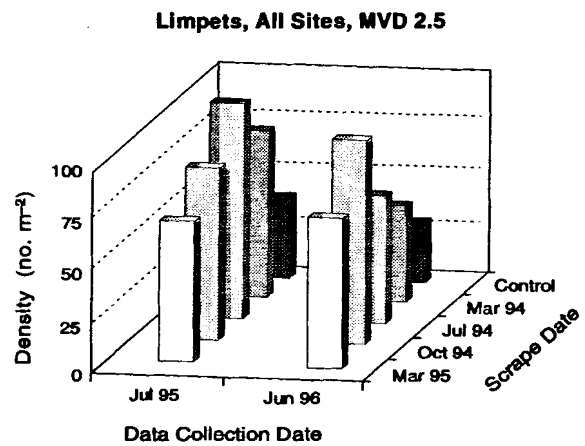


Figure 13. Densities (individuals m^{-2}) of *Littorina sitkana* and *L. scutulata* averaged across all sites. Data are means of site means. N = 8 at MVDs = 1.5 and 2.5. N = 7 at MVD = 3.5. MVD = meter vertical drop. Scrape Date = control quadrats or dates when quadrats were scraped. Data Collection Date = date when percent cover data were collected.





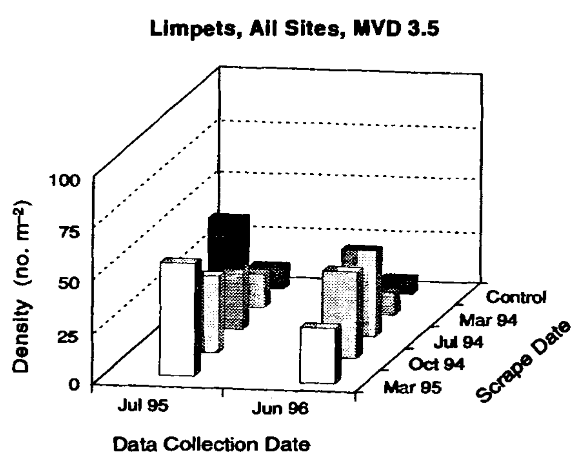
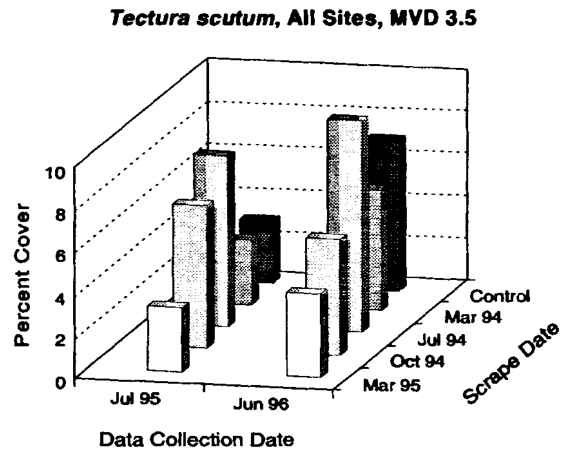


Figure 14. Densities (individuals m^{-2}) of limpets averaged across all sites. Data are means of site means. N = 8 at MVDs = 1.5 and 2.5. N = 7 at MVD = 3.5. MVD = meter vertical drop. Scrape Date = control quadrats or dates when quadrats were scraped. Data Collection Date = date when percent cover data were collected.



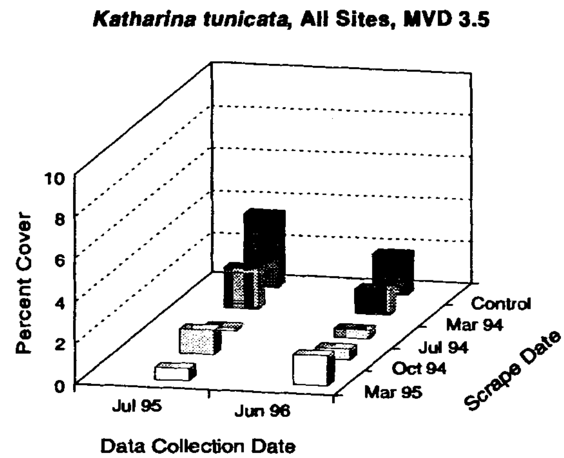


Figure 15. Densities (individuals m^{-2}) of the limpet *Tectura scutum* and the chiton *Katharina tunicata* at MVD 3.5 across all sites. Data are means of site means. N = 7. MVD = meter vertical drop. Scrape Date = control quadrats or dates when quadrats were scraped. Data Collection Date = date when percent cover data were collected.

Many small limpets occurred in the quadrats, with typically more than 80% <8 mm in length. Limpets are difficult to identify at small sizes and were recorded as Lottiidae. However, limpets >8 mm were identified to species when possible. Figure 14 includes all limpets averaged across the sites. Limpets were often more dense on scraped quadrats compared to control quadrats, especially at MVDs 2.5 and 3.5. Limpets, as well as *Littorina* spp., appeared in the quadrats soon after they were scraped. For example, quadrats scraped in March 1995 tended to have densities similar to, or greater than, control quadrats only four months later in July (Figures 13 and 14). Small limpets were often observed living on and among young and adult barnacles before anything else was observed in the quadrats. Limpet densities were lower at MVD 3.5 than at higher tidal levels. However, the limpet *Tectura scutum* typically occurs at MVD 3.5. Although the densities of this limpet were low (Figure 15), individuals were often very large (>15 mm) and can collectively graze a relatively large area. Densities of the chiton *Katharina tunicata,* another large intertidal grazer found at low tidal heights, are also shown in Figure 15. The total numbers of *K. tunicata,* which typically occurs in and among the large tests of *Semibalanus cariosus,* were low in all quadrats. However, these chitons were usually >50 mm in length and could graze large total areas.

Univariate analyses (individual taxonomic group analyses)

A comparison was made between the surface percent cover and 3-dimensional methods to determine whether the earlier surface data could be combined with the later 3-D collections during this study. This comparison would also demonstrate if the 3-D data were comparable to data collected previously in the area by other researchers using the simpler method. Figure 16 compares the two methods for organisms that generally occur above other organisms (overstory), both above and below other organisms (midstory), and beneath most other organisms (understory). The two methods are comparable for the brown algae, *Alaria* spp. (slope = 0.996, $r^2 = 0.994$) and *Fucus gardneri* (slope = 0.92, $r^2 = 0.96$). These algae are overstory organisms and, if present, appear directly under the intersecting grid points for both methods. The two methods did not correlate as well for organisms that often occur beneath other invertebrates or algae. The blue mussel *Mytilus trossulus* often grows on top of barnacles but beneath algae such as *F. gardneri* or *Odonthalia floccosa*. The surface percent cover method underestimated blue mussels by 36% (slope = 0.64, $r^2 = 0.712$). Similarly, the midstory algal species *Odonthalia floccosa* is under-represented as intertidal cover using the surface percent cover method (slope = 0.60, $r^2 = 0.648$). Barnacles often occur beneath other organisms, especially in the middle and lower intertidal zones. The correlation between the two data collection methods is low for barnacle data (slope = 0.45, $r^2 = 0.445$). This comparison of the two methods indicates that the 3-dimensional data more accurately reflect the cover of individual species and that the simpler, surface percent cover method would not be adequate for anything other than overstory organisms. Thus, the statistical comparisons reported for this study were made only for the data collected by the 3-D method starting in July 1995.

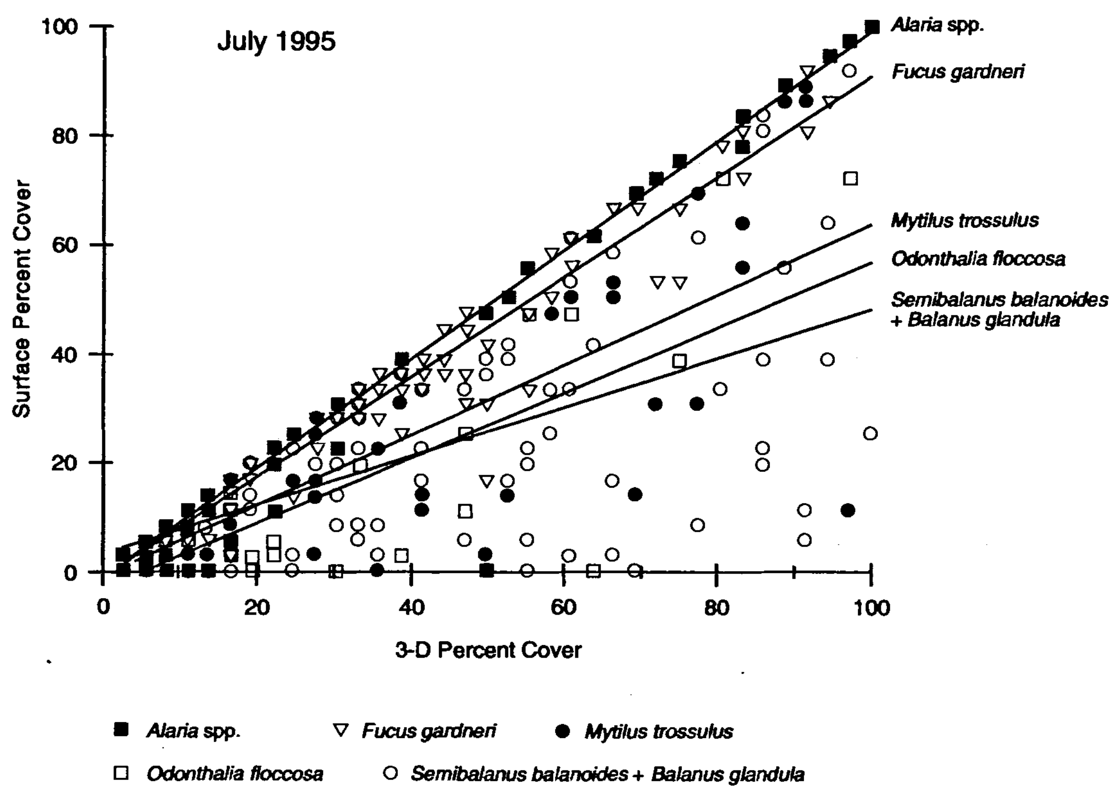


Figure 16. Linear regressions of percent cover data collected in July 1995 using "surface" and "3-D" data collection methods. Slopes and r^2 values are as follows: *Alaria* spp. (slope = 0.996, $r^2 = 0.994$), *Fucus gardneri* (slope = 0.92, $r^2 = 0.96$), *Mytilus trossulus* (slope = 0.64, $r^2 = 0.71$), *Odonthalia floccosa* (slope = 0.60, $r^2 = 0.65$), and *Semibalanus balanoides* + *Balanus glandula* (slope = 0.45, $r^2 = 0.44$).

Analyses of percent cover for barnacles resulted in significant interaction effects at MVD 1.5. The comparisons of Balanus (*Semibalanus balanoides* + *Balanus glandula*) percent cover resulted in significant interaction effects ($p < 0.05$) for the site (ST) × time (T) and scrape date (SC) × T interactions, thus rejecting the null hypotheses of no differences in means between both sites and scrape dates over time (Table 5). The key multiple comparisons of the ST × T interaction yielded no significant differences. The multiple comparisons of the SC × T interaction reveal no significant differences for the comparisons of control vs. scrape dates by sampling date. The plots of mean percent cover for sites BB and HI (Figures 17 and 18, respectively) suggest that the main interaction between the sites and the scrape dates was an over-recruitment of barnacles at the HI site, even though its control quadrats had lower mean percent covers than did site BB.

Table 5. Summary of repeated measures ANOVA comparisons for adult Balanus (*Semibalanus balanoides* + *Balanus glandula*) percent cover data at MVD 1.5. The Mauchly's test was significant ($p < 0.0042$) for this comparison so the Greenhouse–Geiser adjustment (G–G Adj.) was used. A negative sign before the p-value of a Tukey multiple comparison indicates that the mean decreased from one category to the next while a positive sign indicates that the mean increased. P-values < 0.05 are in bold print.

Effect	df Effect	MS Effect	F	P-value	G–G Adj. P-value
Site (ST)	1	802.52	0.666	0.4209	
Scraping (SC)	4	1843.58	1.530	0.2187	
ST×SC	4	3017.14	2.504	0.0632	
Error 1	30	1204.91			
Time (T)	3	8139.97	22.603	**0.0000**	**0.0000**
ST×T	3	1081.97	3.004	**0.0345**	**0.0134**
SC×T	12	1949.32	5.413	**0.0000**	**0.0000**
ST×SC×T	12	156.64	0.435	0.9452	0.9062
Error 2	90	360.13			

Summary of Tukey Multiple Comparisons

	July 95	October 95	June 96	September 96
Site x Time				
BB vs. HI	0.9579	1.000	0.9657	0.8602
Scrape Date x Time				
Control vs. March 94	0.0991	0.5956	1.0000	0.9889
Control vs. July 94	0.7256	1.0000	0.7730	0.9291
Control vs. October 94	0.2012	1.0000	0.7952	0.9400
Control vs. March 95	0.2012	0.9497	1.0000	0.9400

The analysis of variance for Balanus percent cover at MVD 2.5 resulted in significant interaction effects (Table 6). The ST × T and SC × T interaction effects are significant. The key multiple comparisons revealed no significant differences between sites by similar sampling period. The significant comparisons for this effect were among the cross-period comparisons (e.g., July 1995 for BB vs. September 1996 for HI) indicating that changes in mean Balanus percent cover between some sampling periods were different between sites but these differences do not represent comparisons of recovery and succession and are not presented. Comparisons of the SC × T interaction effect demonstrate significantly greater percent cover of barnacles for quadrats scraped in March 1995 compared to control quadrats when sampled in October 1995, June 1996, and September 1996. These significant differences are apparent in the plots of mean percent cover for MVD 2.5 at both sites (Figures 17 and 18). These graphs reveal a tremendous increase in barnacle cover for the March 1995 quadrats that greatly exceeds barnacle cover for the controls.

Table 6. Summary of repeated measures ANOVA comparisons for adult Balanus (*Semibalanus balanoides* + *Balanus glandula*) percent cover data at MVD 2.5. The Mauchly's test was significant ($p < 0.0064$) for this comparison so the Greenhouse–Geiser adjustment (G–G Adj.) was used. A negative sign before the p-value of a Tukey multiple comparison indicates that the mean decreased from one category to the next while a positive sign indicates that the mean increased. P-values < 0.05 are in bold print.

