CHANGES IN BENTHIC MARINE MACROPHYTE COMMUNITY

STRUCTURE IN THE STRAIT OF GEORGIA:

LONG-TERM AND GRAZING RESPONSES

by

MURRAY M. MANSON

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(Signature)

Department of _Botany_

The University of British Columbia
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ABSTRACT

Benthic marine macrophyte community structure at two

sites near Bath and Sear Islands in the Strait of Georgia,

British Columbia, was quantified from the high tide level on

the shore to about 10 m below zero tide level. Data obtained

from the sites during the summers of 1972 through 1975 and in

1992 was used to make several comparisons of macrophyte

community structure. 1) Changes in community structure

along the depth gradient from intertidal to subtidal were

investigated. 2) At Bath Island, a period of intensive

grazing by sea urchins, *Strongylocentrotus droebachiensis*,

during 1973 altered the community structure and provided an

opportunity for a comparative study of macrophyte community

change and regeneration at the two sites. 3) Community

structure at both sites in 1992 was compared to that in the

1970's. A multivariate approach was taken for the analyses,

using principal component analysis, canonical variate

analysis (CVA), and a modification of CVA including depth as

an environmental variable. Several macrophyte associations

were consistently found by the analyses.

1) An association of *Fucus* spp., *Mastocarpus papillatus*,

Neorhodomela larix, *Porphyra* spp., and *Ulva* spp. defined the

community structure of intertidal quadrats. 2) A subtidal

foliose red and kelp species association was found in

ungrazed areas. 3) A grazed form of the subtidal

association was characterized by low variability and high

abundances of *Calliarthron tuberculosum* and *Ulvaria obscura*.
4) After grazing pressure was removed, community structure
was characterized by initial increases in *Ulva* spp. and
Sargassum muticum during the first year, followed by regrowth
of foliose red and kelp species. 5) A 1992 upper subtidal
association characterized by high abundances of *S. muticum*
and *Lomentaria hakodatensis*, *Gigartina exasperata*, *Corallina
officinalis*, and *Gelidium* spp. contrasted with a 1970's
association of such species as *Callophyllis* spp.,
Cryptopleura ruprechtiana, *Polyneura latissima*, and
Desmarestia viridis.

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INTRODUCTION

The Strait of Georgia, located between the eastern
shore of Vancouver Island and the coast of mainland British
Columbia, is in immediate proximity with the majority of the
population of B.C. and Washington State. Heavy use by both
recreational and commercial vessels, fisheries, and effluent
disposal facilities results in the inevitable occurrence of
disturbances to the biota of the strait. A further source of
potential disturbance comes from communities located along
the Fraser River and its tributaries. Freshwater runoff from
the Fraser River has a strong influence on the southern half
of the Strait of Georgia, so the quality of this runoff also
has the potential to impact the biota of the strait. Because
of this heavy traffic and the significant importance of the
Strait of Georgia to the economy of B.C., techniques for
studying disturbances to the natural biota should be
developed. Without the ability to assess the extent of
change caused by a particular disturbance event, there is no
possibility to determine the success of cleanup efforts or
the cost of a disturbance to the various industries with
financial interest in the biota of the strait.

The concept of disturbance and recovery has been
investigated experimentally by many marine ecologists,
particularly in benthic marine communities (Dethier 1984,
Sousa 1985, Witman 1985, deEston and Bussab 1990). A
condition that removes much of the living biomass from a

community (as disturbance will be defined here) can be imposed experimentally, and the effects on community structure followed for as long as necessary. The community structure may be altered in several ways after such a disturbance (Connell 1987), 1) all species removed by the disturbance are replaced by new species; 2) gradual replacement of colonizing species between disturbances either a) in a predictable, progressive succession of species; or b) in an unpredictable, non-successional pattern of species.

The essence of successional change has been the subject of intensive debate among ecologists, with little clear agreement. Marine ecological field experiments in particular have not supported the traditional models of succession (Sousa 1980). For example unpredictable episodic events seem to be important to succession both in the creation of space (Dethier 1984, Sousa 1984) and in the events controlling dispersal of propagules (Reed *et al*. 1988, Reed *et al*. 1992), making succession unpredictable. The availability of propagules at the time of disturbance is another stochastic factor that can lend to the unpredictable nature of marine benthic successions (Lubchenco and Menge 1978). Also, early successional species may have varying effects on the colonization of later species so that a single model of succession is not tenable (Farrell 1991).

One particular aspect of disturbance in marine hard-substrata that has received considerable attention from marine ecologists is that of the effects of sea urchin

grazing on kelp community structure. Paine and Vadas (1969) describe how intensive grazing by sea urchins reduces the diversity of algal assemblages during grazing, but increases the diversity during recolonization. This work seems to have spurred the development of the widely accepted sea otter keystone species hypothesis in the Northeast Pacific (Estes and Palmisano 1974, Estes *et al.* 1978), and possibly the concurrent lobster keystone species hypothesis of the Northwest Atlantic discussed by Elner and Vadas (1990). A myriad of work has generally concluded that intensive grazing by sea urchins can create "urchin barrens" (i.e. Pearse and Hines 1979, Duggins 1981, Harrold and Reed 1985, Dean *et al.* 1989), and removal of the urchins results in the reestablishment of kelp dominated communities (Foreman 1977).

The process of disturbance has been distinguished from that of stress, which does not result in the active removal of biomass (thus creating new space), but limits the growth or reproduction of a selection of species in the community (Clayton 1990). Both disturbance and stress could be present in the natural environment, affecting community structure, but different approaches are used in experimental investigations of these two conditions (Bender *et al.* 1984). The investigation of stress conditions is further complicated by the relative nature of stress (one species may be stressed while others are unaffected or benefit), the variation possible in the intensity of stress, and the difficulty in discerning the compounding effects that stress conditions may

create. Gradually changing environmental conditions are difficult to measure, and their effects on species composition may be noticeable only over periods of several decades. The long-term studies needed to investigate these effects are costly and rarely carried out but can show changes in community that would otherwise go unnoticed (i.e. changes in marine intertidal communities along the English Channel, Southward 1976).

To investigate a disturbance event or the introduction of a stress condition in the natural environment, the luxury of preplanning is rarely possible, and the process of investigating the effects of the condition becomes considerably more difficult. In order to accurately assess the environmental impact caused by a natural disturbance event, some important information must be included in the study. There must be a quantitative assessment of the biota at the disturbed site before the disturbance event, to act as a baseline to compare the post-disturbance character of the site (Green 1979). Simple presence/absence data can fail to show change, as the relative abundances of species may be all that changes. Information of this sort is difficult and costly to obtain, especially over large areas, and it may require a great deal of luck (or persistant sampling) to have this baseline data for the right place at the time of the disturbance. Also essential to the study is a site of similar quantitative character that escaped the disturbance. The data from this site are used as a control, to indicate

the degree of change which is occurring at the disturbed site, unrelated to the disturbance (Green 1979).

The ease of obtaining quantitative information of a particular community ultimately depends on the habits of the organisms studied, and the limits chosen for the number of species to be included in the study. Macrophytes in particular provide sessile, complex communities that can be relatively easily sampled in a random design, and used to indicate the effects of a disturbance. The difficulty in sampling increases with subtidal sampling, relatively few quantitative studies having been done that include subtidal sampling of the entire depth gradient over which macrophytes can occur (Foster 1990, Chapman 1986).

An important aspect of an environmental impact assessment involves the techniques used to define the community structure at the study sites. The data obtained in studies of community structure are multivariate and highly complex, often not meeting distributional assumptions required for some statistical techniques (Green 1979, Jongman *et al*. 1987), making interpretation difficult. The techniques used for interpretation of the data are thus important to the information gained from the data. As mentioned earlier, in order to assess the extent of change in community structure, the data must be quantitative, so the analysis must consider the quantitative nature of the data. Further, important information on interactive effects can be overlooked by assessing a multivariate data set as a series

of univariate responses. Multivariate methods of analysis are thus advantageous in showing community responses to varying conditions. Currently the most common techniques used by environmental biologists for quantitative multivariate data involve either cluster analysis or some form of ordination (Green 1979, Jongman *et al.* 1987).

Relatively little work has been done involving comparative multivariate analyses of marine macrophyte communities. Cluster analysis was used to compare macrophyte communities after experimental manipulation (deEston and Bussab 1990), and to investigate the effects of sewage effluent on species assemblages (Littler and Murray 1975). Cluster analysis was also one of the techniques used by Foreman (1977), in his investigation of macrophyte community regeneration following grazing by sea urchins. Cluster analysis provides an interesting summary of similarity among quadrats, but does not indicate the basis for similarity.

Ordination techniques have the advantage of providing the loadings that each species has on the quadrat scores. Correspondence analysis (Hill 1973) was used to successfully distinguish between subtidal quadrats, intertidal quadrats, and quadrats located on different substrata in the ordination of west African macrophyte vegetation (John *et al.* 1977). Macrophyte communities on different substrata were assessed on chalk cliffs in England (Tittley and Shaw 1980) using correspondence analysis and another ordination technique, principal coordinate analysis (Pimental 1979).

Multidimensional scaling has also been used to show a separation between community structure of inshore and offshore kelp communities (Velimirov *et al.* 1977). The use of multivariate statistics in comparative studies has been used successfully in studies of terrestrial plant communities (Gibson and Brown 1992, Gittins 1985), and aquatic benthic invertebrate studies (Salmon and Green 1983).

In this study, I have the opportunity to investigate the change in macrophyte community structure following a natural disturbance event. The need for a control site and pre-disturbance quantitative data has been met as a long-term quantitative study of benthic community structure and function was underway at two similar sites in the Strait of Georgia at the time of the disturbance (Foreman 1977, Lindstrom and Foreman 1978). The disturbance event was a period of intensive grazing by the green sea urchin, *Strongylocentrotus droebachiensis*. As the data documenting this disturbance were collected from 1972 through 1975, the opportunity to compare the current (1992) macrophyte community structure at the same sites presents itself. A further aspect of this study will thus be to identify changes in community structure that have occured at the study sites from the 1970's to 1992, indicating how appropriate the existing baseline data would be in future assesments of disturbance events at the sites.

In carrying out the two aspects of this study, the following objectives will be met. 1) Macrophyte species

associated with a particular location on an intertidal to subtidal depth gradient will be identified. 2) To identify the direct effects of sea urchin grazing activity on macrophyte community structure, the macrophyte species composition and abundance will be compared at Bath and Sear Islands before (1972) and during (1973) the urchin grazing activity. 3) Community regeneration will also be investigated by comparing macrophyte community structures of Bath and Sear Island in 1972 to those in 1974 and 1975. 4) The final objective of the study will be to identify long-term changes by comparing the macrophyte community structure in 1972-1975 and in 1992. Throughout the study the focus will be on the community response, rather than that of individual species, by using a multivariate approach to the analysis.

MATERIALS AND METHODS

Study area

This research consists of a conjunction of sampling efforts carried out in the summers of 1972 through 1975, and in the summer of 1992. All of these sampling sessions utilized the same two one-hectare study sites located on the south east shores of Bath Island and Sear Island in the Flat Top Islands area (49° 09' N x 123° 40' W) of the Strait of Georgia. The two study sites are located within 1 km of each other and share the same aspect, though the Bath Island site may be slightly more exposed to open water in the Strait of Georgia. At both sites, the substratum consists of solid sandstone bedrock that is covered with boulders at greater depths. At Bath Island, these boulders are found at about 4.5 m below zero tide, some 70 m out from the high water line on the shore. The Sear Island site is of slightly steeper incline, merging into boulders at 6 m below zero tide line, 70 m out from the high water line on shore.

Sampling Procedures

Details of the 1972 through 1975 sampling sessions are described by Foreman (1977), the sampling dates and number of quadrats sampled during these sessions summarized in Table 1. The following is a description of the sampling protocol

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Table 1. Sampling dates and number of quadrats
sampled at each site.

Site	Year	Sampling Dates	#Quadrats
Bath Island	1972	5/18-7/4	39
	1973	5/15-7/26	41
	1974	4/8-7/31	33
	1975	7/7-7/9	19
	1992	6/22-7/4	63
Sear Island	1972	5/31-7/31	40
	1973	.	.
	1974	4/15-8/12	32
	1975	7/9-7/10	20
	1992	6/25-7/16	63

employed during the 1992 sampling session, designed to facilitate comparison with the data collected from 1972 through 1975. A total of six 100 m transects (three per site) were sampled in the summer of 1992, between June 22 and July 3. Each transect ran perpendicular to the shore from a randomly determined point located along the high water line. Quadrats (one-quarter m^2) were placed at 5 m intervals along the transects where the following variables were recorded; 1) the substratum type was assessed as one of four classes (class 1-sand, class 2-shells, class 3-boulders, class 4-continuous solid bedrock), 2) the depth was recorded (later transformed to meters below zero tide level), 3) the number of sea urchins was recorded, 4) all macrophytes were removed from the substratum via a scraper and an air-driven vacuum as designed by Foreman (1977). A total of 126 samples were collected in 1992 (63 samples from both Bath Island and Sear Island). Following collection, the samples were preserved in 5 percent formalin in seawater until further processing could be carried out. Processing entailed sorting each sample into its constituent species and recording the wet weight per m^2 for each. All samples were processed within 5 months of collection. Voucher specimens were prepared for the U.B.C. Phycological Herbarium, and are available there for inspection.

For the purposes of the Foreman (1977) study of benthic community recovery following urchin grazing, urchins were removed from the Bath Island study site in the summer of 1973

by divers. The effort was continued until after sampling was finished in 1975, to remove the urchins that had moved into the area from outside the perimeter of the study site. To estimate the size distribution of the sea urchin (*Strongylocentrotus droebachiensis*) population at Bath Island in 1992, all sea urchins within 1 m on either side of the second 100 m transect were collected. Test diameters (millimeters) and weight (grams) were recorded for each urchin. The urchins were then returned to the site of collection.

Statistical Analyses

An important assumption underlying the application of many statistical analyses is that the variables be jointly linear, and have a normal (or multinormal) distribution (Green 1979). To determine if the species biomass data collected during this study could validly be tested with the statistical techniques described below, the distributional properties of the data were assessed using the graphical technique of Q-Q probability plots (Gnanadesikan 1977). To create these plots for a multivariate data set, the data must first be summarized in a scalar form. The species' abundances in each quadrat were described as the Mahalanobis distance between each quadrat and the group centroid. This univariate summary was plotted against a chi-squared distribution with 26 degrees of freedom. A comparison was

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made between Q-Q probability plots for both the raw data and log-transformed (natural log) data to determine which would more closely approach linearity. Based on the success of log-transformation to improve the joint linearity of the variables, log-transformed species biomass values were used for the following analyses. Multinormality was rejected for both the raw and log-transformed data sets, so formal tests of dimensionality and equality of vector means were not considered in the analysis (Gittins 1985). The techniques used are considered to be rigorous to violations of multinormality, the most important assumption being the joint linearity of variables (Gittins 1985).

Due to the large number of species encountered, the data were well-suited to analysis using multivariate techniques. Multivariate analyses provide insight into joint species responses, therefore emphasizing community level interpretation of the data. As the purpose of this study was to investigate macrophyte community structure, a multivariate approach was chosen for the analysis. Some of the features of principal components analysis (PCA), canonical variate analysis (CVA), and canonical correlation analysis (CCO) were particularly appropriate for interpretation of this data set in terms of the objectives of the study.