Effect	df Effect	MS Effect	F	P-value	G–G Adj. P-value
Site (ST)	1	3.09	0.003	0.9555	
Scraping (SC)	4	10235.15	10.487	**0.0000**	
ST × SC	4	1264.42	1.296	0.2940	
Error 1	30	975.98			
Time (T)	3	7722.35	21.021	**0.0000**	**0.0000**
ST × T	3	1765.05	4.805	**0.0038**	**0.0111**
SC × T	12	2264.69	6.165	**0.0000**	**0.0000**
ST × SC × T	12	226.58	0.617	0.8229	0.7835
Error 2	90	367.36			

Summary of Tukey Multiple Comparisons

	July 95	October 95	June 96	September 96
Site × Time				
BB vs. HI	0.9502	0.0780	0.9998	0.4323
Scrape Date × Time				
Control vs. March 94	0.2153	0.3567	0.9995	0.9745
Control vs. July 94	1.0000	0.9942	0.7641	0.0543
Control vs. October 94	1.0000	0.5071	0.1419	**(+) 0.0033**
Control vs. March 95	1.0000	**(+) 0.0002**	**(+) 0.0002**	**(+) 0.0002**

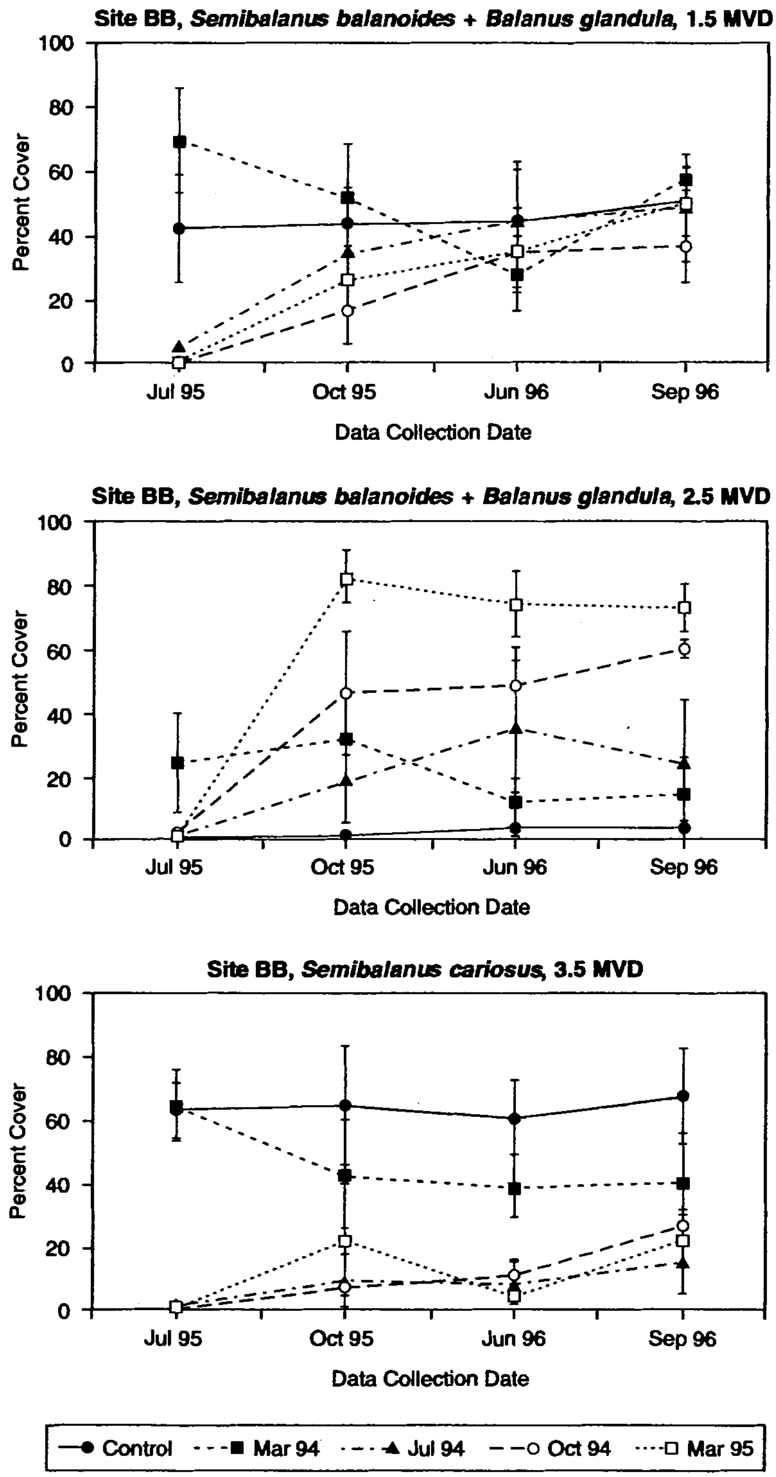


Figure 17. Mean total percent cover of *Semibalanus balanoides* + *Balanus glandula* at MVDs 1.5 and 2.5 and *S. cariosus* at MVD 3.5 in scraped and control quadrats at site BB. Different symbols represent control quadrats or quadrats scraped on different dates, as shown in the legend. The x-axis represents the dates when percent cover data were collected. MVD = meter vertical drop. Error bars represent one standard error of the mean.

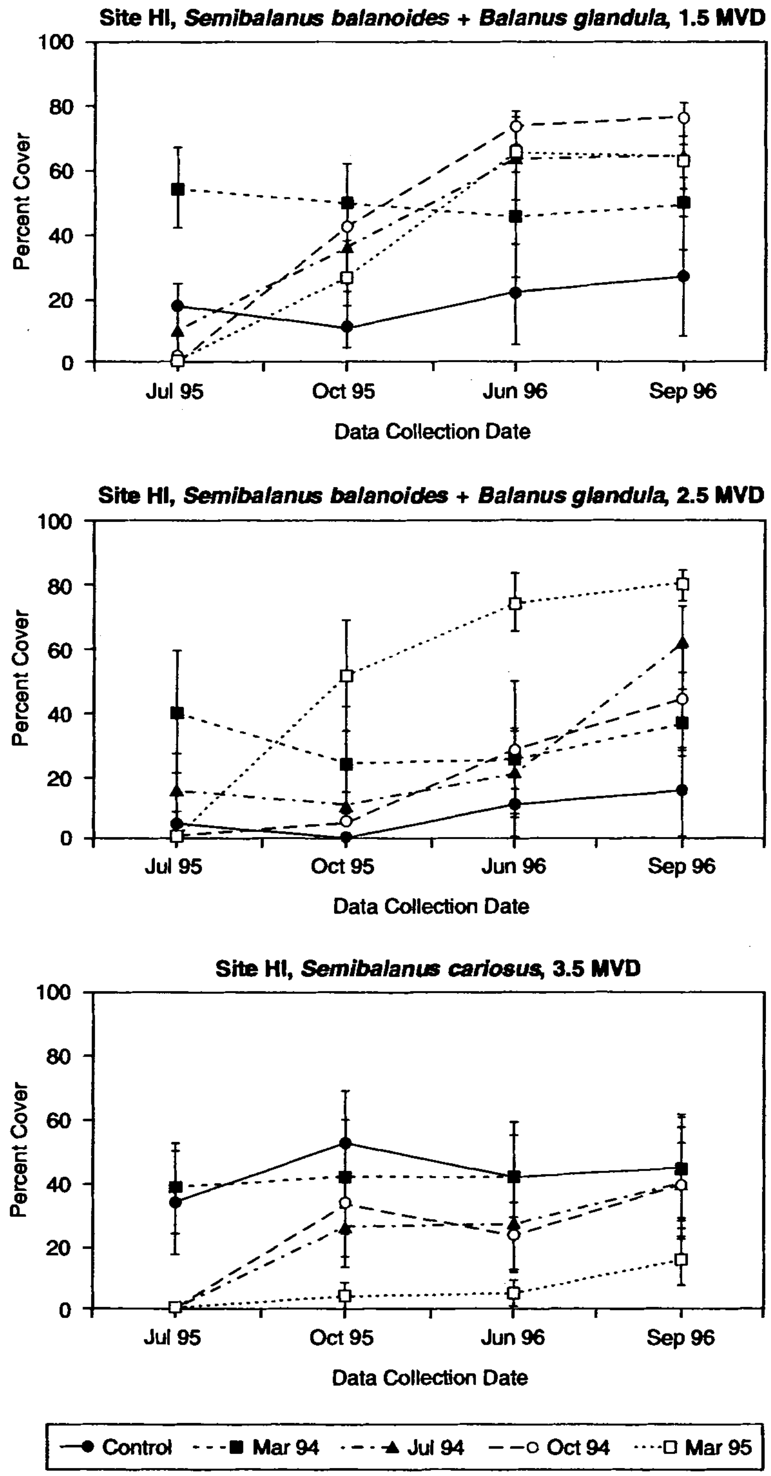


Figure 18. Mean total percent cover of *Semibalanus balanoides* + *Balanus glandula* at MVDs 1.5 and 2.5 and *S. cariosus* at MVD 3.5 in scraped and control quadrats at site HI. Different symbols represent control quadrats or quadrats scraped on different dates, as shown in the legend. The x-axis represents the dates when percent cover data were collected. MVD = meter vertical drop. Error bars represent one standard error of the mean.

Comparisons of *Semibalanus cariosus* at MVD 3.5 rejected the null hypotheses of no differences in mean percent cover; the ST × T and SC × T interaction effects were significant (Table 7). The comparisons of percent cover between stations, limited to comparisons for matching sampling periods, revealed no significant differences. The significant comparisons within the set of cross-period comparisons are not presented. The comparisons of the SC × T interaction reveal that percent cover of *S. cariosus* for the July 1994, October 1994 and March 1995 quadrats for each sampling period were generally significantly less than that of the controls. None of the comparisons for the March 1994 quadrats are different from the controls. Mean percent cover for *S. cariosus* (Figures 17 and 18) in treated quadrats was generally less than in controls although percent cover in March 1994 quadrats was similar to control quadrats, particularly at site HI (Figure 18).

Table 7. Summary of repeated measures ANOVA comparisons for adult *Semibalanus cariosus* percent cover data at MVD 3.5. The Mauchly's test was not significant ($p = 0.0933$). A negative sign before the p-value of a Tukey multiple comparison indicates that the mean decreased from one category to the next while a positive sign indicates that the mean increased. A logarithmic transformation [$\log(X + 1)$] was used to correct for inequality of variances. P-values < 0.05 are in bold print.

Effect	df Effect	MS Effect	F	P-value
Site (ST)	1	27.78	0.016	0.9006
Scraping (SC)	4	12172.50	6.948	**0.0004**
ST × SC	4	1786.55	1.020	0.4123
Error 1	30	1751.83		
Time (T)	3	1693.03	9.748	**0.0000**
ST × T	3	496.53	2.859	**0.0414**
SC × T	12	421.89	2.429	**0.0089**
ST × SC × T	12	162.81	0.937	0.5140
Error 2	90	173.69		

Summary of Tukey Multiple Comparisons

	July 95	October 95	June 96	September 96
Site × Time				
BB vs. HI		0.9988	0.9944	0.9992
Scrape Date × Time				
Control vs. March 94	1.0000	0.6043	0.9834	0.8698
Control vs. July 94	**(+) 0.0002**	**(–) 0.0002**	**(–) 0.0005**	**(–) 0.0050**
Control vs. October 94	**(–) 0.0002**	**(–) 0.0002**	**(–) 0.0004**	0.0705
Control vs. March 95	**(–) 0.0002**	**(–) 0.0002**	**(–) 0.0002**	**(–) 0.0002**

The analysis of variance for percent cover of *Fucus gardneri* at MVD 1.5 provides evidence against the null hypotheses of no differences in mean cover due to scrape date, site, or sample date. All main effects are significant (Table 8). Comparisons between sites indicate that the percent cover of *F. gardneri* at site BB was significantly greater than at site HI. Tukey multiple comparisons between the control quadrats and the percent cover of *F. gardneri* for the various scrape dates indicate significant differences in percent cover between the controls and the October 1994 and March 1995 quadrats. Comparisons between sampling periods reveal that the percent cover of *F. gardneri* increased with time. The results of these multiple comparisons are supported by the plots of mean percent cover for *F. gardneri* at sites BB and HI (Figures 19 and 20, respectively). For all scrape dates, the percent cover of *F. gardneri* at site BB was much greater than the cover of *F. gardneri* at site HI. For MVD 1.5 at both sites, the mean percent covers of the October 1994 and March 1995 treatments were the lowest of all quadrats during all four sampling periods. Generally, the percent cover of scraped quadrats increased for each sampling period.

Table 8. Summary of repeated measures ANOVA comparisons for *Fucus gardneri* percent cover data at MVD 1.5. The Mauchly's test was significant ($p < 0.0001$) for this comparison so the Greenhouse–Geiser adjustment (G–G Adj.) was used. A negative sign before the p-value of a Tukey multiple comparison indicates that the mean decreased from one category to the next while a positive sign indicates that the mean increased. P-values < 0.05 are in bold print.

Effect	df Effect	MS Effect	F	P-value	G–G Adj. P-value
Site (ST)	1	50.43	8.250	**0.0074**	
Scraping (SC)	4	39.67	6.490	**0.0007**	
ST × SC	4	5.58	0.912	0.4694	
Error 1	30	6.11			
Time (T)	3	7.34	12.083	**0.0000**	**0.0000**
ST × T	3	0.41	0.679	0.5670	0.5032
SC × T	12	0.85	1.399	0.1809	0.2197
ST × SC × T	12	0.21	0.350	0.9769	0.9362
Error 2	90	0.61			

Summary of Tukey Multiple Comparisons

Site	P-value
BB vs. HI	**(–) 0.0076**

Scrape Date	March 94	July 94	October 94	March 95
Control vs.	0.9523	0.4388	**(–) 0.0202**	**(–) 0.0309**

Sampling Date	July 95	October 95	June 96
October 1995	**(+) 0.0104**	—	—
June 1996	**(+) 0.0024**	0.9644	—
September 1996	**(+) 0.0001**	**(+) 0.0335**	0.1059

The ST main effect and SC × T interaction effect for percent cover of *F. gardneri* at MVD 2.5 are both significant, rejecting the null hypotheses of no differences in mean cover among sites and scraped dates over time (Table 9). Multiple comparisons reveal that site BB had significantly greater percent cover than site HI. The comparisons of control to scraped quadrats by sampling period reveal that in July 1995, *F. gardneri* cover in quadrats scraped in July 1994, October 1994, and March 1995 was significantly less than in the control quadrats. In October 1995, only those quadrats scraped in October 1994 remained different from the controls. The plots of mean percent cover (Figures 19 and 20) support the results of the comparisons and show that site BB had greater percent cover for all treatments. A trend of increasing cover for *F. gardneri* over the sampling periods for all scraped quadrats except for those scraped in March 1994 at site BB, is also shown in Figures 19 and 20.

Table 9. Summary of repeated measures ANOVA comparisons for *Fucus gardneri* percent cover data at MVD 2.5. The Mauchly's test was significant (p = 0.0010) for this comparison so the Greenhouse–Geiser adjustment (G–G Adj.) was used. A negative sign before the p-value of a Tukey multiple comparison indicates that the mean decreased from one category to the next while a positive sign indicates that the mean increased. P-values < 0.05 are in bold print.

Effect	df Effect	MS Effect	F	P-value	G–G Adj. P-value
Site (ST)	1	82.33	25.453	**0.0000**	
Scraping (SC)	4	13.75	4.250	**0.0076**	
ST × SC	4	1.81	0.559	0.6940	
Error 1	30	3.24			
Time (T)	3	18.71	24.712	**0.0000**	**0.0000**
ST × T	3	1.30	1.717	0.1691	0.1877
SC × T	12	3.12	4.119	**0.0000**	**0.0006**
ST × SC × T	12	1.38	1.820	0.0564	0.0893
Error 2	90	0.76			

Summary of Tukey Multiple Comparisons

Site	P-value
BB vs. HI	**(–) 0.0002**

Scrape Date	July 95	October 95	June 96	September 96
Control vs. March 94	1.0000	0.9724	1.0000	1.0000
Control vs. July 94	**(–) 0.0142**	0.8434	0.3782	1.0000
Control vs. October 94	**(–) 0.0012**	**(–) 0.0059**	0.5481	1.0000
Control vs. March 95	**(–) 0.0004**	0.2650	1.0000	0.8435

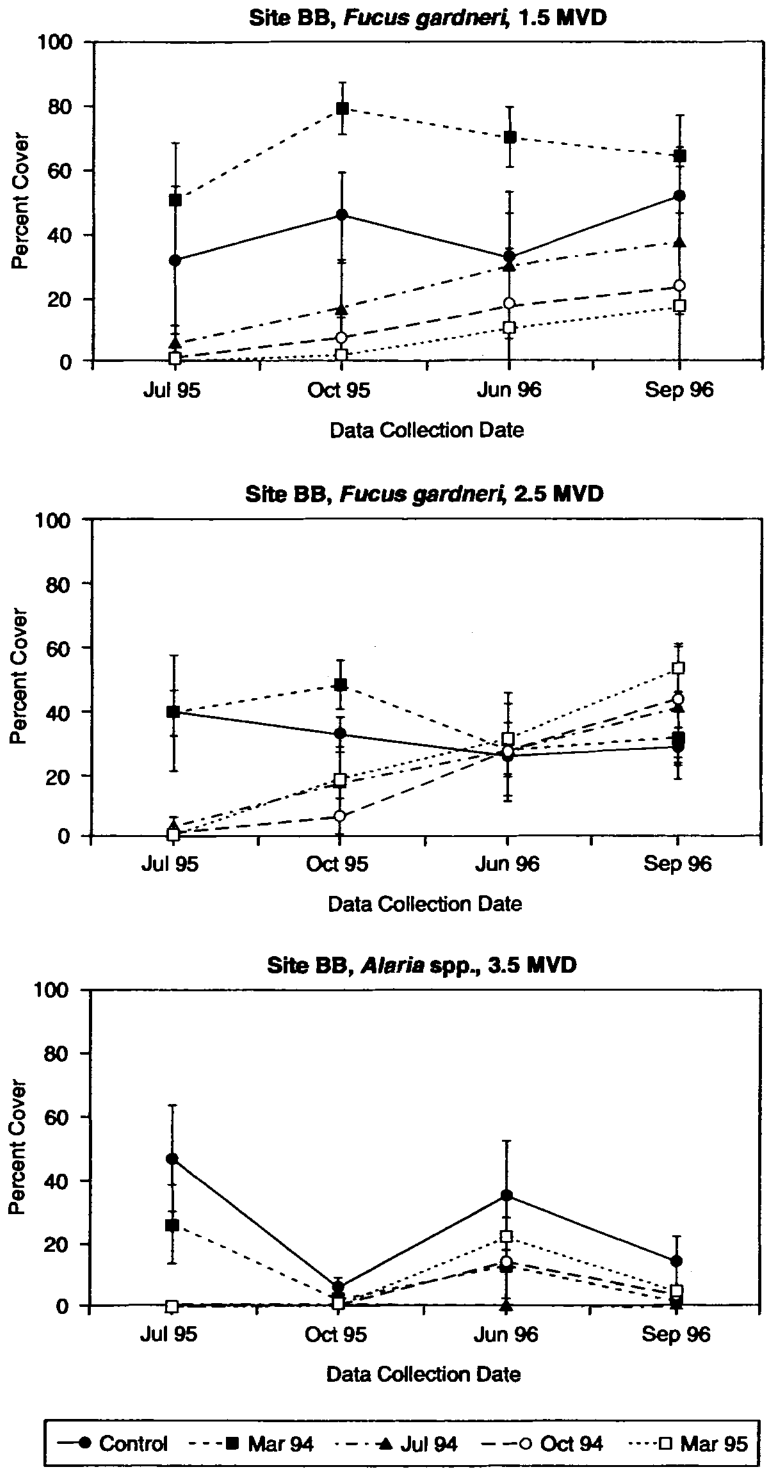


Figure 19. Mean total percent cover of *Fucus gardneri* at MVDs 1.5 and 2.5 and *Alaria* spp. at MVD 3.5 in scraped and control quadrats at site BB. Different symbols represent control quadrats or quadrats scraped on different dates, as shown in the legend. The x-axis represents the dates when percent cover data were collected. MVD = meter vertical drop. Error bars represent one standard error of the mean.

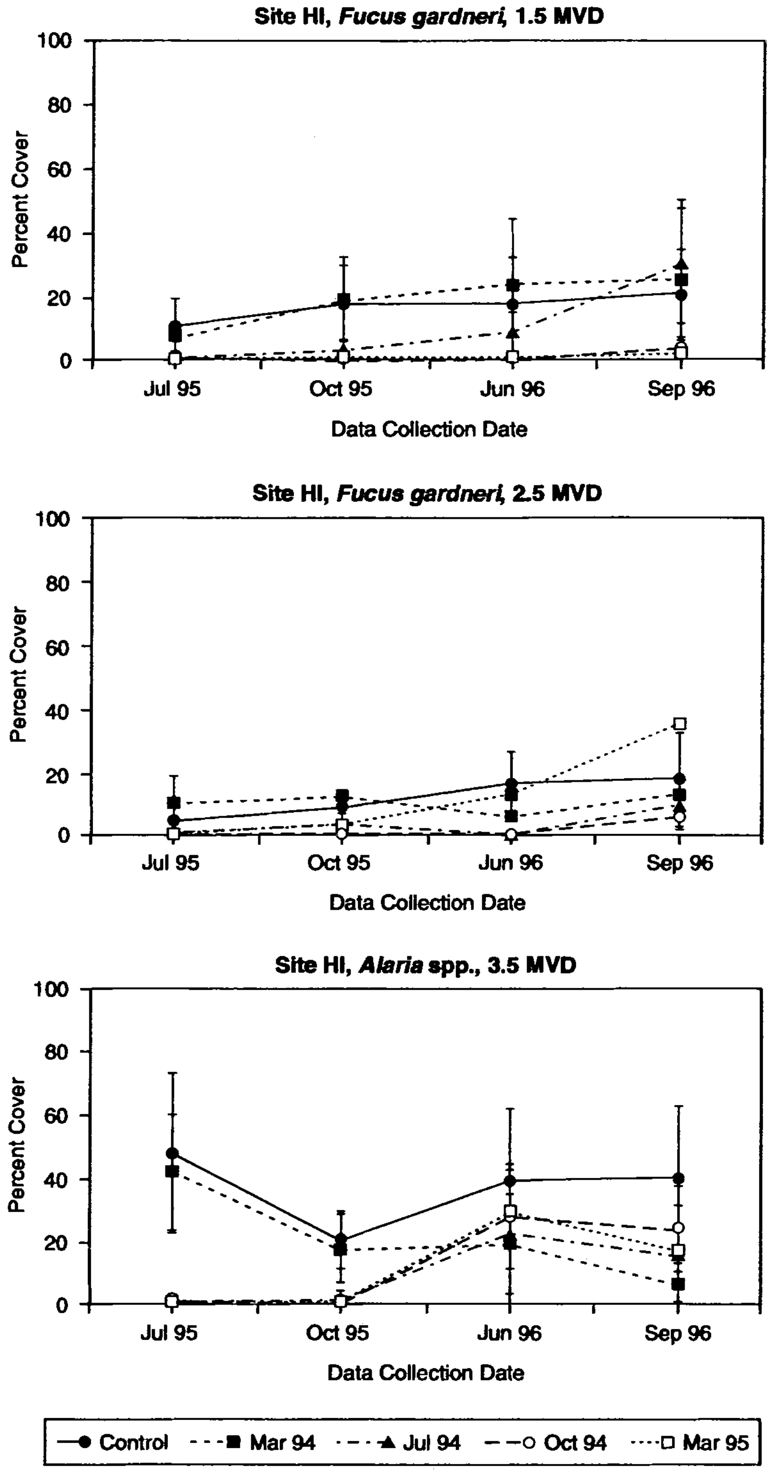


Figure 20. Mean total percent cover of *Fucus gardneri* at MVDs 1.5 and 2.5 and *Alaria* spp. at MVD 3.5 in scraped and control quadrats at site HI. Different symbols represent control quadrats or quadrats scraped on different dates, as shown in the legend. The x-axis represents the dates when percent cover data were collected. MVD = meter vertical drop. Error bars represent one standard error of the mean.

The results of the rmANOVA comparisons for *Alaria* spp. percent cover data at MVD 3.5 provide evidence rejecting the null hypothesis of no scrape date effects between sampling periods (Table 10). The SC × T interaction effect is significant and multiple comparisons indicate that the *Alaria* spp. percent cover in scraped quadrats, excluding March 1994, was significantly less than in control quadrats in July 1995.

Table 10. Summary of repeated measures ANOVA comparisons for *Alaria* spp. percent cover data at MVD 3.5. The Mauchly's test was significant ($p < 0.0001$) for this comparison so the Greenhouse–Geiser adjustment (G–G Adj.) was used. A negative sign before the p-value of a Tukey multiple comparision indicates that the mean decreased from one category to the next while a positive sign indicates that the mean increased. P-values < 0.05 are in bold print.

Effect	df Effect	MS Effect	F	P-value	G–G Adj. P-value
Site (ST)	1	3310.38	2.405	0.1314	
Scraping (SC)	4	3334.13	2.423	0.0700	
ST × SC	4	50.95	0.037	0.9972	
Error 1	30	1376.19			
Time (T)	3	2061.54	6.723	**0.0004**	**0.0034**
ST × T	3	274.50	0.895	0.4469	0.4046
SC × T	12	786.90	2.566	**0.0057**	**0.0225**
ST × SC × T	12	134.44	0.438	0.9436	0.8771
Error 2	90	306.62			

Summary of Tukey Multiple Comparisons

Scrape Date	July 95	October 95	June 96	September 96
Control vs. March 94	0.9932	1.0000	0.6461	0.5297
Control vs. July 94	(–) **0.0003**	0.9983	0.2908	0.8260
Control vs. October 94	(–) **0.0003**	0.9964	0.9406	0.9932
Control vs. March 95	(–) **0.0003**	0.9950	0.9992	0.9599

Plots of mean percent cover in control quadrats at sites BB and HI (Figures 19 and 20, respectively) show the intra-annual variability expected for an annual alga. Note that the percent cover of most scraped quadrats was lower than in control quadrats. The March 1994 scraped quadrats had cover similar to control quadrats in July and October 1995, but decreased below control levels in June and September 1996.

Comparisons of percent cover for *Mytilus trossulus* at MVD 1.5 show significant main effects, thus the null hypothesis of no differences in percent cover due to scrape date or sampling date was rejected. For these comparisons, the SC and T main effects are significant (Table 11). The multiple comparisons of all the control quadrats vs. all scraped quadrats for all sites BB and HI combined reveals that the scraped quadrats had significantly lower cover of *M. trossulus* than control quadrats. Figure 21 indicates that quadrats scraped in March 1994 at site BB had converged with controls by June 1996. Comparisons of percent cover by sampling date indicate that the October 1995, June 1996, and September 1996 sampling dates had greater cover of *M. trossulus* than did the July 1995 sampling date. Figures 21 and 22 show mean *M. trossulus* percent cover for sites BB and HI, respectively. With the exception of quadrats scraped in March 1994 at site BB and sampled in June 1996 and September 1996, scraped quadrat cover was much lower than control quadrat cover at both sites, even by the last sampling date in September 1996. At the exposed site HI, *M. trossulus* was slow to recover in scraped quadrats and will apparently take significantly longer than 2.5 years to recover from removal during any season.

Table 11. Summary of repeated measures ANOVA comparisons for *Mytilus trossulus* percent cover data at MVD 1.5. The Mauchly's test was significant ($p < 0.0376$) for this comparison so the Greenhouse–Geiser adjustment (G–G Adj.) was used. A negative sign before the p-value of a Tukey multiple comparison indicates that the mean decreased from one category to the next while a positive sign indicates that the mean increased. P-values < 0.05 are in bold print.

Effect	df Effect	MS Effect	F	P-value	G–G Adj. P-value
Site (ST)	1	0.81	0.215	0.6465	
Scraping (SC)	4	37.55	9.923	**0.0000**	
ST×SC	4	5.77	1.524	0.2204	
Error 1	30	3.78			
Time (T)	3	1.55	5.425	**0.0019**	**0.0043**
ST×T	3	0.22	0.773	0.5120	0.4839
SC×T	12	0.33	1.175	0.3128	0.3235
ST×SC×T	12	0.29	1.005	0.4510	0.4457
Error 2	90	0.28			

Summary of Tukey Multiple Comparisons

Scrape Date	March 94	July 94	October 94	March 95
Control vs.	**(–) 0.0282**	**(–) 0.0004**	**(–) 0.0003**	**(–) 0.0003**

Sampling Date	July 95	October 95	June 96
October 1995	**(+) 0.0316**	—	—
June 1996	**(+) 0.0276**	1.0000	—
September 1996	**(+) 0.0015**	0.7351	0.7636

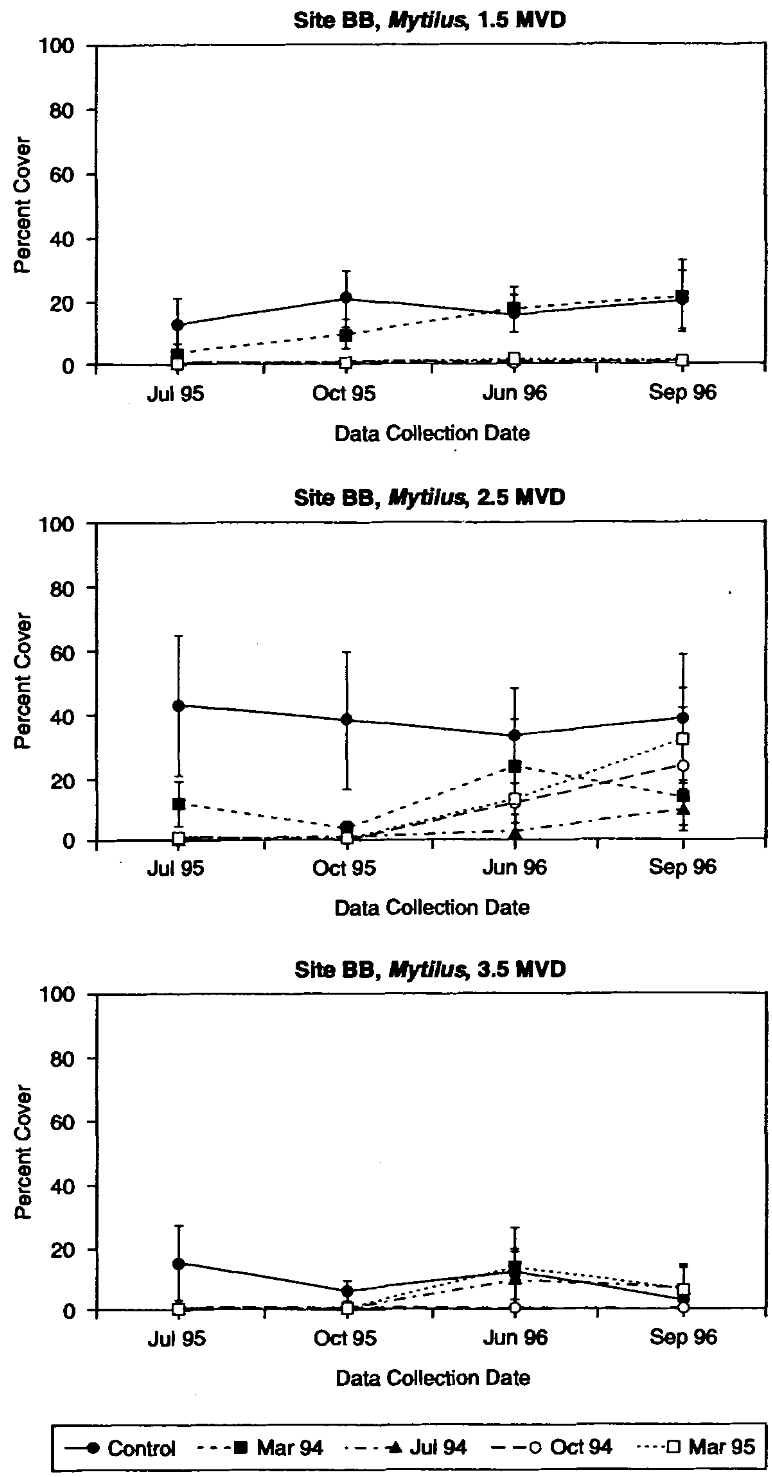


Figure 21. Mean total percent cover of *Mytilus trossulus* in scraped and control quadrats at site BB. Different symbols represent control quadrats or quadrats scraped on different dates, as shown in the legend. The x-axis represents the dates when percent cover data were collected. MVD = meter vertical drop. Error bars represent one standard error of the mean.

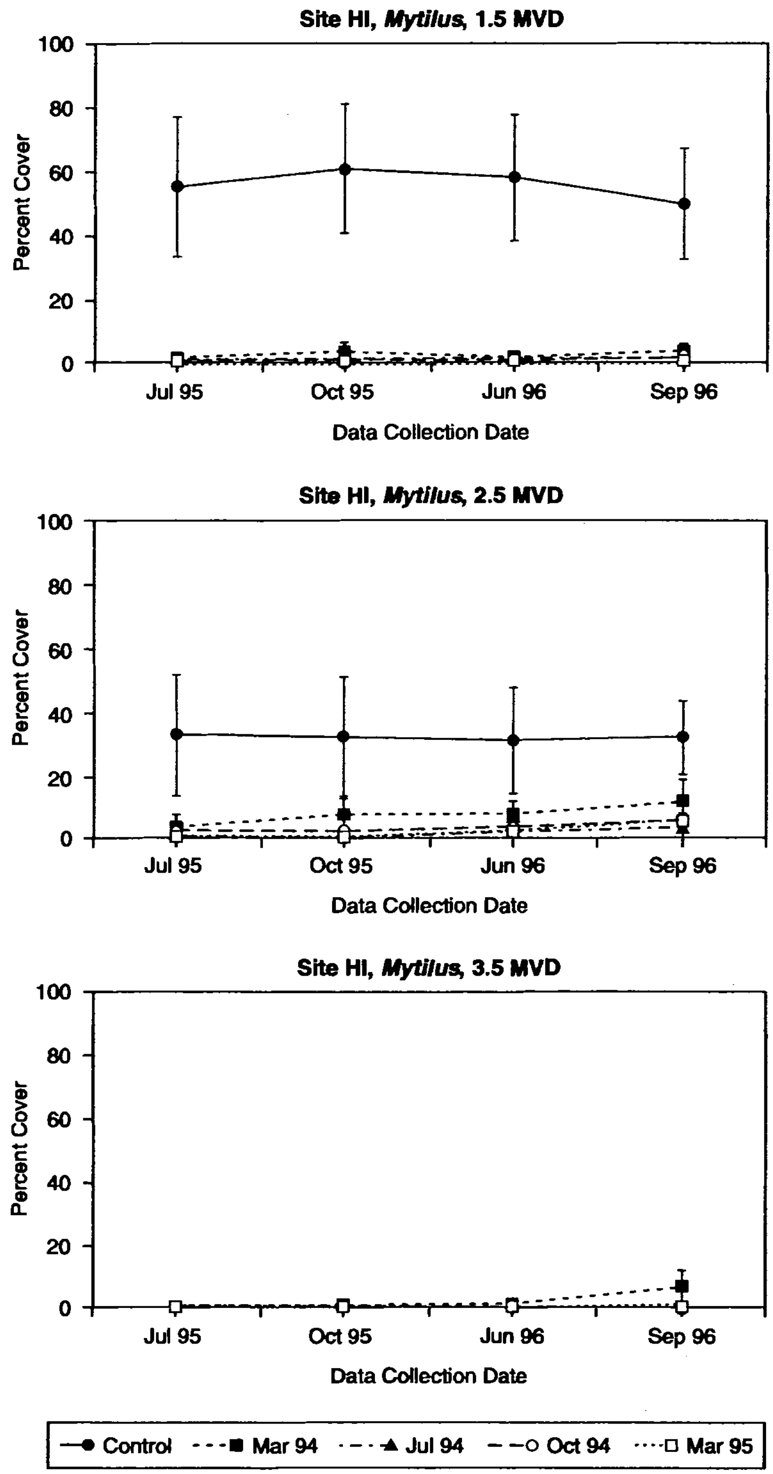


Figure 22. Mean total percent cover of *Mytilus trossulus* in scraped and control quadrats at site HI. Different symbols represent control quadrats or quadrats scraped on different dates, as shown in the legend. The x-axis represents the dates when percent cover data were collected. MVD = meter vertical drop. Error bars represent one standard error of the mean.