The ability of PCA to order quadrats along a single axis based on the relative abundance of several important species results in a reduction in dimensionality of the data set. In this manner, quadrats with similar locations on the axis have similar species compositions (Jongman *et al.* 1987). By using the quadrat scores on the component axes as variables, interpretation of complex data sets is simplified, and joint species responses are emphasized.

The component loadings from a PCA show how each species influences the axes, so species that have similar loadings can be interpreted as associations (Jongman *et al.* 1987). The loadings were used to define the species associations in this study.

The focus of this study on comparing the macrophyte community structure at Bath and Sear Islands during different years was addressed by summarizing the component scores of the quadrats from each site/year group (i.e. Bath Island/1972 (B72), Bath Island/1992 (B92), Sear Island/1972 (S72)), and using descriptive statistics and graphics to facilitate their comparison. These statistics are based on 95 percent confidence intervals of the component scores for each site/year (Jolicoeur and Mosimann 1960). The confidence intervals can be calculated for each site/year on each component axis, and graphically represented as ellipses. The ellipses for each site/year can then be compared in terms of

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their location on the axes, area (A), eccentricity (ecc), and angle (θ) of intersection of the major axis of the ellipse with the first component axis. The area of the ellipse provides an indication of the amount of variation in the quadrat scores within the site/year. Eccentricity is a measure of the shape of the ellipse in terms of the relative lengths of the major and minor axes (ecc = $a^{-1}(a^2-b^2)^{1/2}$; where 'a' is half the length of the major axis, and 'b' half the length of the minor axis), and is bounded by 0 and 1. Biologically, eccentricity represents the extent to which the scores within the site/year on the component axes are correlated to one another; eccentricity values approaching 1 indicating that the presence or absence of one species association is strongly correlated with that of another. The angle θ indicates the relative extent to which each component influences the spread of points within the site/year. Similar values for θ at two site/years would indicate similar species compositions at those site/years.

PCA was carried out on the correlation matrices of two different subsets of the data to show the major associations of macrophytes; 1) all quadrats, all species encountered more than 15 times in the data set, 2) quadrats between 3 m above and 6 m below zero tide, species encountered more than 15 times (excluding most microscopic filamentous and polysiphonous species) with high component loadings on one of the first three component axes from the previous analysis. By using the correlation matrices (Pearson correlation

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coefficients), the size differences among macrophyte species would not influence the associations (Pielou 1984). Although this method may disproportionately weight the importance of rare species, it was necessary because the differences in biomass among macrophytes were so great that the first three axes derived from a covariance matrix described variation in only the large kelp species. Further, by minimizing the number of rare species in the analysis, this effect should be reduced.

Canonical Variate Analysis

Canonical ordination techniques have the advantage of performing an ordination on two sets of related data, such that the correlation between the two ordinations is maximized (Gittins 1985). One common use of canonical ordination among ecologists is canonical correlation analysis (CCO) which involves correlating a set of species abundances with a set of environmental variables measured for the same quadrats. Thus, CCO shows the patterns of species variation that most strongly correlate to patterns of variation in the environmental data.

Canonical variate analysis (CVA) is a variation of CCO where dummy variables are assigned to represent specific groups of quadrats. The analysis is then carried out as a CCO, with the dummy variable set substituted for the environmental data set. Patterns of variation in the species

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abundance data are thus correlated to the quadrat groups to maximize the ratio of the between group sum of squares of quadrat scores to the within group sum of squares along each axis (Jongman *et al.* 1987). The CVA thus emphasizes the differences in scores between the groups of quadrats.

CVA was useful to this study since part of the objective was to compare the species wet-weights recorded for quadrats grouped according to the site/year from which they were collected. The axes resulting from this ordination, calculated to maximize the correlation between species wet-weights and site/year quadrat groups, should emphasize the differences in macrophyte species composition and abundance among the site/years. When viewed in light of the grazing histories of the site/years, information on how grazing affects macrophyte community structure can be inferred.

CVA was performed to correlate the same log-transformed species data set used in the second PCA with an 8 variable binary code used to delineate the site/year groups of quadrats. For example, quadrats sampled at Bath Island during 1973 were coded with a score of 1 for the first dummy variable and 0 for the other seven (i.e. 1,0,0,0,0,0,0,0), while B74 was coded with 0 for the first variable, 1 for the second, and 0 for the others (i.e. 0,1,0,0,0,0,0). The ninth site/year (B72) received 0 for all dummy variables (i.e. 0,0,0,0,0,0,0,0).

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The above CVA was also carried out in a modified form, with depth included as a ninth variable in addition to the dummy variable set. Otherwise, this analysis used the same data as the CVA. This was done to show how species composition compared among the site/years along the depth gradient.

RESULTS

A list of all of the species encountered in the study
is included in Appendix 1. A total of 158 species were
encountered during the 5 years of sampling. Figure 1 shows
the size distribution of *Strongylocentrotus droebachiensis*
at Bath Island in 1992.

Distributional Properties of the Data

The Q-Q probability plots are shown in Figure 2. The
log-transformed species abundances (wet weights) show a
substantial improvement in linearity, relative to the raw
species abundances. However, the deviation from linearity at
the extremes of the distributions in the plot indicate that
the data were not multivariate normal. The failure of the
data to meet the assumption of multinormality has removed the
opportunity for formal hypothesis tests and attachment of
probabilities to the results of the analyses. The percent of
variance accounted for by the various ordinations indicates
the strength of the conclusions arrived at via the analyses.
It follows that the results should be interpreted with some
reservation.
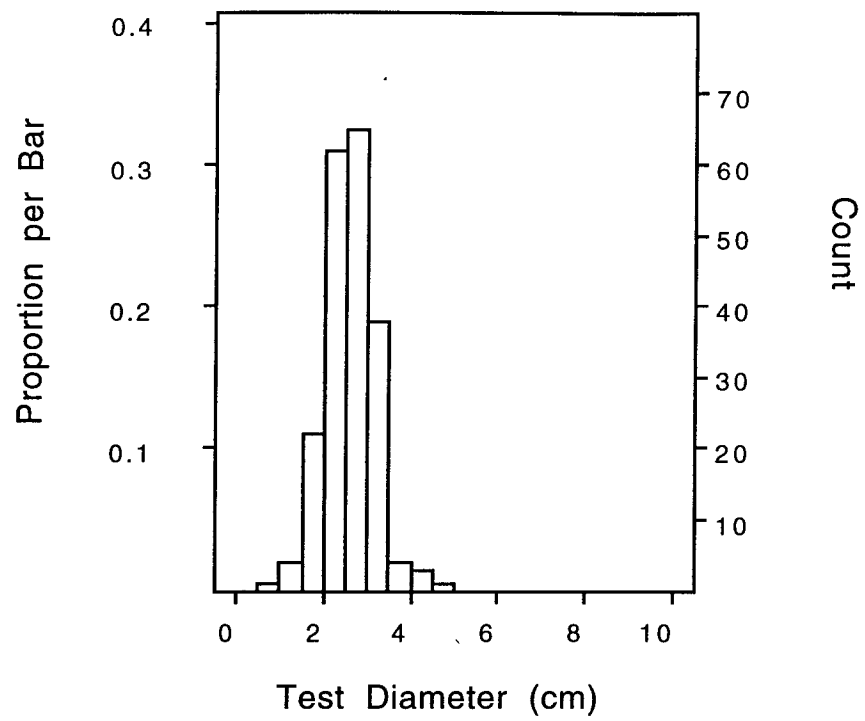
Figure 1.   Number and proportion of sea urchin test diameters (cm) collected from Bath Island in 1992.
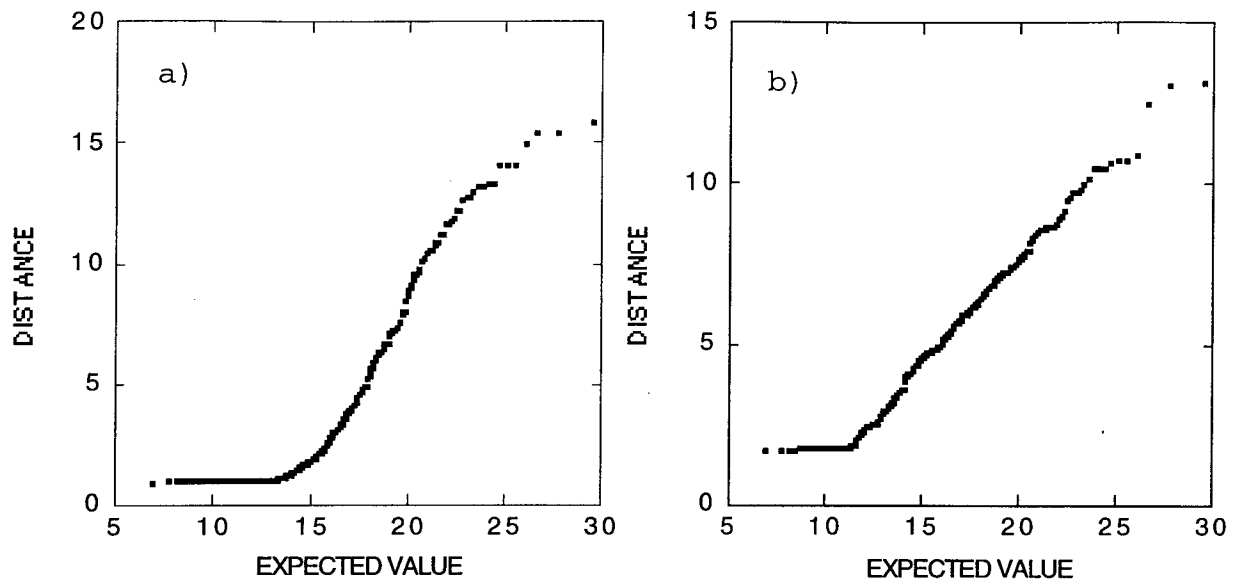
Figure 2. Q-Q probability plots of a) raw species abundances
and b) log-transformed species abundances.Distance measure is
Mahalanobis distance from group centroid, expected value
based on Chi-squared distribution (32 degrees of freedom).