The rmANOVA comparisons of *M. trossulus* percent cover at MVD 2.5 result in significant main effects, thus rejecting the null hypothesis of no differences in percent cover due to scrape date or sampling date (Table 12). The SC and T main effects results are significant. Multiple comparisons of the scrape dates show that control quadrats had significantly greater percent cover of *M. trossulus* than the July 1994, October 1994, and March 1995 scraped quadrats. The comparisons of sampling dates indicate significantly greater cover in June and September 1996 compared to July 1995 and significantly greater cover in September 1996 than in October 1995 or June 1996 (Table 12). Figures 21 and 22 indicate little inter- or intra-annual variability in *M. trossulus* cover, as is expected for a sessile, relatively long-lived intertidal invertebrate. For sites BB and HI combined, scraped quadrats had not converged with control quadrats by the last sampling date in September 1996.

Table 12. Summary of repeated measures ANOVA comparisons for *Mytilus trossulus* percent cover data at MVD 2.5. The Mauchly's test was significant ($p < 0.0001$) for this comparison so the Greenhouse–Geiser adjustment (G–G Adj.) was used. A negative sign before the p-value of a Tukey multiple comparison indicates that the mean decreased from one category to the next while a positive sign indicates that the mean increased. P-values < 0.05 are in bold print.

Effect	df Effect	MS Effect	F	P-value	G–G Adj. P-value
Site (ST)	1	1.67	0.287	0.5960	
Scraping (SC)	4	23.93	4.122	**0.0089**	
ST×SC	4	0.87	0.150	0.9614	
Error 1	30	5.80			
Time (T)	3	11.89	21.060	**0.0000**	**0.0000**
ST×T	3	0.97	1.747	0.1632	0.1862
SC×T	12	0.96	1.698	0.0802	0.1255
ST×SC×T	12	0.35	0.627	0.8141	0.7384
Error 2	90	0.56			

Summary of Tukey Multiple Comparisons

Scrape Date	March 94	July 94	October 94	March 95
Control vs.	0.3498	**(–) 0.0090**	**(–) 0.0365**	**(–) 0.0393**

Sampling Date	July 95	October 95	June 96
October 1995	1.0000	—	—
June 1996	**(+) 0.0010**	**(+) 0.0011**	—
September 1996	**(+) 0.0014**	**(+) 0.0001**	**(+) 0.0406**

Multivariate analyses (community level analyses)

The multi-dimensional scaling ordinations were conducted for the scraped and control quadrats at each site. The resulting ordination plots, coded to separate out all scrape date × site combinations, are too complex to interpret (as illustrated in Figure 23). Thus, the ordination plots presented in Figures 24 and 25 are coded to separate out scrape date only. The ordination plots illustrate trends by showing how similar each quadrat is to all other quadrats. The proximity of a quadrat to all other quadrats is a measure of the similarity of their multi-species data sets, or their intertidal communities. The three plots in Figures 24 and 25 represent ordinations for data from the three MVDs. The codes in the plots represent the quadrat scrape date: C = control quadrats, 1 = quadrats scraped in March 1994, 2 = quadrats scraped in July 1994, 3 = quadrats scraped in October 1994, and 4 = quadrats scraped in March 1995. The data should be interpreted based on how each data point ordinates relative to all other data points within a plot. Thus, by superimposing scrape date codes onto the ordinations (Figures 23–25), we can interpret the role of season of disturbance (scrape date) along a gradient, or direction, in the plot. There are no scales on the axes, and distances in separate MDS plots cannot be compared. However, shifts in relative distances of a series or point relative to other series or points in one plot can be compared to relative distances in another. Also, note that the orientation in space for an ordination is irrelevant. A plot could be reversed or placed upside down and the interpretations would be identical; the relative inter-point distances between every point and all other points is what is important.

Quadrats scraped in March 1994 ordinated closest to control quadrats at all MVDs, but had not yet converged with controls in July 1995 (Figure 24: stress = 0.098 for MVD 1.5, 0.136 for MVD 2.5, and 0.120 for MVD 3.5). The stress coefficients indicate acceptable (<0.15) to good (<0.1) fits between the inter-point distances in the ordination plots based on the Bray–Curtis dissimilarity data. The two March 1994 scraped quadrats that ordinated furthest from their controls were from sites JB and C2. As the data represented in Figure 24 were collected in July 1995, when most scraped quadrats were less than a year old, there had been limited time for recovery. The data points tend to ordinate within "scrape date" groups rather than within "site" groups. In other words, the communities in quadrats scraped at the same time but at different sites were more similar to each other than were quadrats within a site scraped on different dates. Quadrats scraped in October 1994 and March 1995 ordinated together. The sampling date (July 1995) for these data was shortly after the spring settlement of barnacles and both sets of quadrats had a similar "monoculture" of spat. This indicates that space made available on rocks in the fall remains vacant until spring and is, therefore, similar to a March disturbance relative to recruitment dynamics.

September 1996 was the last sampling date for this study and the ordination plots in Figure 25 (stress = 0.218 for MVD 1.5, 0.199 for MVD 2.5, and 0.179 for MVD 3.5) represent the longest time that the quadrats had to recover since being scraped. The stress values indicate that the ordinations in the plots do not accurately reflect the dissimilarities between each data set as calculated by the Bray–Curtis dissimilarity index. Thus, interpretations must be general and detailed interpretation of individual points can't be made. In general, the control quadrats ordinate separately from the scraped quadrats. However, unlike the MDS plots for data collected in July 1995, the codes did not separate out by scrape date. The ordination distances between the quadrats scraped in March 1994 and those scraped in July 1994, October 1994, and March 1995 were not as distinct as they were in July 1995. The quadrats that tended to ordinate furthest from control quadrats were those scraped in July 1994, suggesting that a summer disturbance follows a different recovery process that delays return to the pre-disturbance community.

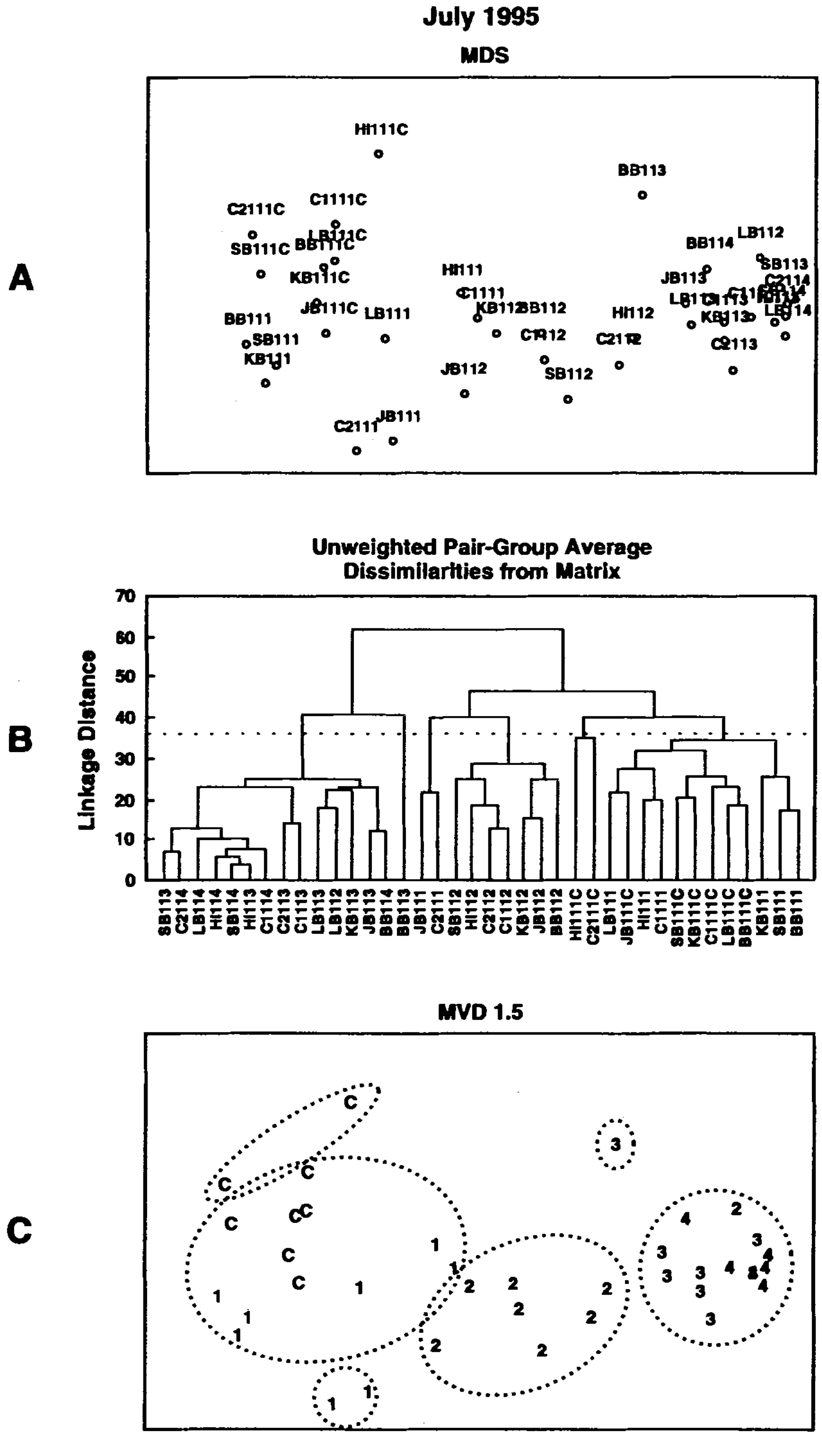


Figure 23. Example of coding style for multi-dimensional scaling. The coding is for multi-species data combined across all sites and scrape dates (+ controls) within a meter vertical drop. The labels in graphs A and B contain codes for site (first two letters or letter and number for C1 and C2), meter vertical drop (first number), data collection date (second number), and quadrat type (last number representing control or scrape date). Graph A illustrates the MDS ordination with original codes, graph B represents results from a cluster analysis, and graph C shows MDS ordination results coded for quadrat type, including controls. The dotted lines delineate clusters at the 36% similarity level, as shown in B.

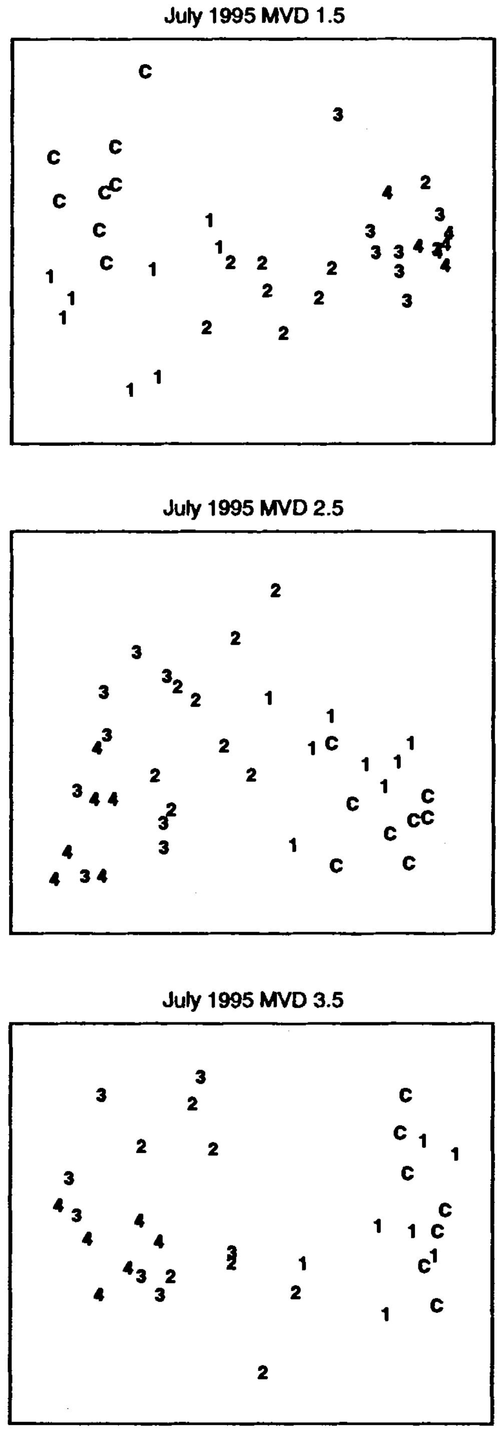


Figure 24. Multi-dimensional scaling ordination of July 1995 multi-species data from control and scraped quadrats at eight sites. Series codes are: C = control quadrats, 1 = quadrats scraped in March 1994, 2 = quadrats scraped in July 1994, 3 = quadrats scraped in October 1994, 4 = quadrats scraped in March 1995. The eight data points within each series represent the eight sites. MVD = meter vertical drop.

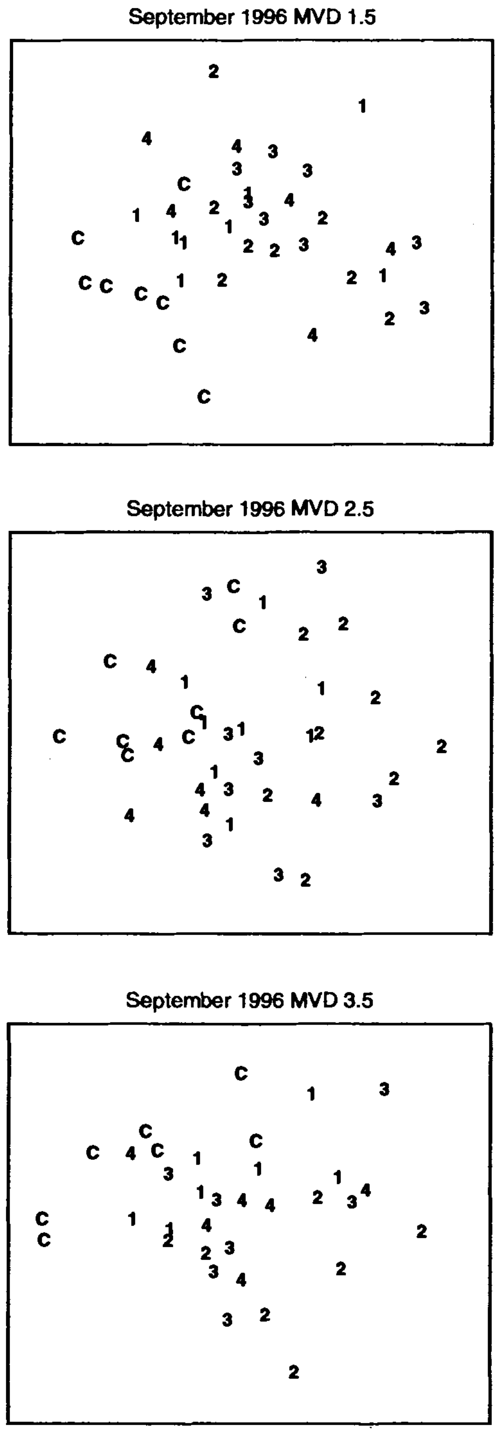


Figure 25. Multi-dimensional scaling ordination of September 1996 multi-species data from control and scraped quadrats at eight sites. Series codes are: C = control quadrats, 1 = quadrats scraped in March 1994, 2 = quadrats scraped in July 1994, 3 = quadrats scraped in October 1994, 4 = quadrats scraped in March 1995. The eight data points within each series represent the eight sites. MVD = meter vertical drop.

The ordinations shown in Figure 24 exhibit the classic horseshoe, or arch, effect. This is a common feature of ordinations from single, strong environmental gradients. In the case of these ordinations, the environmental gradient is "scrape date". Samples toward opposite ends of the environmental gradient have few species in common, thus having high dissimilarities. When the plot arches near the tail, this indicates that dissimilarities near 100% have been reached [Clarke and Warwick 1994]. By September 1996 (Figure 25), after the quadrats had a longer time to recover from being scraped, the separation along the "scrape date" environmental gradient is not as strong and the horseshoe effect is absent. This is further indication that all scraped quadrats were more similar to control quadrats in September 1996 than they were in July 1995.

Figures 26–31 extract individual sites from the MDS plots presented in Figures 24 and 25. The eight individual plots within each figure were not created from separate dissimilarity matrices, but were extracted from the MDS ordination for all sites combined. The extraction by site is for aiding interpretations of how quadrats within a site ordinate relative to each other. Figure 26 extracts the site data from the MDS ordination at MVD 1.5 shown in Figure 24. The arrows indicate the direction from most recently scraped quadrats (March 1995) towards older quadrats and finally towards control quadrats. Exceptions are for sites KB and JB where the most recently scraped quadrats were in October 1994.

The general direction of the arrows in Figures 26–28 for all sites is along a gradient in the same direction within each figure, indicating that in July 1995 the ordination within each original MDS is driven by scrape date. At MVD 1.5 (Figure 26), the most exposed sites—HI, C1, and C2—had control quadrats most dissimilar from the next closest (ordinated) scraped quadrat. In other words, the quadrats scraped in March 1994 (those quadrats with the longest time to recover after being scraped) ordinated further from their control quadrats at these sites than they did at the other five sites. This indicates that the exposed sites initially recovered more slowly than the less exposed sites. Data collected in September 1996 (Figures 29–31) ordinate in patterns different than those observed for the July 1995 data. The arrows do not point in the same direction along a gradient in each plot. Thus, as also shown in Figure 25, there is not a strong environmental gradient related to scrape date as seen for July 1995 sampling data. However, a different pattern emerges that was not as apparent when the data for all sites were shown in one ordination (Figure 25). The quadrats scraped in March 1995 tended to be more similar to the control quadrats than quadrats scraped in July and October 1994, even though the latter had five and eight months longer to recover, respectively. This pattern is particularly evident at MVDs 2.5 and 3.5 (Figures 30 and 31). For most site-extracted plots that show this pattern, the scrape date that ordinates furthest from controls is July 1994, indicating that by September 1996 their invertebrate and algal communities were most dissimilar to undisturbed control quadrats.

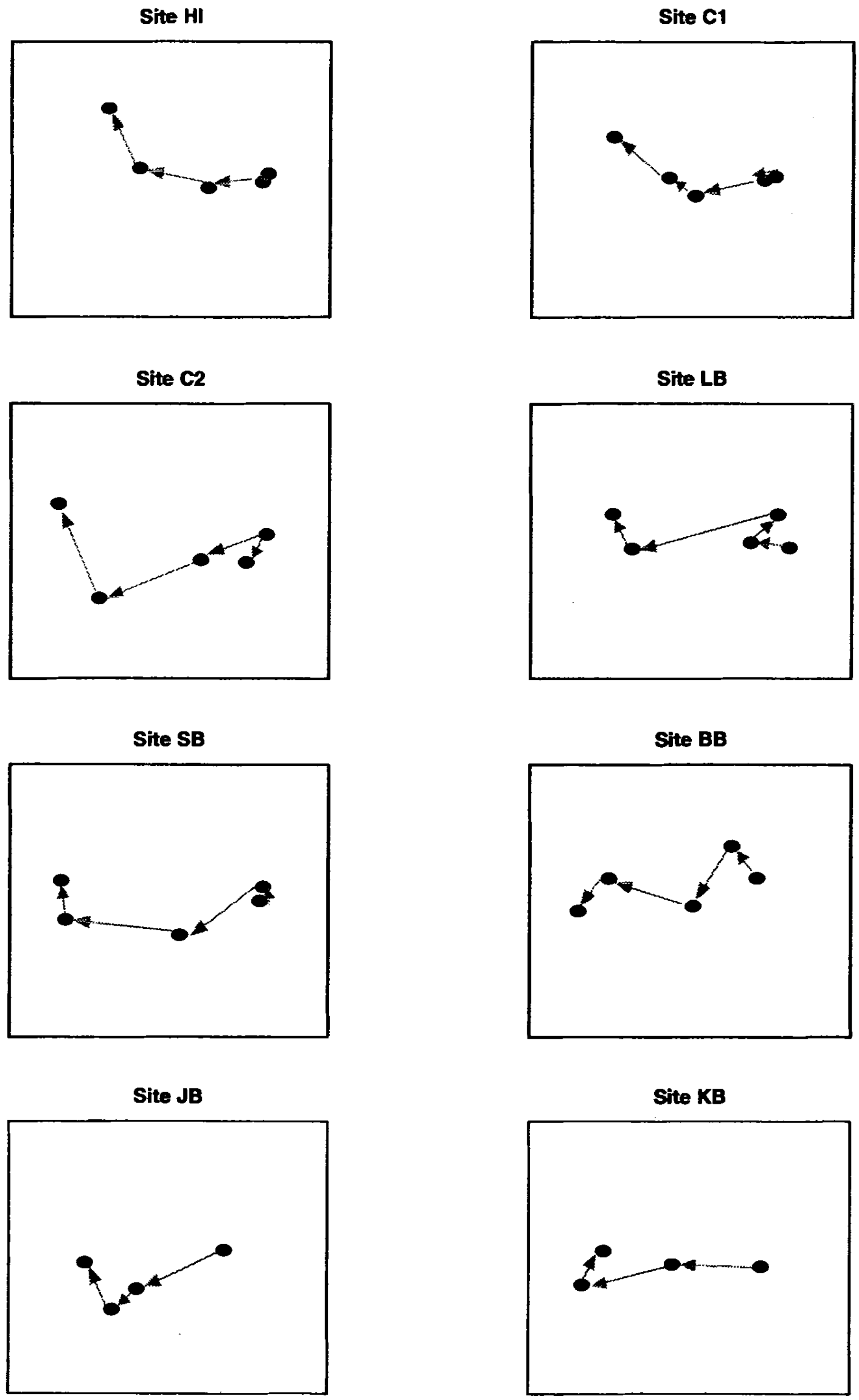


Figure 26. MDS ordination of July 1995 multi-species data at MVD 1.5, redrawn from Figure 24. Individual sites are extracted and plotted without all other ordination points. The arrows point in the direction from quadrats scraped in March 1995 → quadrats scraped in October 1994 → quadrats scraped in July 1994 → quadrats scraped in March 1994 → control quadrats. Quadrats were not scraped in March 1995 at sites JB or KB. The relative axes scales are the same for all plots.

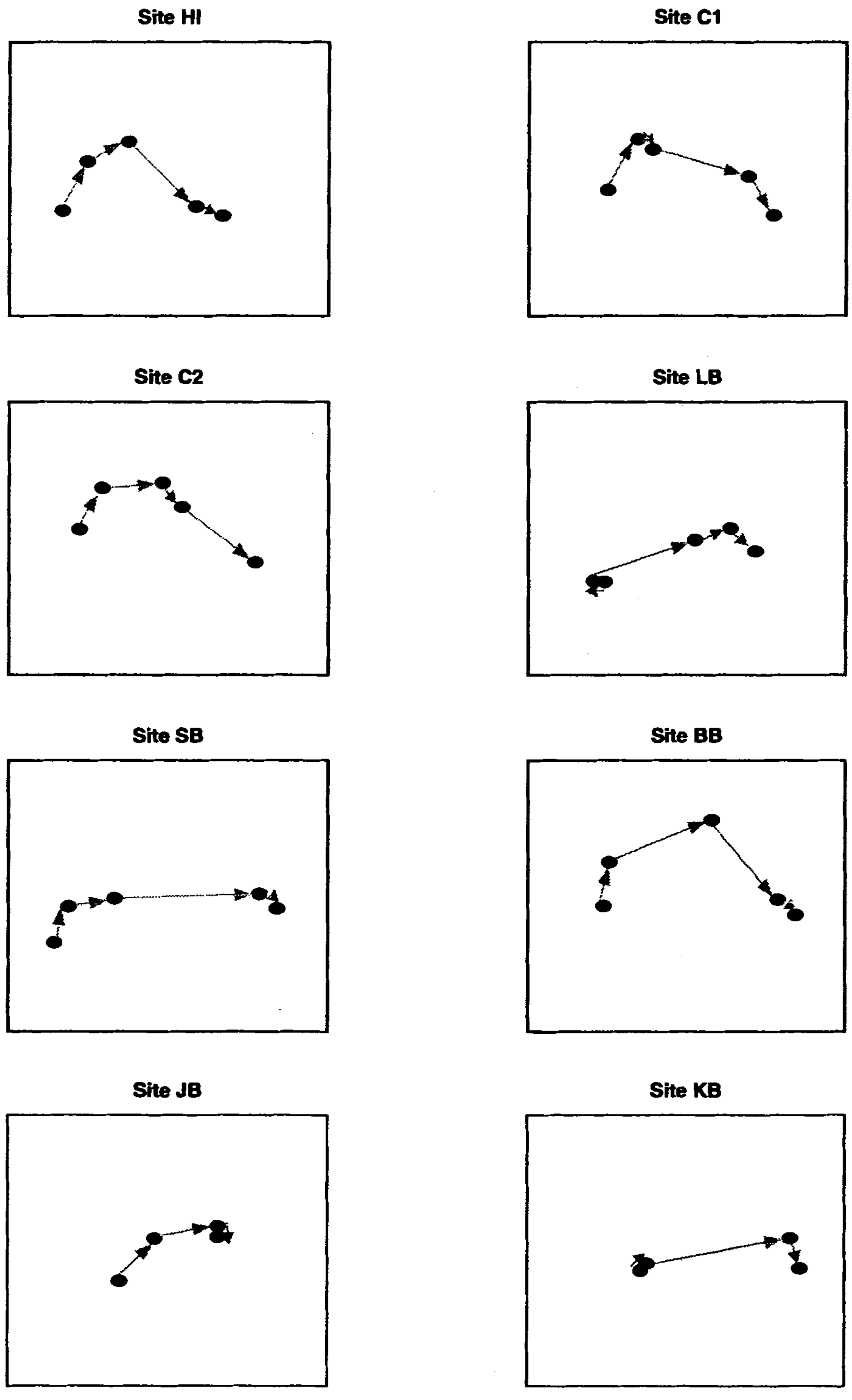


Figure 27. MDS ordination of July 1995 multi-species data at MVD 2.5, redrawn from Figure 24. Individual sites are extracted and plotted without all other ordination points. The arrows point in the direction from quadrats scraped in March 1995 → quadrats scraped in October 1994 → quadrats scraped in July 1994 → quadrats scraped in March 1994 → control quadrats. Quadrats were not scraped in March 1995 at sites JB or KB. The relative axes scales are the same for all plots.

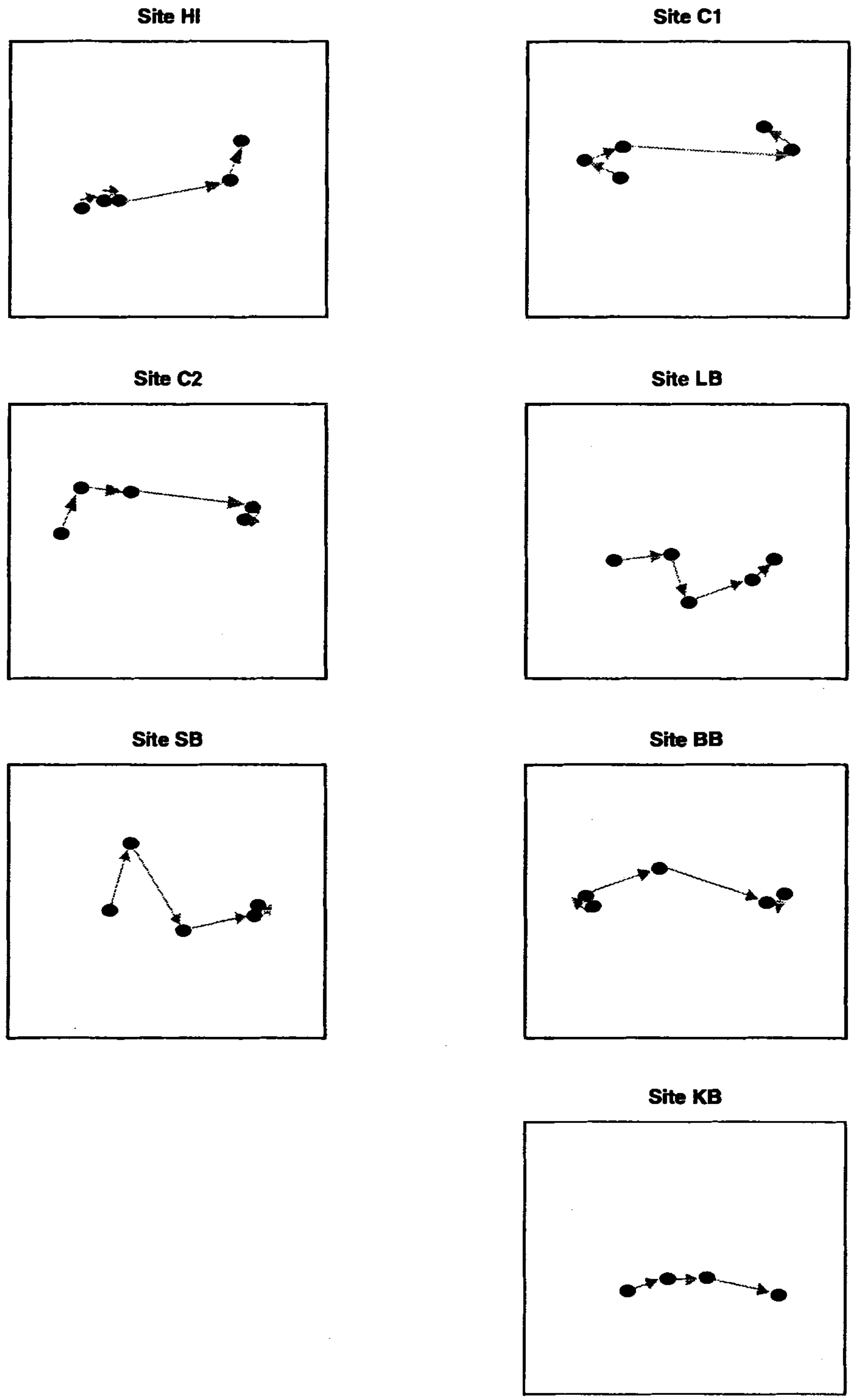


Figure 28. MDS ordination of July 1995 multi-species data at MVD 3.5, redrawn from Figure 24. Individual sites are extracted and plotted without all other ordination points. The arrows point in the direction from quadrats scraped in March 1995 → quadrats scraped in October 1994 → quadrats scraped in July 1994 → quadrats scraped in March 1994 → control quadrats. Site JB had no quadrats at MVD 3.5. Quadrats were not scraped in March 1995 at sites JB or KB. The relative axes scales are the same for all plots.

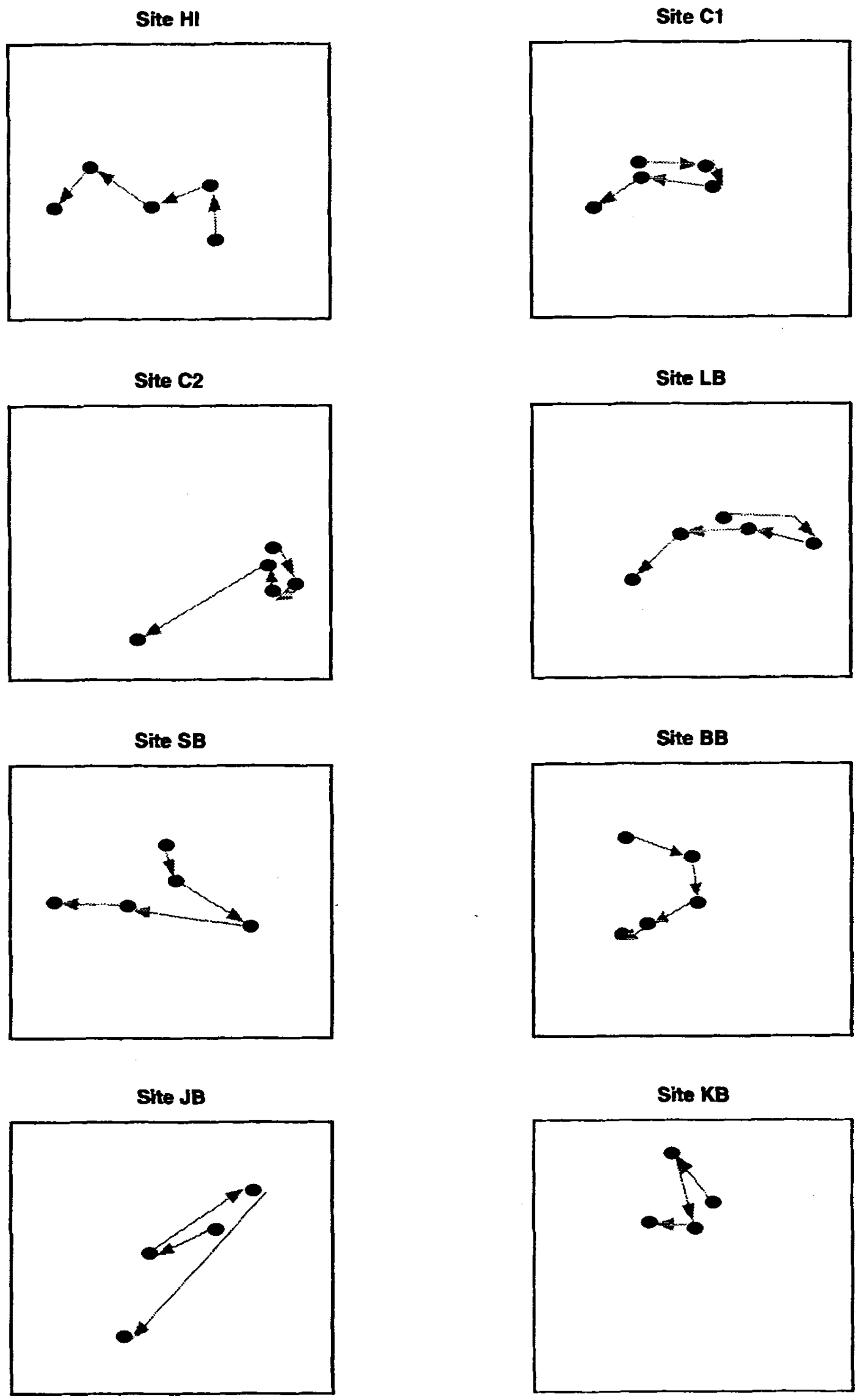


Figure 29. MDS ordination of September 1996 multi-species data at MVD 1.5, redrawn from Figure 25. Individual sites are extracted and plotted without all other ordination points. The arrows point in the direction from quadrats scraped in March 1995 → quadrats scraped in October 1994 → quadrats scraped in July 1994 → quadrats scraped in March 1994 → control quadrats. Quadrats were not scraped in March 1995 at sites JB or KB. The relative axes scales are the same for all plots.