The PCA of the first log-transformed data subset (all quadrats, species occurring more than 15 times) yielded 66 component axes, the most important of which accounted for only 7.6% of the variation in the data set (Table 2). The component loadings from the first three axes resulting from this analysis are included in Table 2, but will not be interpreted further as the following analysis summarizes the main points in a more concise manner.

The PCA of the second log-transformed data subset (quadrats between 3 m above and 6 m below zero tide, species with high component loadings on one of the first three component axes from the first PCA) yielded 27 component axes, the first three accounting for 23.2%, 9.7%, and 8.3% of the variation in the data subset (Table 3). The component loadings on the first axis indicate a number of species with strong, positive correlations, and others with strong negative correlations. Those species with strong positive correlations include *Laurencia spectablis* (0.732), *Plocamium cartilagineum* (0.727), *Prionitis* spp. (0.703), *Iridaea splendens* (0.781), and *Constantinea subulifera* (0.779). Strong negative correlations occur with *Fucus* spp. (-0.405) and *Mastocarpus papillatus* (-0.419) (Table 3).

The second axis also indicates groups of positively and negatively correlating species. Strong positive correlations are found between the second axis and *Gelidium* spp. (0.443),

Table 2. Eigenvalues, percent variance accounted for, and component loadings for the first three axes from the principal components analysis of raw species abundances in all quadrats.

	Axis 1	Axis 2	Axis 3
Eigenvalue	5.044	2.702	2.314
% Variance	7.643	4.094	3.506

Species	Component Loadings		
Laurencia spectablis	0.367	-0.312	-0.116
Herposiphonia plumula	0.750	0.172	0.055
Pterosiphonia dendroidea	0.444	0.188	-0.151
Amplisiphonia pacifica	0.460	0.096	0.164
Ulvaria obscura	0.108	-0.184	0.067
Plocamium cartilagineum	0.694	-0.042	0.288
Corallina officinalis	0.175	-0.490	0.007
Odonthalia floccosa	0.100	0.019	-0.150
Ceramium pacificum	0.371	-0.401	0.081
Constantinea subulifera	0.458	0.045	-0.509
Prionitis spp.	0.309	-0.427	-0.112
Iridaea splendens	0.389	-0.071	-0.369
Antithamnion defectum	0.478	0.233	0.005
Gelidium spp.	0.024	-0.547	0.006
Pterosiphonia gracilis	0.045	0.172	0.042
Ulva spp.	-0.040	-0.138	0.014
Microcladia borealis	-0.006	-0.114	-0.128
Fucus spp.	-0.107	0.096	0.020
Polysiphonia spp.	0.016	0.122	-0.025
Bossiella chiloensis	-0.022	-0.088	0.044
Calliarthron tuberculosum	0.011	0.008	-0.002
Callophyllis flabellulata	0.691	0.091	-0.229
Gymnogrongus leptophyllus	0.016	-0.332	-0.087
Cryptopleura ruprechtiana	0.592	-0.036	-0.005
Polyneura latissima	0.605	0.061	0.517
Platythamnion pectinatum	0.014	0.084	0.061
Sargassum muticum	0.003	-0.586	0.016
Bossiella spp.	0.003	-0.108	-0.003
Mastocarpus papillatus	-0.104	0.084	0.025
Agarum fimbriatum	-0.061	0.070	0.045
Laminaria saccharina	0.113	-0.009	-0.134
Desmarestia viridis	0.205	0.032	-0.216
Bonnemaisonia nootkana	0.004	0.141	0.090

Colonial Diatoms	0.003	-0.045	-0.042
Callophyllis heanophylla	0.056	0.006	-0.090
Nereocystis luetkeana	-0.005	0.034	-0.052
Neorhodomela larix	-0.042	-0.189	-0.073
Branchioglossum bipinnatifidum	0.009	-0.384	0.039
Colpomenia peregrina	-0.025	-0.166	-0.004
Costaria costata	-0.009	0.009	0.030
Rhodoptilum plumosum	-0.038	0.059	0.028
Gigartina exasperata	0.101	-0.482	0.111
Enteromorpha spp.	-0.044	0.033	0.016
Leathesia difformis	-0.026	-0.052	0.011
Rhodymenia pertusa	0.312	0.161	-0.503
Platythamnion villosum	0.143	0.190	-0.041
Rhodoglossum roseum	0.217	-0.015	-0.226
Pugetia fragilissima	-0.057	-0.011	0.031
Lomentaria hakodatensis	-0.027	-0.417	0.041
Ceramium californicum	0.009	0.104	0.094
Laminaria bongardiana	0.249	0.130	-0.395
Hollenbergia subulata	0.027	0.173	0.190
Porphyra spp.	-0.060	0.077	0.024
Sphacelaria spp.	0.014	0.007	0.014
Heterosiphonia densuiscula	-0.025	0.202	0.177
Callophyllis violacea	0.594	-0.050	-0.227
Schizymenia pacifica	0.090	-0.012	-0.073
Nienburgia andersoniana	0.315	0.136	-0.166
Pleonosporium vancouveranium	0.055	-0.025	0.019
Laminaria farlowii	-0.020	-0.341	-0.036
Microcladia coulteri	0.534	0.023	0.559
Fauchea spp.	-0.039	-0.046	0.115
Cryptosiphonia woodii	-0.014	0.016	0.002
Haraldiophyllum mirable	0.540	0.037	0.554
Weeksia coccinea	-0.039	0.057	0.039
Cladophora spp.	-0.023	-0.032	0.028

Table 3. PCA of log-transformed species data. Only
eigenvalues >2 shown.