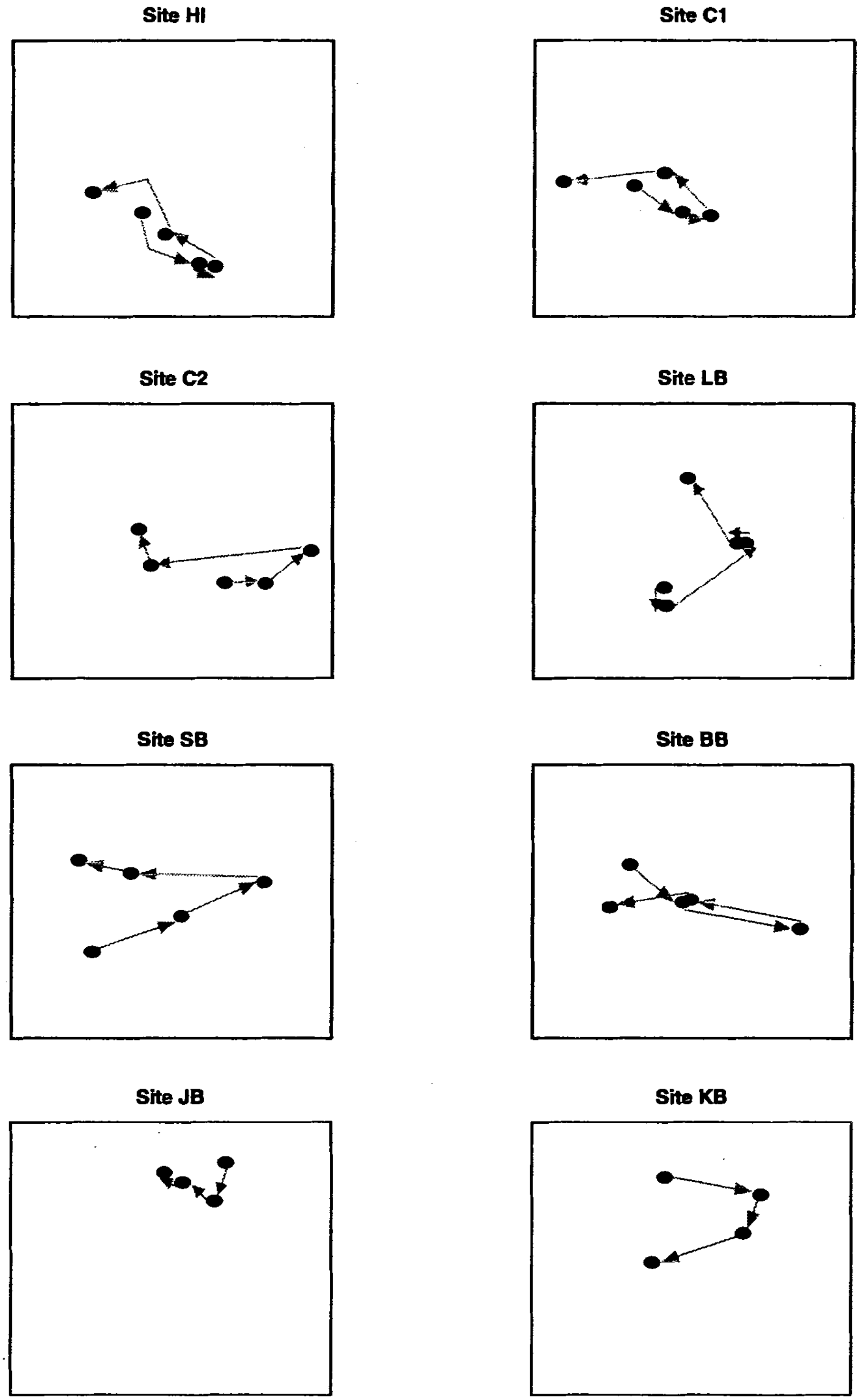


Figure 30. MDS ordination of September 1996 multi-species data at MVD 2.5, redrawn from Figure 25. Individual sites are extracted and plotted without all other ordination points. The arrows point in the direction from quadrats scraped in March 1995 → quadrats scraped in October 1994 → quadrats scraped in July 1994 → quadrats scraped in March 1994 → control quadrats. Quadrats were not scraped in March 1995 at sites JB or KB. The relative axes scales are the same for all plots.

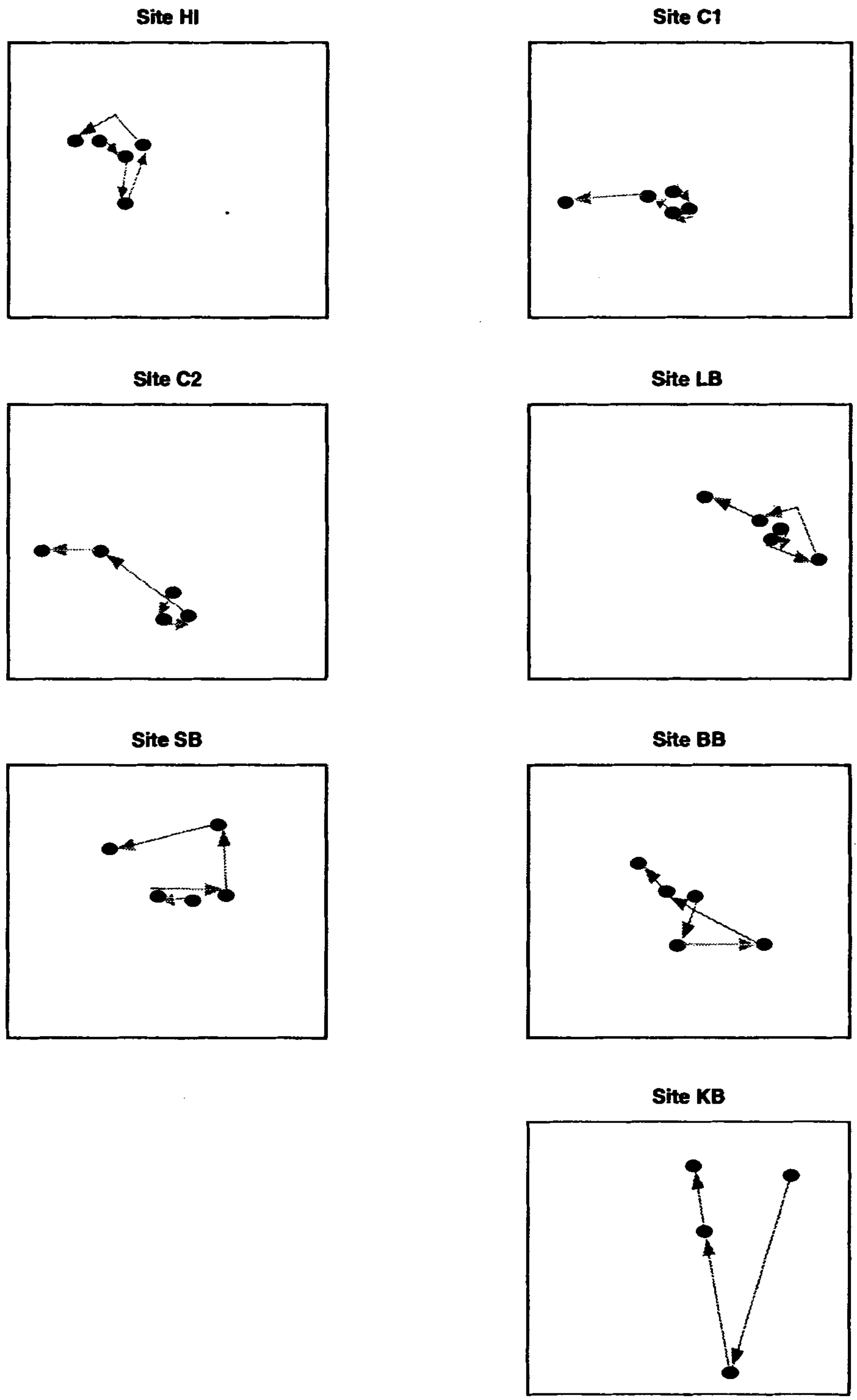


Figure 31. MDS ordination of September 1996 multi-species data at MVD 3.5, redrawn from Figure 25. Individual sites are extracted and plotted without all other ordination points. The arrows point in the direction from quadrats scraped in March 1995 → quadrats scraped in October 1994 → quadrats scraped in July 1994 → quadrats scraped in March 1994 → control quadrats. Site JB had no quadrats at MVD 3.5. Quadrats were not scraped in March 1995 at sites JB or KB. The relative axes scales are the same for all plots.

Discussion

The two major goals of this study were to establish a multi-year sampling program in rocky-intertidal assemblages of outer Kachemak Bay and to assess the intertidal invertebrate and algal recruitment and successional patterns leading to recovery after seasonal disturbances across a range of wave-exposed sites. Eight locations were selected and established as permanent rocky habitat monitoring sites. Calcium sulfate dissolution measurements made at each one showed substantial differences in water motion and the sites were subjectively ranked as exposed versus sheltered. The site on Hesketh Island (HI) and two on one of the Herring Islands (C1 and C2) are exposed to most local storm waves in addition to residual ocean swells that occur as a result of storms many miles away. These sites also had the highest dissolution rates. The three sites ranked as having moderate wave exposure—LB, SB, and BB—all have similar dissolution rates that were slightly lower than at the more exposed sites. The site in Jakolof Bay (JB) had a higher dissolution rate during spring-tide series than expected by its ranked wave exposure. JB is near the entrance to the bay where a geographic constriction causes tidal currents to increase dramatically relative to surrounding water, resulting in a high dissolution rate. The most sheltered site, KB, had the lowest dissolution rate during the study. Generally, the subjective ranking of sites based on observations, orientation relative to prevailing storm direction, and fetch matched the measured dissolution rates. The method provides an additional inexpensive, quick tool for assessing or understanding differences in water movement at intertidal sites. Highsmith et al. [1994] showed, through multi-variate analyses, that community level species similarities among sites across the entire *Exxon Valdez* spill region were best described by wave exposure, rather than by local geography or any other variable studied.

The eight established sites were successfully surveyed in March 1994; permanently marked during each of the treatment visits in March 1994, July 1994, October 1994, and March 1995; and monitored during four sampling periods between July 1994 and September 1996. Intertidal zonation was reflected at the sites by the shift in dominant barnacles by tidal height, as well as a shift from the perennial alga *Fucus gardneri* dominating algal cover in the upper and mid intertidal zone to *Alaria* spp. dominating in the low intertidal zone. The control quadrat measurements are a time-series of data representing late spring/early summer and fall periods for two years and provide inter- and intra-annual comparisons of rocky-intertidal habitat in outer Kachemak Bay. These data indicate that over the course of the study the dominant intertidal invertebrates exhibited a relatively stable population, or spatial cover. There was relatively little variation between seasons and years for the major barnacle species, *Semibalanus balanoides* and *Balanus glandula*, in the upper and middle intertidal zones and *S. cariosus* in the lower intertidal zone. In a closely related California study in the mid-1980s [Kinnetic Laboratories, Inc. 1992; Minerals Management Service 1996], investigators also found that, although there were differences among sites, there was relatively little seasonal or year-to-year variation in the abundances of the most common species at a given site over a six-year period.

The data presented in this report span a relatively short period of time compared to similar intertidal monitoring studies in Alaska [Highsmith et al. 2000; Coates et al. 1999], but the relative stability of the dominant space-occupying invertebrates and algae in undisturbed habitat was similar among the studies. In 1996, Pentec Environmental, Inc. [1996] revisited several rocky-intertidal shorelines that had been surveyed between 1974 and 1978. They reported no major shifts in species dominance or in the health of the intertidal communities outside of the natural variations shown in 1974–1978, indicating that rocky sites in Kachemak Bay had experienced an extended (18+ years) period of stability. An earlier rocky-intertidal habitat study conducted in outer Kachemak Bay [Carroll 1994] did show inter- and intra-annual variability for several dominant organisms. These inconsistencies can be attributed to two main differences between this and the current Kachemak Bay study. First, the earlier study conducted by Carroll [1994] recorded only those organisms that occurred directly beneath each grid point when collecting percent cover data. Thus, organisms that typically occur as midstory or understory organisms, such as barnacles, were underestimated when overstory algal cover was high. For example, he showed that *S. cariosus* exhibited large seasonal shifts in percent cover, even though this organism is a relatively slow-growing, long-lived sessile invertebrate. The current study collected data through overstory, midstory and understory layers which more accurately reflect the abundance of organisms. Secondly, Carroll [1994] reported a massive winter-kill of many sessile invertebrates due to extremely low air temperatures immediately before his sites were established. His study was designed to document recovery from this stress, and his control sites, or sites that were not experimentally treated, were recovering from this natural clearing disturbance. The timing of the winter freeze that he documented as creating widespread disturbances to the intertidal zone of outer Kachemak Bay occurred in January, similar to the timing of the disturbances created in March 1994 and 1995 for this study.

The study design for determining whether the timing of disturbances affected recovery patterns over a range of wave-exposed rocky-intertidal habitat was complex: eight sites, three tidal heights, five treatments (control quadrats and four scrape dates), and four data collection dates. Statistical analyses or descriptions of the patterns for individual species at each site × tidal height × treatment combination were not possible within the scope of this study. A species by species report for each site, MVD, and scrape treatment across the four sampling dates would most likely show differing trends for each species or taxon based in part on the variables already mentioned, but also on an organism's life history and reproduction cycle, feeding strategy, dependence on other species for food or protection, tolerance of temperature or salinity extremes, growth rate, and whether it was sessile or mobile. Highsmith et al. [1994] showed injury and recovery assessment trends across three sampling dates after the *Exxon Valdez* oil spill for over 50 invertebrate and algal taxa at each of three tidal heights and four habitat types. Injury and recovery trends differed among species, and within species they often differed across habitats and tidal heights. The present study focused on several dominant organisms for statistically comparing recovery trends of the various scraped quadrats to those of control quadrats at two sites, and relied upon multivariate techniques to compare combined algal and invertebrate multi-species data for the treatment × site × MVD combinations. The data for several individual taxa were combined across all sites to illustrate general recovery trends within the region.

Barnacles were significant contributors to intertidal cover in the mid to upper intertidal zone on outer Kachemak Bay rocky shores. Balanus (*Semibalanus balanoides* + *Balanus glandula*) were also the dominant organisms recruiting to the space made available in scraped quadrats. Recruitment was not a limiting factor for recovery in the high and mid intertidal zone, as Balanus cover was generally higher in scraped quadrats than control quadrats. Barnacle recruitment into scraped quadrats was very high in the spring. In the quadrats scraped in March 1995, there was a decrease in total cover between spat in July 1995 and mature barnacles in September 1996, due to juvenile mortality. The ratios of barnacle spat to Balanus percent cover were relatively constant across sites. For most sites and tidal heights, the September 1996 data revealed that barnacle percent cover on the most recently scraped quadrats was still substantially higher than the controls, due in large part to over-recruitment into the bare space provided by the scraping. The dominant barnacle in the low intertidal is *S. cariosus*, which recruited at a much lower rate and still had not reached control levels by the end of the study in September 1996, except at site HI in quadrats scraped in March 1994.