	Axis 1	Axis 2	Axis 3
Eigenvalue	6.257	2.622	2.230
% Variance	23.174	9.710	8.261
Species	Component Loadings		
Laurencia spectablis	0.732	0.013	-0.031
Plocamium cartilagineum	0.727	0.020	0.121
Odonthalia floccosa	0.587	-0.042	0.222
Corallina officinalis	0.612	0.339	-0.136
Ceramium pacificum	0.587	0.252	0.322
Prionitis spp.	0.703	0.040	0.327
Iridaea splendens	0.781	-0.039	0.261
Constantinea subulifera	0.779	-0.057	0.174
Ulvaria obscura	0.294	-0.112	-0.090
Laminaria spp.	0.442	-0.039	-0.504
Ulva spp.	0.063	0.472	0.275
Fucus spp.	-0.405	0.208	0.553
Gelidium spp.	0.434	0.443	-0.418
Callophyllis spp.	0.674	-0.450	0.197
Calliarthron tuberculosum	0.118	-0.256	-0.179
Cryptopleura ruprechtiana	0.619	-0.387	0.312
Sargassum muticum	0.388	0.726	-0.050
Mastocarpus papillatus	-0.419	0.156	0.458
Desmarestia viridis	0.363	-0.427	0.018
Neorhodomela larix	-0.041	0.287	0.255
Polyneura latissima	0.352	-0.218	0.126
Gigartina exasperata	0.396	0.462	-0.280
Lomentaria hakodatensis	0.239	0.557	-0.110
Porphyra spp.	-0.176	0.048	0.269
Agarum fimbriatum	0.009	0.000	-0.241
Costaria costata	0.221	-0.070	-0.482
Nereocystis luetkeana	0.228	-0.382	-0.325

Ulva spp.(0.472), *Sargassum muticum* (0.726), *Gigartina exasperata* (0.462), and *Lomentaria hakodatensis* (0.557), while strong negative correlations are found with *Nereocystis luetkeana* (-0.382) and *Cryptopleura ruprechtiana* (-0.387).

Axis 3 shows a positive correlation with *Ceramium pacificum* (0.322), *Prionitis* spp. (0.327), *Fucus* spp. (0.553), *Cryptopleura ruprechtiana* (0.312), and *Mastocarpus papillatus* (0.458). A negative correlation exists with *Laminaria* spp. (-0.504), *Gelidium* spp. (-0.418), *Costaria costata* (-0.482), and *Nereocystis luetkeana* (-0.325).

Figures 3 and 4 show the relationship between quadrat depth and quadrat scores on the first and second component axes. Low scoring quadrats on the first axis apparently occur above 0 tide level to 3 m, intertidally (Fig. 3), corresponding to the *Fucus* spp. and *M. papillatus* association. The first axis therefore seems to separate intertidal quadrats from subtidal ones. On the second axis (Fig. 4), both high scoring and low scoring quadrats are present deeper than 0 tide level. However, virtually all of the high scoring sites were sampled in 1992, while the low scoring sites appear to have been sampled exclusively during the 1970's. Above 0 tide level to 3 m, high scores are present for quadrats sampled from both time periods, indicating that a second intertidal macrophyte association is present. The second axis seems to describe both an *Ulva* spp. dominated intertidal association and a 1992 subtidal
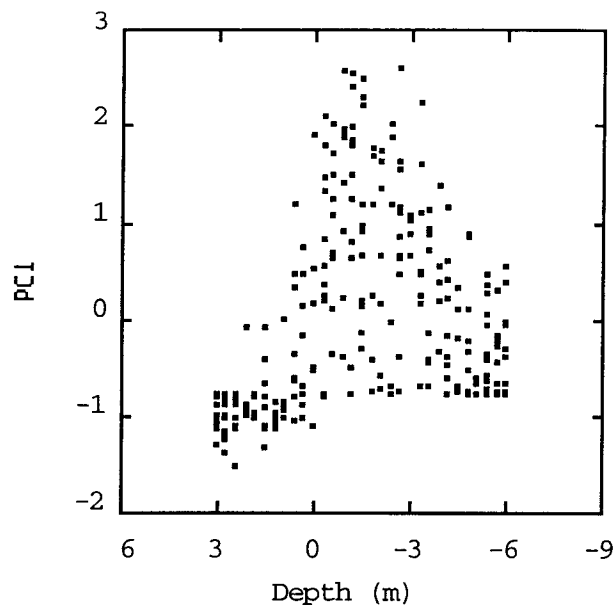
Figure 3. Quadrat scores on the first principal axis from the PCA of log-transformed species abundances vs. quadrat depth (m). Negative values for depth indicate depth below zero tide level.
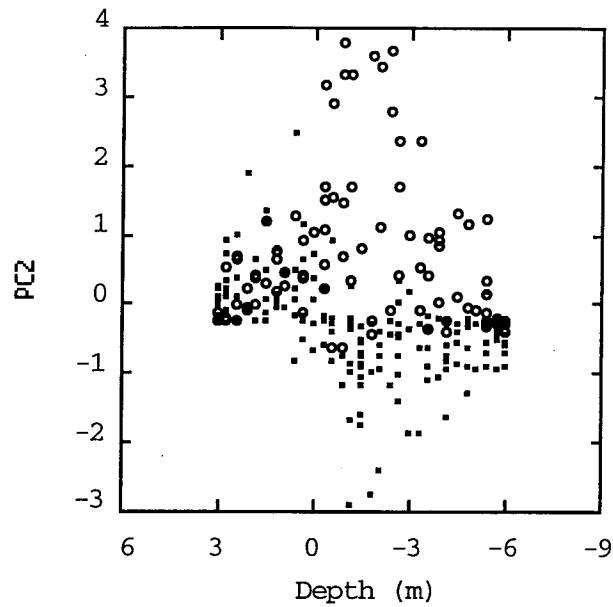
Figure 4. Quadrat scores on the second principal axis from
the PCA of log-transformed species abundances vs. quadrat
depth (m); quadrats sampled in 1992 (○) and during the 1970's
(·). Negative values for depth indicate depth below zero
tide level.

association at the positive end, and a 1970's subtidal association at the negative end.

Figures 5a through 5i show the quadrat scores for each site/year on the first two component axes, with 95% confidence intervals indicated by the ellipses. Table 4 summarizes the changes in area (A), angle of orientation (θ), and eccentricity (ecc) of the ellipses that are apparent by visual inspection of Figures 5a through 5i. At Bath Island, a decrease in area and an increase in eccentricity from 1972 to 1973 corresponds to the year the urchins arrived at the site (Figs. 5a, 5b; Table 4). The decrease in area seems to result from a decrease in quadrat scores at the positive end of axis 1, and from a decrease at the negative end of axis 2. From 1973 through 1975, the area is increasing, apparently due to the decreasing eccentricity values which indicate lower correlations among species. In 1992, Bath Island has similar area and eccentricity to 1974 and 1975, but differs greatly in angle of orientation (Figs. 5b through 5e; Table 4). The Sear Island site/years tend to have similar angles of orientation to the corresponding Bath Island site/years, but have much greater values for their area and eccentricity. The low angles of orientation of the two 1992 site/years are dramatically different from those of the 1970's, suggesting that the 1992 site/years are similar to each other in terms of their species compositions. However, in terms of area (within site/year variation) and eccentricity (the extent to which species associations are correlated), the 1992