Gregarious settlement, in which larvae colonize in response to indicators of their own species, may account for the high initial recruitment of barnacles into newly scraped quadrats. Gregarious response is stronger in barnacles, especially *Balanus glandula*, than other intertidal organisms [Larman and Gabbott 1975]. For most barnacle species, planktotrophic larvae are released in early spring to coincide with spring phytoplankton availability [Crisp 1976]. Thus, larval settlement is highest during spring. Carroll [1994] documented barnacle recruitment onto artificial plates at two sites and two tidal heights in outer Kachemak Bay. The date on which recruits were first observed on test surfaces during his three-year study varied by only 4 days, from 8–11 May. However, he detected differences in the total length of time that the barnacles recruited during each year. In 1991, barnacles "trickled" in during much of the spring and summer. In 1992 and 1993, recruitment began with an initial heavy pulse, resulting in maximum density of recruits by the beginning of June. The pattern Carroll [1994] detected in 1992 and 1993 was similar to the results for this study. Barnacle spat were the initial colonizers of quadrats having bare space available in the spring and the highest densities of spat were detected during the summer sampling dates, July 1995 and June 1996. Significantly fewer barnacle spat were detected in October 1995 and September 1996, probably due to mortality and advancement to larger size classes. Some barnacles recruited later, as evidenced by the presence of adult Balanus in quadrats sampled July 1995 that had been scraped in July 1994. Strathmann and Branscomb [1979] observed that larvae of the barnacles *B. glandula* and *S. cariosus* recruited more heavily into algal cover transplanted from low intertidal substrates to the upper intertidal zone than among algae resident in the upper intertidal area. Thus, the absence or presence of specific algal species could enhance recovery after a disturbance by affecting microhabitats utilized by other species, such as barnacles.

Percent cover values for *Fucus gardneri* indicated variable recruitment and recovery. This species is the major structural component of rocky shorelines throughout much of Alaska's coastline and was heavily damaged by the EVOS and subsequent clean-up activities [DeVogelaere and Foster 1993; Stekoll and Deysher 1996; Highsmith et al. 2000]. Quadrats scraped in March 1994 generally had the highest *Fucus* cover of any scraped quadrats during the study and were more similar to the control quadrats at the end of the study than for any other scrape date. Also, the overall cover of *Fucus* was lowest at the most exposed sites (Figure 8). Percent cover values may fluctuate annually, as there appear to be some differences in cover at the control sites from year to year. Interactions between organisms may play a part in highly variable recruitment as well. For example, barnacles can facilitate the settlement of *Fucus* eggs [Carroll 1994; Highsmith et al. 2000), although long-term survival of *Fucus* plants on barnacle tests is lower than for plants growing in substrate cracks [Stekoll and Deysher 1996].

A study conducted in Herring Bay revealed decreased grazer densities when *Fucus gardneri* was removed from quadrats [Highsmith et al. 2000]. In that study, limpets and littorine snail abundances decreased on rocky substrate directly beneath *Fucus* canopy after the plants were removed. While limpet densities increased to pre-*Fucus* removal levels after one month, *L. sitkana* densities still remained depressed two months later. In the current study, littorine densities equal to or greater than those in control quadrats were found in scraped quadrats by July 1995. Quadrats scraped in March were dominated by barnacle spat, yet contained greater numbers of littorines than did control quadrats, even in the total absence of *Fucus* cover. Under the experimental conditions of these two studies, littorines appear to take at least two months but less than 16 months to recruit back into scraped quadrats.

Alaria spp. are commonly found in association with *Semibalanus cariosus* in the low intertidal zone. The holdfasts of these algae are often attached directly to the barnacle tests, suggesting that the presence of *S. cariosus* may facilitate *Alaria* recruitment. Compared to the other species included in this study, *Alaria* recovery in the low zone appears to be much slower, though *Alaria* cover was highest on sites with the highest *S. cariosus* cover. *Alaria* spp. were one of the algal genera damaged by the EVOS [Highsmith et al. 1994]. Recruitment of *Fucus* into the space made available by the removal of *Alaria* at oil/clean-up impacted beaches resulted in higher cover of *Fucus* at oiled sites compared to non-oiled sites in the low intertidal area. The current study results do not show this replacement at MVD 3.5, although *Alaria* cover in control quadrats was highest at sites with low *Fucus* cover.

Only limited recruitment patterns appeared to be related to the wave exposure gradient, perhaps because barnacle spat recruitment was high at most sites. Both *Semibalanus cariosus* and *Alaria* spp. showed higher percent cover at the three exposed sites than at the protected sites, especially by September 1996 (Figure 7). In contrast, *Fucus gardneri* had higher cover at protected sites (Figure 8), with significant differences at MVD 1.5 between sites HI (exposed) and BB (protected) (Table 8). *F. gardneri* did not recruit into scraped quadrats until after barnacles had recruited into the space and, as noted above, *Alaria* spp. recovery may be dependent upon prior *S. cariosus* recruitment.

General successional patterns emerged as the quadrats were sampled over time. Barnacle spat recruitment was highest in quadrats that had the most bare space available when data were collected in July 1995 (i.e., quadrats scraped most recently). By September 1996, however, barnacle spat cover was low, in part because bare space was becoming limiting in many of the scraped quadrats, with total percent cover near 80%. Also, barnacle spat grew into adult barnacles (*Semibalanus balanoides* and *Balanus glandula*), increasing total adult barnacle cover. In fact, in most scraped quadrats, the percent cover of adult barnacles was higher than in control quadrats as a result of the over-recruitment of spat onto the available bare space when the quadrats were created. Rolan and Gallagher [1991] reported similar trends for *Semibalanus balanoides* following an oil spill at Sullom Voe, with a rapid initial population increase following the spill that reached densities higher than those reported in pre-spill data. They, however, attributed the increase to spill-related loss of a major barnacle predator. As barnacle spat matured in the scraped quadrats, adult barnacle percent cover was lower than previously found for barnacle spat, indicating spat mortality, possibly due to overcrowding. In contrast, over-recruitment did not occur in the larger, low intertidal species, *Semibalanus cariosus*. This barnacle had not recovered by the last sampling date, except in scraped quadrats that had the most time to recover (>2.5 years).

Mytilus trossulus recovery was incomplete for all scraped quadrats at sites BB and HI combined. Recovery appeared to be further along at the wave-protected site BB (Figure 21), compared to the wave-exposed site HI (Figure 22), but significant differences in recovery rates were not detected by the rmANOVA. However, recovery shown for *M. trossulus* is probably underestimated. Although the 3-dimensional percent cover method used to collect these data did measure understory organisms, it did not detect more than one layer of the same organism. Once a taxon was encountered, it was not recorded again if it occurred more than once. This decision was made because most algal species fold over onto themselves and individuals would otherwise be recorded twice or even three times. However, for organisms such as *M. trossulus*, that often recruit to byssal threads of established individuals, our 3-D method is not truly counting individual mussels in a three dimensional manner. Recovery of mussel beds in cleared areas during a California study [Kinnetic Laboratories, Inc. 1992; Minerals Management Service 1996] was slow and took up to ten years or more at most sites. Suchanek [1978], however, reported that for exposed rocky shorelines in southeastern Alaska, mussels settled densely in bare space and grew quickly to reproductive size, often occupying 75–80% of the substratum.

Recovery from disturbance was incomplete in the most recently scraped quadrats by the last sampling date in September 1996, although some sites were further along in the recovery process than others. Quadrats scraped in July and October 1994 were furthest from recovery compared to control quadrats. Quadrats scraped in March 1994 and March 1995 were more similar to control quadrats. Quadrats scraped in March, before barnacle larval settlement, had the most bare space available for recruitment. A similar study conducted in California also showed that recovery varied with time of clearing [Kinnetic Laboratories, Inc. 1992; Minerals Management Service 1996]. Their study showed that in an *Endocladia/Mastocarpus papillatus* assemblage, quadrats scraped in spring had recovered to a greater extent than those cleared in the fall. Sousa [1979a, b] reported that seasonality of recruitment is crucial in determining the sequence in which species colonize newly cleared space, with the species that is least seasonal in its recruitment usually becoming established first. Our data contradict this statement since barnacles dominate in quadrats scraped during all seasons, even though their recruitment is extremely seasonal.

On the central Oregon coast, Farrell [1991] reported that the general order of succession was the same for experimental clearings: *Chthamalus dalli* → *Balanus glandula* → macroalgae (including *Fucus*). *Fucus* colonized only after barnacles had done so, similar to the findings of this study. Although the general order of succession was the same for different clearings, the time required ranged from less than 12 months to greater than 36 months. Farrell [1991] attributed the differences in the rates of succession to variations in the timing of successful *Balanus* recruitment. For our study, scraped quadrat recovery also depended on the recruitment of barnacles, which delayed recovery stages for almost a year for quadrats scraped in the summer and fall until the following spring's barnacle settlement.

Multi-dimensional scaling has become a widely accepted model for demonstrating ecological patterns in a variety of marine communities. Applied to this study, it successfully illustrated the differences in intertidal communities among controls and quadrats scraped on different dates. In addition, the method showed the relative convergence of quadrats scraped in March 1994 and 1995 compared to quadrats scraped in July and October 1994. Additionally, the dissimilarities of scraped quadrats compared to control quadrats was reduced between July 1995 and September 1996. MDS methods have been applied extensively in studies of environmental impacts of pollution on soft sediment subtidal habitats to show differences in community structure between polluted and non-polluted sites or to show shifts in community structure along a pollution gradient [Gray et al. 1988; Agard et al. 1993; Warwick 1993]. MDS was also utilized to assess benthic communities following the EVOS in subtidal environments of Prince William Sound [Feder and Blanchard 1998; Jewett et al. 1999]. Highsmith et al. [1994] used MDS methods to evaluate recovery of invertebrate and algal communities on rocky substrates after the *Exxon Valdez* disturbance and subsequent clean-up activities. MDS methods had not been applied to many rocky-intertidal studies previously and their data showed that site exposure to waves explained the ordinations and oiling category did not. Hansen and Ingolfsson [1993] used MDS methods to evaluate patterns in species composition of Iceland's rocky shorelines and found that the degree of site exposure was an important factor in structuring intertidal communities. Since then a number of studies have used MDS to evaluate rocky-intertidal habitats [Chapman and Underwood 1998; Conlan et. al. 1998; Dye 1998; Lasiak 1998].

No direct relationship between recovery rate and site wave exposure was apparent from the MDS analyses. MDS analyses performed after the EVOS for intertidal invertebrates and algae from rocky shores [Highsmith et al. 1994] indicated that sites with similar wave exposures were more similar than sites within a given geographical area. This suggests that effects due to wave exposure may be masked in this study as a result of the high variability observed. Unfortunately, data collection in Highsmith et al. [1994] was short term relative to recovery, and specific assessment of the interaction between community recovery rates and wave exposure was not possible during that study. Wave action may contribute to the productivity of more exposed coastlines by providing food and nutrients, limiting self-shading algae, and protecting sessile species from grazing and predation [Leigh et al. 1987]. Sessile invertebrates tend to reach their largest individual size at wave-swept sites [Paine 1976], but mobile grazers and predators are generally smaller [Menge 1974; Paine 1976; Denny et al. 1985; Brown and Quinn 1988]. Although individuals may be smaller, some invertebrates can be more abundant on exposed shorelines. Brown and Quinn [1988] found smaller, but more abundant, *Nucella* and limpets on exposed shorelines. However, the reverse may also occur. In Herring Bay, higher abundances of a littorine snail were found at protected than exposed sites [Highsmith et al. 2000], although the differences in wave exposure were much less than across the eight sites in this study. The effects of wave exposure on intertidal organisms are not always clear and the results of this study, primarily the assessment of specific organisms rather than community level analyses, suggest only weak to moderate influences on recruitment and recovery of scraped sites within this particular study area.

Recovery rates will vary with the scale of the disturbance, with intertidal communities taking longer to recover from disturbances that substantially increase distances to source populations for recruits. Recovery rates detected during this study were higher for several dominant intertidal organisms (e.g., Balanus and *Fucus gardneri*) than for the same species damaged by the *Exxon Valdez* oil spill. *Fucus gardneri* recovery in the high intertidal zone was not complete by September 1996 of this study. However, most scraped quadrats had significantly increased *Fucus* cover and were beginning to approach levels similar to control quadrats. *Fucus* damaged in high intertidal areas impacted by the EVOS had not recovered to the levels found on unoiled shorelines seven years after the spill. The higher recovery rate is most likely a result of the size of scraped quadrats compared to the vast intertidal areas affected by the spill. The scraped quadrats in this study were surrounded by healthy, undisturbed intertidal communities. The presence of nearby barnacles may encourage gregarious settlement of larvae. *Fucus gardneri* egg dispersal distance is very limited, with settlement occurring near the adult plant [Stekoll and Deysher 1996]. Thus, in our study, nearby plants provide a source of eggs for the disturbed sites. In a heavily oil- or treatment-damaged area, *Fucus* cover along whole shoreline segments may be dramatically reduced, thus greatly retarding *Fucus* recovery rates. Studies in Herring Bay showed slow increases in limpet and littorine densities on oiled sites in the years following the EVOS. These studies also showed slow steady increases in densities in cleared sites at unoiled shorelines adjacent to heavily oiled areas, indicating that the available recruits to the entire area were affected by the extensive loss of adults at oiled sites. We observed relatively short recovery periods for limpets and littorines in our quadrats, suggesting availability of potential recruits was not a recovery restraint in this study.

Conclusions

1. Recovery from disturbances occurs on different time scales for different species, different habitats and different geographic locations. We have shown during this study that time of disturbance relative to seasonal reproductive events of major space-occupying species can affect the time-course of recovery. However, the study did not continue long enough for all end points to be reached nor for confirmation of overall community recovery by documenting achievement of stability (i.e., no further significant change or difference from controls). Consequently, a primary conclusion of this study is that long-term monitoring of experimentally disturbed sites is needed in Kachemak Bay in order to fully understand the specific events and time-course of recovery from seasonal disturbances. However, this study does provide a data and knowledge base for continued intertidal monitoring and research in the region that should be incorporated into a long-term program. As there may be habitat and local geographic differences in recruitment and post-recruitment dynamics, research of the type conducted in this project should also be conducted on a long-term basis at other locations within Kachemak Bay and Cook Inlet.

2. The specific objectives of the study in the rocky-intertidal habitat of outer Kachemak Bay were to: a) determine whether the season in which a disturbance occurs affects recovery rates or successional processes, b) quantify inter- and intra-annual abundance patterns for major space-occupying species, and c) determine the effect of wave exposure on community structure and response to seasonal disturbances. To address these objectives, eight rocky-intertidal sites were established over a gradient of wave exposures and permanently marked such that baseline data can continue to be collected in the future (see conclusion 1). Data were collected from undisturbed control quadrats during two summer and two fall sampling periods in 1995 and 1996 to quantify inter- and intra-annual abundance patterns for major space-occupying species. In addition to control quadrats at each site, experimental quadrats were cleared of all biota during different seasons and followed over time to see if the timing of a disturbance affects recovery rates and/or successional processes. The data collected from these sites could provide pre-spill data in the event of a catastrophic oil spill at upstream coastal areas in the Gulf of Alaska or in Cook Inlet.

3. The season in which a disturbance to rocky-intertidal habitats in southcentral Alaska takes place affects recruitment, successional, and recovery patterns of several dominant intertidal algae and invertebrates. In this study, summer and fall disturbances took longer to recover from than disturbances in the spring, prior to the period of peak settlement of barnacle larvae. It appears that barnacle recruitment is a precursor for recruitment of other major species common

in the undisturbed community. Therefore, early barnacle recruitment appears to be the key to higher recovery rates. For this study, recovery by intertidal organisms from disturbances was not shown to be a function of wave exposure. The recruitment, successional, and recovery trends were similar across all sites, perhaps due to rather uniform barnacle cover, regardless of exposure. Although most bare space is colonized within months of being created, especially at exposed sites, the initial species composition is much different from controls, so measurement of total percent cover, independent of species composition, is not a good predictor of recovery rates from disturbances.

4. In control quadrats, the data indicate a relatively stable intertidal community where the dominant organisms showed little inter-annual variability. Several species did exhibit intra-annual variability in percent cover (i.e., differences between summer and fall) which were expected given their life histories. In experimental quadrats, barnacle spat densities were highest in the most recently scraped set and lowest in the oldest set due to less space being available for settlement in the older quadrats. Spat densities declined during summer and fall due to some combination of growth out of the size class and post-settlement mortality. For all sites combined, the percent cover levels for the barnacles *Semibalanus balanoides* and *Balanus glandula*, which had over-recruited into scraped quadrats, had not returned to control percent cover levels, which were usually lower, as of the last sampling date at MVDs 1.5 and 2.5. At MVD 3.5, the barnacle *S. cariosus* and the kelp *Alaria* spp. had not increased to control levels in quadrats that had more than two years to recover after being scraped. *Fucus gardneri* was also still recovering except in scraped quadrats that had 2.5 years to recover. The blue mussel *Mytilus trossulus* had not increased to control levels for all scraped quadrats combined at sites BB and HI as of the last sampling date. Based on the results for site HI, mussels may take much longer than 2.5 years to recover. As having zero means is inevitable for some species and quadrats in a relatively short-term study, the parametric analyses of the results need to be interpreted with some caution.