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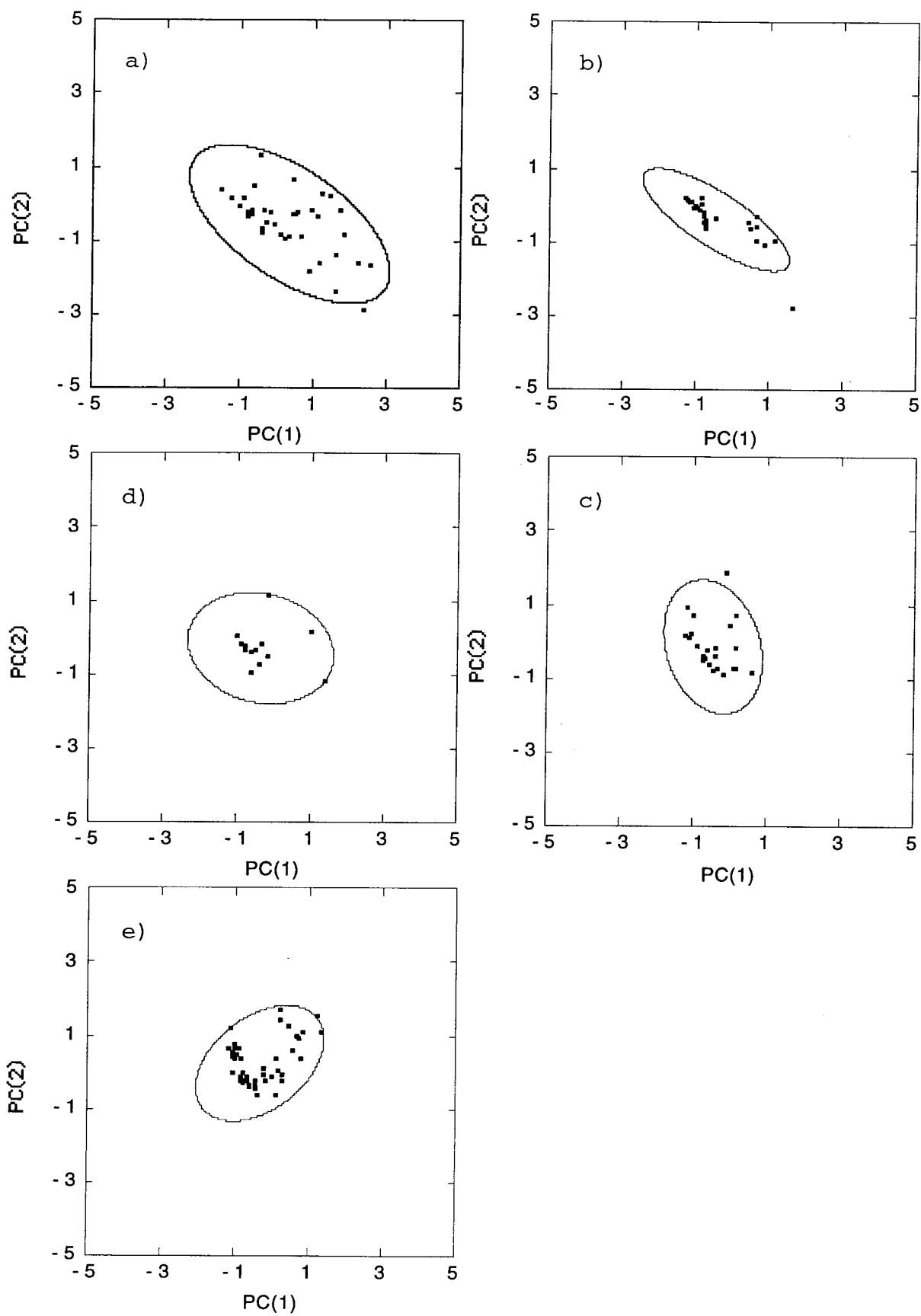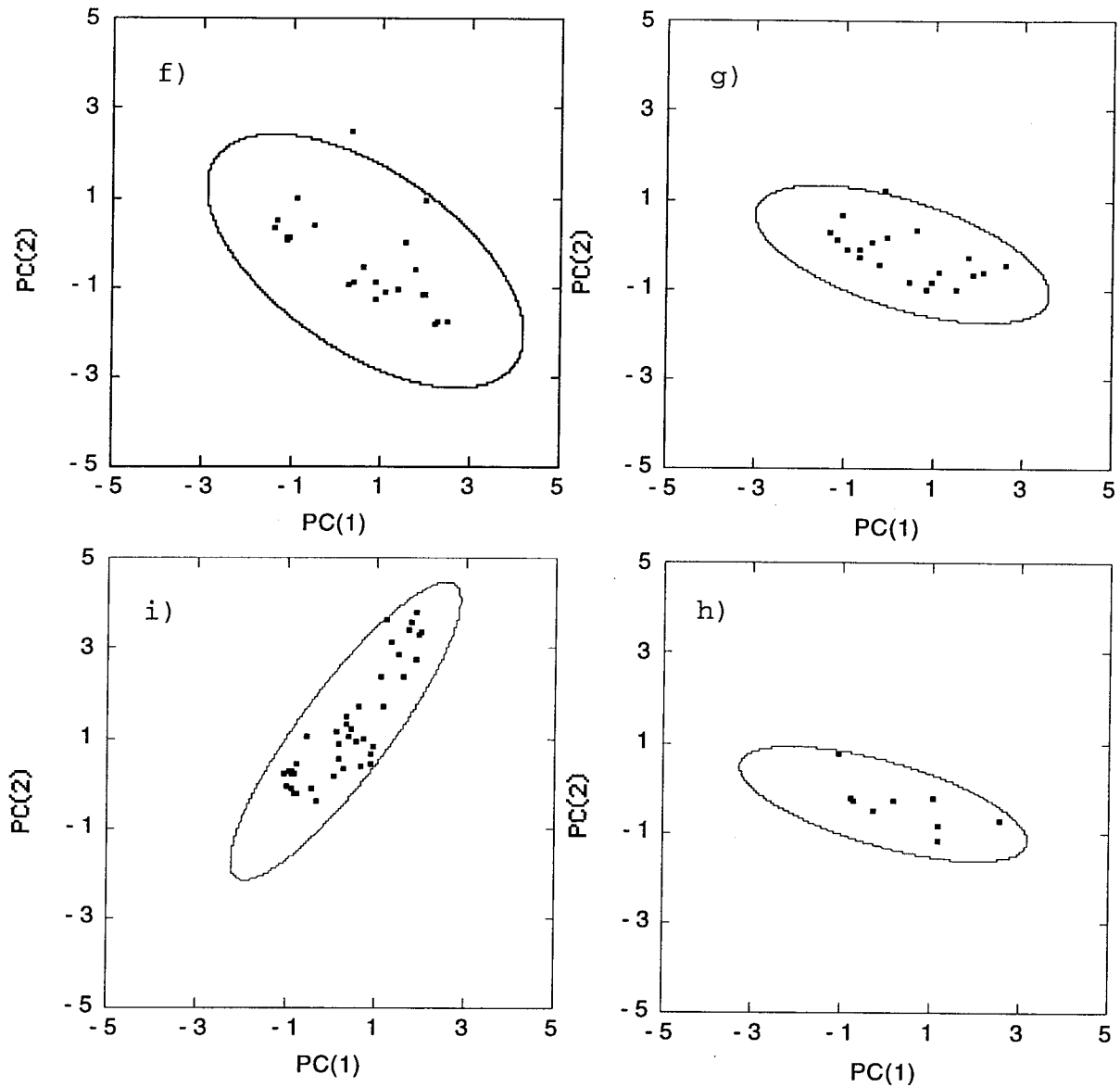
Figure 5. Quadrat scores on second principal axis vs. scores
on first principal axis from the PCA of log-transformed
species abundances (all quadrats between 3 m above and 6 m
below zero tide). Ellipses represent 95% confidence
intervals; a) B72, b) B73, c) B74, d) B75, e) B92, f) S72, g)
S74, h) S75, i) S92.

TABLE 4. Statistics describing the 95% confidence ellipses from PCA of log-transformed data. θ, angle of major axis with x axis; ecc, eccentricity. See text for explanation of descriptive statistics.

Site/Year	ecc	θ	Area
B72	.893	145	565.5
B73	.951	148	205.0
B74	.706	108	320.4
B75	.650	164	373.1
B92	.768	38	314.2
S72	.866	145	1061.9
S74	.932	162	552.9
S75	.958	164	395.8
S92	.973	53	490.1

site/years are more similar to the site/years from their respective islands, particularly in 1974 and 1975, than to each other.

Canonical Variates Analysis

Formal multivariate tests of the equality of site/year community centroids and the dimensionality of canonical space could not be applied based on the failure of the data set to meet the assumption of multinormality. The first three canonical variates were thus chosen for interpretation based only on the strength of the canonical correlations (0.709, 0.680, 0.560; Table 5).

The correlation coefficients between the canonical variates, u_k and v_k, and the variables in the dummy and species variable sets are shown in Table 5. These correlation coefficients will be used for interpretation of the canonical variates.

Species that show a relatively strong positive correlation with v_1 include *Ulvaria obscura* (0.357), *Callophyllis* spp.(0.563), *Cryptopleura ruprechtiana* (0.538), *Desmarestia viridis* (0.311), *Polyneura latissima* (0.330), and *Nereocystis luetkeana* (0.414). Those species showing relatively strong negative correlations with v_1 are *Sargassum muticum* (-0.419), *Corallina officinalis* (-0.284), *Gelidium* spp. (-0.329), *Ulva* spp. (-0.432), and *Gigartina exasperata* (-0.276). This variate extracts 7.56% of the

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TABLE 5. Canonical correlation coefficients, redundancies, % variance extracted, and canonical loadings from the CVA of log-transformed species abundances.

Correlation Coefficient	0.709	0.680	0.560
Canonical Variate	v1	v2	v3
Species	Canonical Loadings		
Laurencia spectablis	-0.009	0.289	0.038
Plocamium cartilagineum	0.108	0.427	0.012
Odonthalia floccosa	0.053	0.146	-0.225
Corallina officinalis	-0.284	0.510	0.134
Ceramium pacificum	-0.002	0.171	0.122
Prionitis spp.	0.096	0.309	0.127
Iridaea splendens	0.224	0.363	0.124
Constantinea subulifera	0.184	0.476	0.059
Ulvaria obscura	0.357	-0.258	0.348
Laminaria spp.	0.070	0.481	-0.032
Ulva spp.	-0.432	0.068	0.194
Fucus spp.	0.104	-0.096	0.021
Gelidium spp.	-0.329	0.577	0.170
Callophyllis spp.	0.563	0.338	0.065
Calliarthron tuberculosum	-0.090	-0.275	-0.200
Cryptopleura ruprechtiana	0.538	0.254	0.119
Sargassum muticum	-0.419	0.319	0.130
Mastocarpus papillatus	0.183	0.080	0.074
Desmarestia viridis	0.311	0.230	-0.472
Neorhodomela larix	-0.177	-0.011	-0.104
Polyneura latissima	0.330	0.161	0.095
Gigartina exasperata	-0.276	0.396	0.453
Lomentaria hakodatensis	-0.272	0.326	0.281
Porphyra spp.	0.153	-0.126	0.106
Agarum fimbriatum	-0.079	0.208	0.038
Costaria costata	0.046	0.267	-0.254
Nereocystis luetkeana	0.414	0.217	-0.268
% Variance	7.560	9.470	3.940
Redundancy	3.800	4.380	1.240

Canonical Variate	u1	u2	u3
		Canonical Loadings	
B73	-0.073	0.278	-0.215
B74	-0.101	0.571	0.261
B75	-0.066	0.137	-0.082
B92	0.454	0.379	-0.160
S72	-0.477	-0.436	0.182
S74	-0.337	0.012	0.615
S75	-0.128	-0.029	0.060
S92	0.697	-0.562	0.265
% Variance	13.400	13.400	7.900
Redundancy	6.720	6.200	2.480

variance in the species data set and 3.8% of the variation in the site/year data (Table 5). The site/year communities that correlate with u_1 are B92 (0.454) and S92 (0.697) in a positive manner, and S72 (-0.477) and S74 (-0.337) in a strong negative manner. The u_1 variate extracts 13.4% of the variation in the site/year data, and accounts for 6.72% of the variation in the species data (Table 5). The relationship between v_1 and u_1 is shown graphically in Figure 6a. From this it can be seen that the high scores of S92 and B92 on u_1 correspond to their low scores on v_1. The site/years S92 and B92 differ from the rest of the site/year communities due to a high proportion of *S. muticum, C. officinalis, Gelidium* spp., *Ulva* spp., and *G. exasperata*.

The v_2 variate correlates positively with species such as *Constantinea subulifera* (0.476), *Laminaria* spp. (0.481), *Gelidium* spp. (0.577), *Plocamium cartilagineum* (0.427), and *Corallina officinalis* (0.510). Negatively correlated species include *Ulvaria obscura* (-0.258) and *Calliarthron tuberculosum* (-0.275) (Table 5). The second variate extracts 9.47% of the variance in the species data. The u_2 variate correlates positively with B73, B74, B75 and B92 and negatively with S72, S75, and S92. Figure 6b shows that the sites correlating positively with u_2 have low scores on v_2, corresponding to higher amounts of *U. obscura* and *C. tuberculosum*, while the other site/years have greater amounts of *C. subulifera, Laminaria* spp., *Gelidium* spp., *P. cartilagineum*, and *C. officinalis*.

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a)

b)