5. Multi-dimensional scaling methods, using time of disturbance as an environmental variable, illustrated differences in community recovery status among quadrats scraped during different seasons. By September 1996, analyses indicate relative convergence of quadrats scraped in March 1994 and 1995, compared to quadrats scraped in July and October 1994. No direct relationship with recovery rate and site wave exposure was apparent from the MDS analyses. The dissimilarities of scraped quadrats compared to control quadrats were reduced between July 1995 and September 1996, suggesting community recovery was in progress but not complete after 2.5 years.

6. We cannot provide a rigorous, statistically-based estimate of recovery time for scraped intertidal quadrats. Simple inspection of the data presented suggest that some species at some tidal heights at some locations reach control levels approximately 2 to 2.5 years after scraping but that some of the same species plus other species at different heights and locations did not reach control levels over the same period. Even for those cases where there is not a significant difference between scraped and control quadrats by the end of the present study, monitoring should continue for at least an additional two years to ensure the recovering quadrats have stabilized. A difficulty in making recovery estimates is the potential for additional disturbance of the experimental quadrats. For example, extremely cold weather coincided with very low tide series in 1989, 1999 and 2000, usually in January. Nearly all mid to upper intertidal barnacles and mussels in the vicinity of the present study were killed in 1989 [Carroll 1994]. Shells and tests of dead mussels and barnacles were still present in early April but by June they had fallen off and there was a heavy set of barnacle spat. Based on the results of this study, severe winter kill would reset the recovery process back to the beginning, with time to recovery similar to that for

our March 1994 or March 1995 scraped quadrats in which there was early barnacle recruitment. However, recovery of species with poor dispersal capabilities, such as *Fucus gardneri*, would probably take much longer than suggested by our data due to the lack of nearby adult plants. Our estimate of the time boundaries for a community study of the type presented here would be 5–10 years, following the latest major disturbance, whether experimental or otherwise.

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Study Products

Kachemak Bay Algal Voucher Collection: stored at the University of Alaska Fairbanks Kasitsna Bay Laboratory.

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Highsmith, R.C., S.M. Saupe and A.L. Blanchard. 2001. Kachemak Bay experimental and monitoring Studies: Recruitment, succession, and recovery in seasonally disturbed rocky-intertidal habitat. Final Report. OCS Study MMS 2001-053, University of Alaska Coastal Marine Institute, University of Alaska Fairbanks, 66 p.

Saupe, S.M., and R.C. Highsmith. 1995. Recruitment and succession after disturbances to the intertidal zone in outer Kachemak Bay, Alaska. Oral presentation at the University of Alaska Coastal Marine Institute Annual Research Review, February 1995, Fairbanks.

Saupe, S.M., and R.C. Highsmith. 1995. Recruitment and succession after disturbances to the intertidal zone in outer Kachemak Bay, Alaska. Oral presentation at the Kachemak Bay Conference, Homer, AK.

Saupe, S.M., and R.C. Highsmith. 1996. Recruitment and succession after disturbances to the intertidal zone in outer Kachemak Bay, Alaska. Oral presentation at the University of Alaska Coastal Marine Institute Annual Research Review, February 1996, Fairbanks.

Saupe, S.M., and R.C. Highsmith. 1997. Recruitment and succession after disturbances to the intertidal zone in outer Kachemak Bay, Alaska. Oral presentation at the University of Alaska Coastal Marine Institute Annual Research Review, February 1997, Fairbanks.

Saupe, S.M., and R. C. Highsmith. 1997. Recruitment and succession after disturbances to the intertidal zone in outer Kachemak Bay, Alaska. Watershed '97, The Cook Inlet Symposium, Anchorage.

Saupe, S.M., and R.C. Highsmith. 1999. Recruitment and succession after disturbances to the intertidal zone in outer Kachemak Bay, p. 37 (abstract). *In* Proceedings Seventh MMS Information Transfer Meeting. Alaska OCS Region, Minerals Management Service, January 1999, Anchorage. (http://www.mms.gov/Alaska/ess/itm/itm99/itm.htm)

References

Agard, J.B.R., J. Gobin and R.M. Warwick. 1993. Analysis of marine macrobenthic community structure in relation to pollution, natural oil seepage and seasonal disturbance in a tropical environment (Trinidad, West Indies). Mar. Ecol. Prog. Ser. 92:233–243.

Berlow, E.L. 1997. From canalization to contingency: Historical effects in a successional rocky intertidal community. Ecol. Monogr. 67:435–460.

Bray, J.R., and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325–349.

Brown, K.M., and J.F. Quinn. 1988. The effect of wave action on growth in three species of intertidal gastropods. Oecologia (Berlin) 75:420–425.

Carroll, M.L. 1994. The ecology of a high-latitude rocky intertidal community: Processes driving population dynamics in Kachemak Bay, Alaska. Ph.D. dissertation, University of Alaska Fairbanks, 225 p.

Chapman, M.G., and A.J. Underwood. 1998. Inconsistency and variation in the development of rocky intertidal algal assemblages. J. Exp. Mar. Biol. Ecol. 224:253–264.

Clarke, K.R., and R.M. Warwick. 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Bourne Press Ltd., Bournemouth, U.K., 137 p.

Coates, D.A., A.K. Fukuyama, J.R. Skalski and S. Kimura. 1999. Monitoring of biological recovery of Prince William Sound intertidal sites impacted by the *Exxon Valdez* oil spill: 1997 Biological Monitoring Survey. Prepared for NOAA Hazardous Materials Response and Assessment Division, Seattle, 130 p.

Conlan, K.E., H.S. Lenihan, R.G. Kvitek and J.S. Oliver. 1998. Ice scour disturbance to benthic communities in the Canadian High Arctic. Mar. Ecol. Prog. Ser. 166:1–16.

Crisp, D.J. 1976. Settlement responses in marine organisms, p. 83–124. *In* R.C. Newell [ed.], Adaptation to Environment. Essays on the Physiology of Marine Animals. Butterworth, London/Boston.

Denny M.W., T.L. Daniel and M.R. Koehl. 1985. Mechanical limits to size in wave-swept organisms. Ecol. Monogr. 55:69–102.

DeVogelaere, A.P., and M.S. Foster. 1993. Damage, recovery and restoration of intertidal *Fucus* following the *Exxon Valdez* oil spill. Study for the Environmental Protection Agency, 45 p.

DeVogelaere, A.P., and M.S. Foster. 1994. Damage and recovery in intertidal *Fucus* assemblages following the *Exxon Valdez* oil spill. Mar. Ecol. Prog. Ser. 106:263–271.

Dobroski, C.J., and R.B. Bogardus. 1990. A standardized approach to the ecological monitoring of oil spills, p. 197–217. *In* Proc. Thirteenth Arctic and Marine Oil Spill Program Technical Seminar, 6–9 June 1990, Edmonton, Alberta.

Dye, A.H. 1998. Community-level analyses of long-term changes in rocky littoral fauna from South Africa. Mar. Ecol. Prog. Ser. 164:47–57.

Farrell, T.M. 1991. Models and mechanisms of succession: An example from a rocky intertidal community. Ecol. Monogr. 61:95–113.

Feder, H.M., and A. Blanchard. 1998. The deep benthos of Prince William Sound, Alaska, sixteen months after the *Exxon Valdez* oil spill. Mar. Poll. Bull. 36:118–130.

Field, J.G., K.R. Clarke and R.M. Warwick. 1982. A practical strategy for analyzing multi-species distribution patterns. Mar. Ecol. Prog. Ser. 8:37–52.

Foster, M.S., A.P. DeVogelaere, C. Harrold, J.S. Pearse and A.B. Thum. 1986. Causes of spatial and temporal patterns in rocky intertidal communities of central and northern California. Prepared for the Minerals Management Service, U.S. Dept. of the Interior by Kinnetic Laboratories, Inc. in association with the University of California, Santa Cruz, and Moss Landing Marine Laboratories. Contract no. 14-12-0001-30057. Vol. 1–2. OCS Study MMS 85-0049. 126 p.

Foster, M.S., C. Harrold and D.D. Hardin. 1991. Point vs. photo-quadrat estimates of the cover of sessile marine organisms. J. Exp. Mar. Biol. Ecol. 146:193–203.

Gerard, V.A. 1982. In situ water motion and nutrient uptake by the giant kelp *Macrocystis pyrifera*. Mar. Biol. 69:51–54.

Gilfillan, E., D.S. Page, E.J. Harner and P.D. Boehm. 1995. Shoreline ecology program for Prince William Sound, Alaska, following the *Exxon Valdez* oil spill: Part 3 – Biology, p. 398–443. *In* P.G. Wells, J.N. Butler and J.S. Hughes [eds.], *Exxon Valdez* Oil Spill: Fate and Effects in Alaskan Waters. Am. Soc. Test. Mater. Spec. Tech. Publ. 1219, Philadelphia.

Gray, J.S., M. Aschan, M.R. Carr, K.R. Clarke, R.H. Green, T.H. Pearson, R. Rosenberg and R.M. Warwick. 1988. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. Mar. Ecol. Prog. Ser. 46:151–165.

Hansen, J.R., and A. Ingolfsson. 1993. Patterns in species composition of rocky shore communities in sub-arctic fjords of eastern Iceland. Mar. Biol. 117:469–481.

Hawkins, S.J., and R.G. Hartnoll. 1983. Changes in a rocky shore community: An evaluation of monitoring. Mar. Env. Res. 9:131–181.

Highsmith, R.C., M.S. Stekoll, W.E. Barber, L. McDonald, D. Strickland and W.P. Erickson. 1994. Comprehensive assessment of coastal habitat. Vol. I. *Exxon Valdez* oil spill state/federal natural resource damage assessment final report (Coastal Habitat Study No. 1A). NTIS No. PB99-110447. *Exxon Valdez* Oil Spill Trustee Council. 796 p.

Highsmith, R.C., M.S. Stekoll, P. van Tamelen, S.M. Saupe, T.L. Rucker and L. Deysher. 2000. Herring Bay experimental and monitoring studies. Final status report. Monitoring and Restoration Project No. 96086-C. *Exxon Valdez* Oil Spill Trustee Council. 229 p.

Hiscock, K. [ed.]. 1985. Rocky shore survey and monitoring workshop, 1–4 May 1984. British Petroleum International Ltd., London.

Houghton, J.P., A.K. Fukuyama, D.C. Lees, P.J. Hague, H.L. Cumberland, P.M. Harper and W.B. Driskell. 1993. Evaluation of the condition of Prince William Sound shorelines following the *Exxon Valdez* oil spill and subsequent shoreline treatment. Vol. II: 1992 Biological Monitoring Survey. NOAA Tech. Memo. NOS ORCA 73, Seattle.

Houghton, J.P., D.C. Lees, W.B. Driskell, S.C. Lindstrom and A.J. Mearns. 1996. Recovery of Prince William Sound intertidal epibiota from *Exxon Valdez* oiling and shoreline treatments, 1989 through 1992. Am. Fish. Soc. Symp. 18:379–411.

Jewett, S.C., T. Dean, R.O. Smith and A. Blanchard. 1999. The *Exxon Valdez* oil spill: Impacts and recovery in the soft-bottom benthic community in eelgrass habitats. Mar. Ecol. Prog. Ser. 185:59–83.

Kim, J.H., and R.E. DeWreede. 1996. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. Mar. Ecol. Prog. Ser. 133:217–228.

Kinnetic Laboratories, Inc. 1992. Study of the rocky intertidal communities of central and northern California. Final report, Vol. I–II. Prepared in association with the University of California, Santa Cruz, Moss Landing Marine Laboratories, and TENERA Corporation for the U.S. Department of the Interior, Minerals Management Service, Pacific OCS Region. Contract No. 14-12-0001-30057. OCS Study MMS 91-0089.

Kruskal, K.B., and M. Wish. 1978. Multidimensional Scaling. Sage Publications, Beverly Hills, 93 p.

Larman, V.N., and P.A. Gabbott. 1975. Settlement of cyprid larvae of *Balanus balanoides* and *Elminius modestus* induced by extracts of adult barnacles and other marine animals. J. Mar. Biol. Assoc. U.K. 55:183–190.

Lasiak, T. 1998. Multivariate comparisons of rocky infratidal macrofaunal assemblages from replicate exploited and non-exploited localities on the Transkei coast of South Africa. Mar. Ecol. Prog. Ser. 167:15–23.

Lees, D.C., and J.P. Houghton. 1977. Reconnaissance of the intertidal and shallow subtidal biotic assemblages in lower Cook Inlet. Final report, append. A–D. Prepared by Dames and Moore for Dept. of Commerce, NOAA/OCSEAP, 170 p.

Lees, D.C., J.P. Houghton, D.E. Erickson, W.B. Driskell and D.E. Boettcher. 1980. Ecological studies of intertidal and shallow subtidal habitats in lower Cook Inlet, Alaska. Final report. Prepared by Dames and Moore for Dept. of Commerce, NOAA/OCSEAP, 403 p.

Leigh, E.G., R.T. Paine, J.F. Quinn and T.H. Suchanek. 1987. Wave energy and intertidal productivity. Proc. Natl. Acad. Sci. 84:1314–1318.

Menge, B.A. 1995. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. Ecol. Monogr. 65:21–74.

Menge, J.L. 1974. Prey selection and foraging period of a predaceous rocky intertidal snail, *Acanthina punctulata*. Oecologia (Berlin) 17:293–316.

Minerals Management Service. 1996. Mussel recovery and species dynamics at four California intertidal sites: 1992 data report. Prepared in association with Kinnetic Laboratories, Inc. for the U.S. Department of the Interior, Minerals Management Service, Pacific OCS Region. Contract No. PC 94-1. OCS Study 96-0009.

Muus, B.J. 1968. A field method for measuring "exposure" by means of plaster balls. A preliminary account. Sarsia 34:61–68.

O'Clair, C.E., and S.T. Zimmerman. 1987. Biogeography and ecology of intertidal and shallow subtidal communities, p. 305–344. *In* D.W. Hood and S.T. Zimmerman [eds.], The Gulf of Alaska: Physical Environment and Biological Resources. National Technical Information Service, Springfield, Virginia.

Paine, R.T. 1976. Size-limited predation: An observational and experimental approach with the *Mytilus–Pisaster* association. Ecology 57:858–873.

Pentec Environmental, Inc. 1996. A survey of selected Cook Inlet intertidal habitats. Final report to Cook Inlet Regional Citizens Advisory Council, Kenai, Alaska. Project number 95-0014E67, 68 p. + append.

Petticrew, E.L., and J. Kalff. 1991. Calibration of a gypsum source for freshwater flow measurements. Can. J. Fish. Aquat. Sci. 48:1244–1249.

Rolan, G.R., and R. Gallagher. 1991. Recovery of the intertidal biotic communities at Sullom Voe following the *Esso Bernicia* oil spill of 1978. 1991 International Oil Spill Conference, San Diego, American Petroleum Institute.

Rosenthal, R.J., and D.C. Lees. 1976. Marine plant community study, Kachemak Bay, Alaska. Prepared by Dames and Moore for the Alaska Dept. of Fish and Game, 288 p.

Seed, R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. II. Growth and mortality. Oecologia 3:317–350.

Sousa, W.P. 1979a. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 79:227–254.

Sousa, W.P. 1979b. Disturbance in marine intertidal boulder fields: The nonequilibrium maintenance of species diversity. Ecology 60:1225–1239.

Stekoll, M.S., and L. Deysher. 1996. Recolonization and restoration of upper intertidal *Fucus gardneri* (Fucales, Phaeophyta) following the *Exxon Valdez* oil spill. Hydrobiologia 326/327:311–316.

Strathmann, R.R., and E.S. Branscomb. 1979. Adequacy of cues to favorable sites used by settling larvae of two intertidal barnacles, p. 77–78. *In* S.E. Stancyk [ed.], Reproductive Ecology of Marine Invertebrates. University of South Carolina Press, Columbia.

Suchanek, T.H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 31:105–120.

Underwood. A.J., and M.G. Chapman. 1998. Variation in algal assemblages on wave-exposed rocky shores in New South Wales. J. Mar. Freshw. Res. 49:241–254.

van Tamelen, P.G., and M.S. Stekoll. 1996. Population response of the brown alga *Fucus gardneri* and other algae in Herring Bay, Prince William Sound, to the *Exxon Valdez* oil spill. Am. Fish. Soc. Symp. 18:193–211.

Warwick, R.M. 1993. Environmental impact studies on marine communities: Pragmatical considerations. Aust. J. Ecol. 18:63–80.

Warwick, R.M., and K.R. Clarke. 1991. A comparison of some methods for analyzing changes in benthic community structure. J. Mar. Biol. Assoc. U.K. 71:225–244.

Whittle, D., L. Maltby, P.H. Warren and L.J. Tattersfield. 1998. Using univariate and multivariate techniques to analyze community response to toxic perturbation by a surfactant, p. 175. *In* Proc. Society of Environmental Toxicology and Chemistry 19th Annual Meeting, Charlotte, North Carolina.

The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Royalty Management Program** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principals of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.