c)
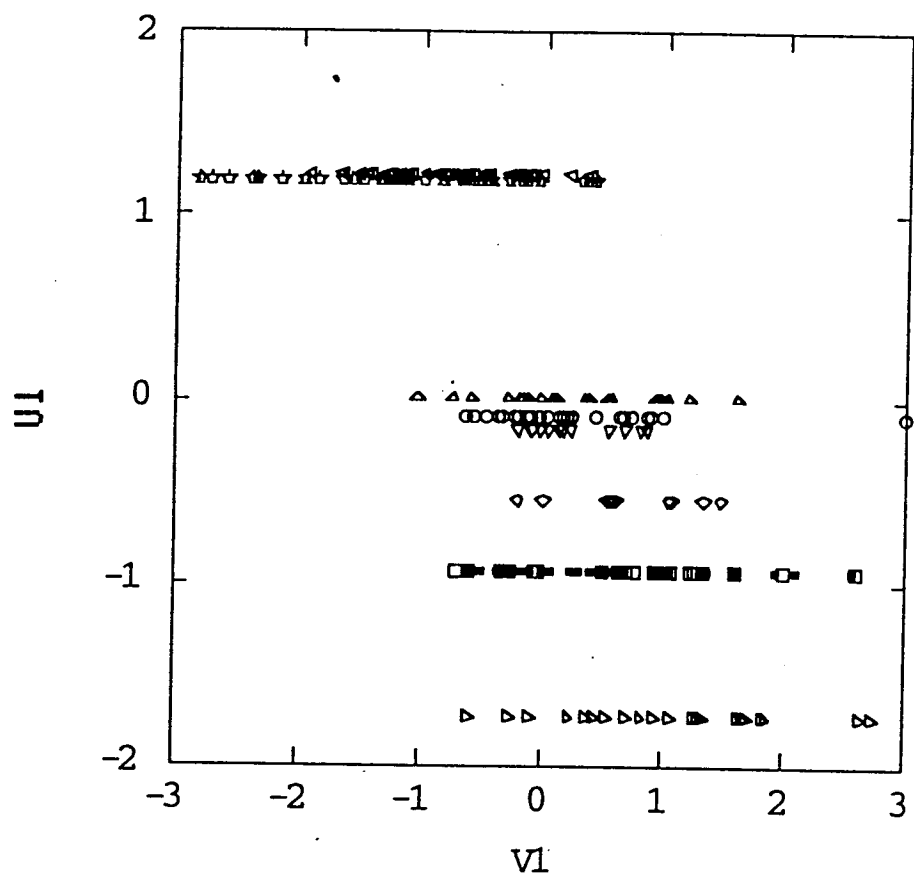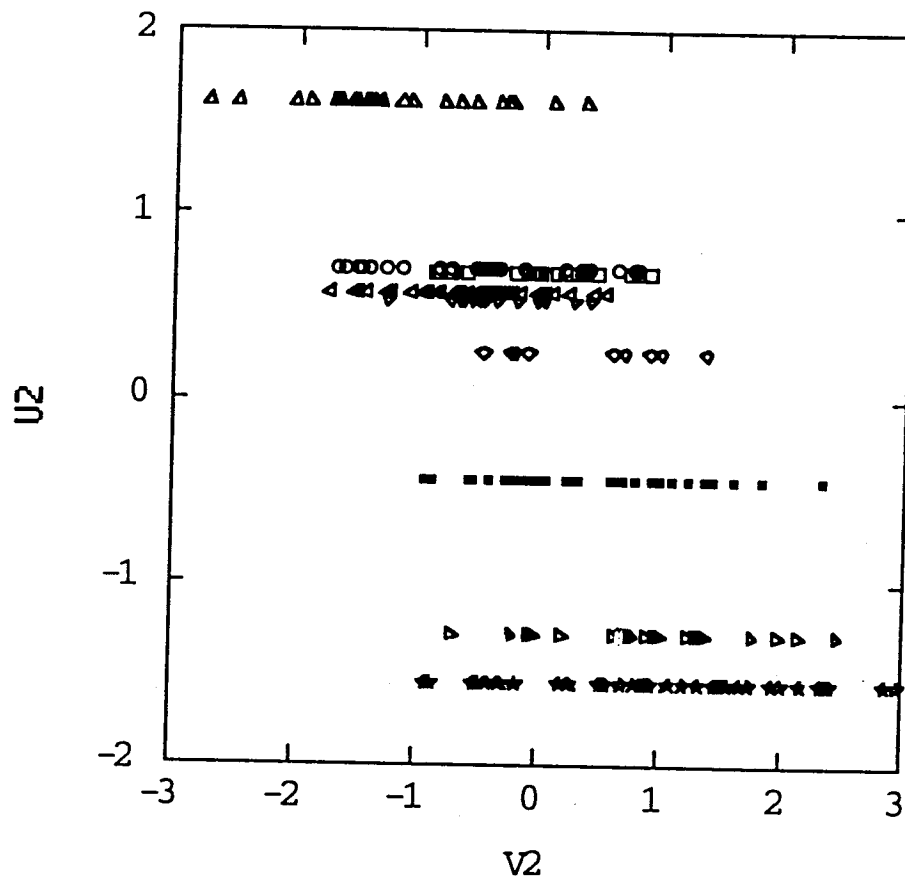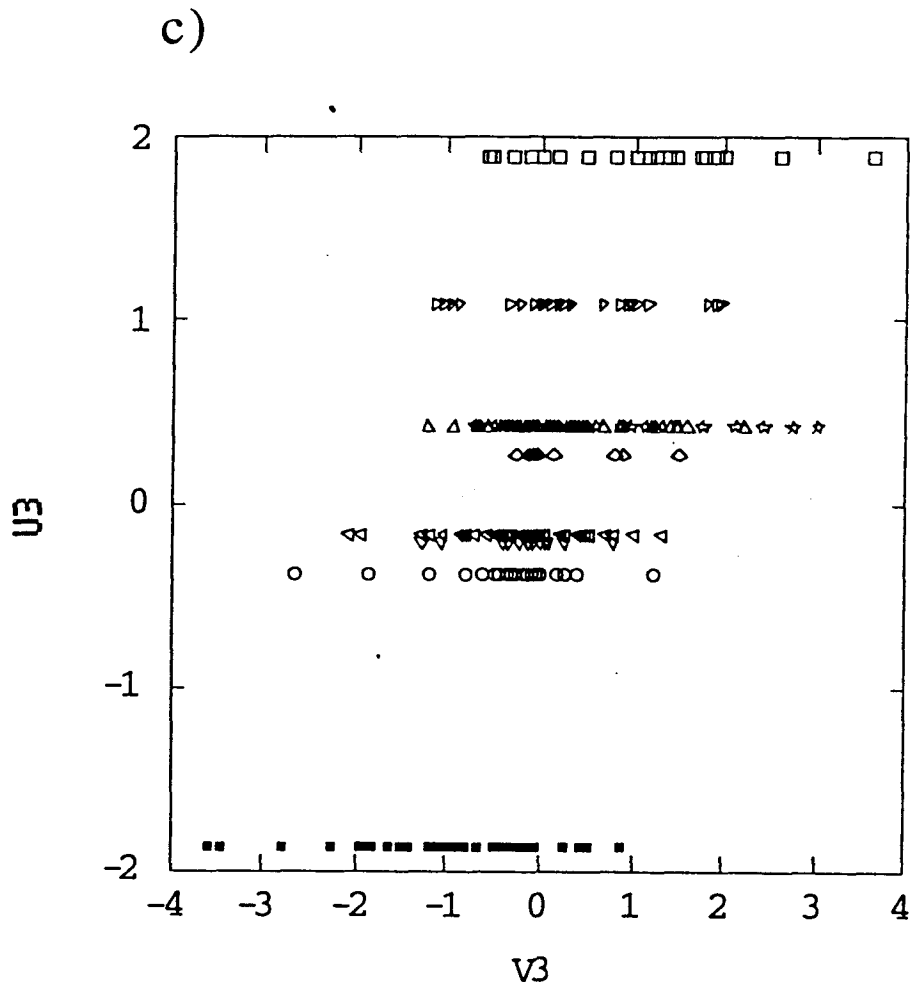
Figure 6. Quadrat scores on v_i and u_i axes from the CVA of
log-transformed species abundances; a) u_1 vs. v_1, b) u_2 vs.
v_2, c) u_3 vs. v_3 (· B72, ○ B73, ▴ B74, ▾ B75, ◂ B92, ▸ S72,
□ S74, ◇ S75, ✦ S92).

Species correlating with the third variate, v_3, are

Ulvaria obscura (0.348) and *Gigartina exasperata* (0.453)

positively, and *Odonthalia floccosa* (-0.225), *Calliarthron*

tuberculosum (-0.200), *Desmarestia viridis* (-0.472), *Costaria*

costata (-0.254), and *Nereocystis luetkeana* (-0.268)

negatively. The v_3 variate extracts 3.94% of the variance in

the species data (Table 5). Figure 6c indicates that the low

scoring sites on u_3 have lower scores on v_3, corresponding to

greater amounts of *O. floccosa, C. tuberculosum, D. viridis,*

C. costata, and *N. luetkeana.*

Figure 7a represents a three dimensional scatter plot of the

quadrats on the u_i axes. Since the u_i scores of the quadrats from

a particular site/year are identical, the quadrats from each

site/year appear as a single point on the graph. Further, the u_i

scores of the quadrats from a particular site/year are correlated

to their scores on the corresponding v_i axis, so site/years with

similar species compositions should have similar locations on the

u_i axes, and thus cluster together in Figure 7a. Figures 7b and

7c are two dimensional representations of Figure 7a, to aid in

visualization of the three dimensions. The site/years B73 and B75

appear close on all three axes, with B92 different from them only

on u_1. Site/year B74 is somewhat similar but differs on u_2. The

site/years S74 and S75 appear to be similar to each other, with

most of their separation occurring on u_3. The other site/years

seem to be unique, sharing similar scores with other site/years on

only one axis. For example, B92 and S92 share a high

40
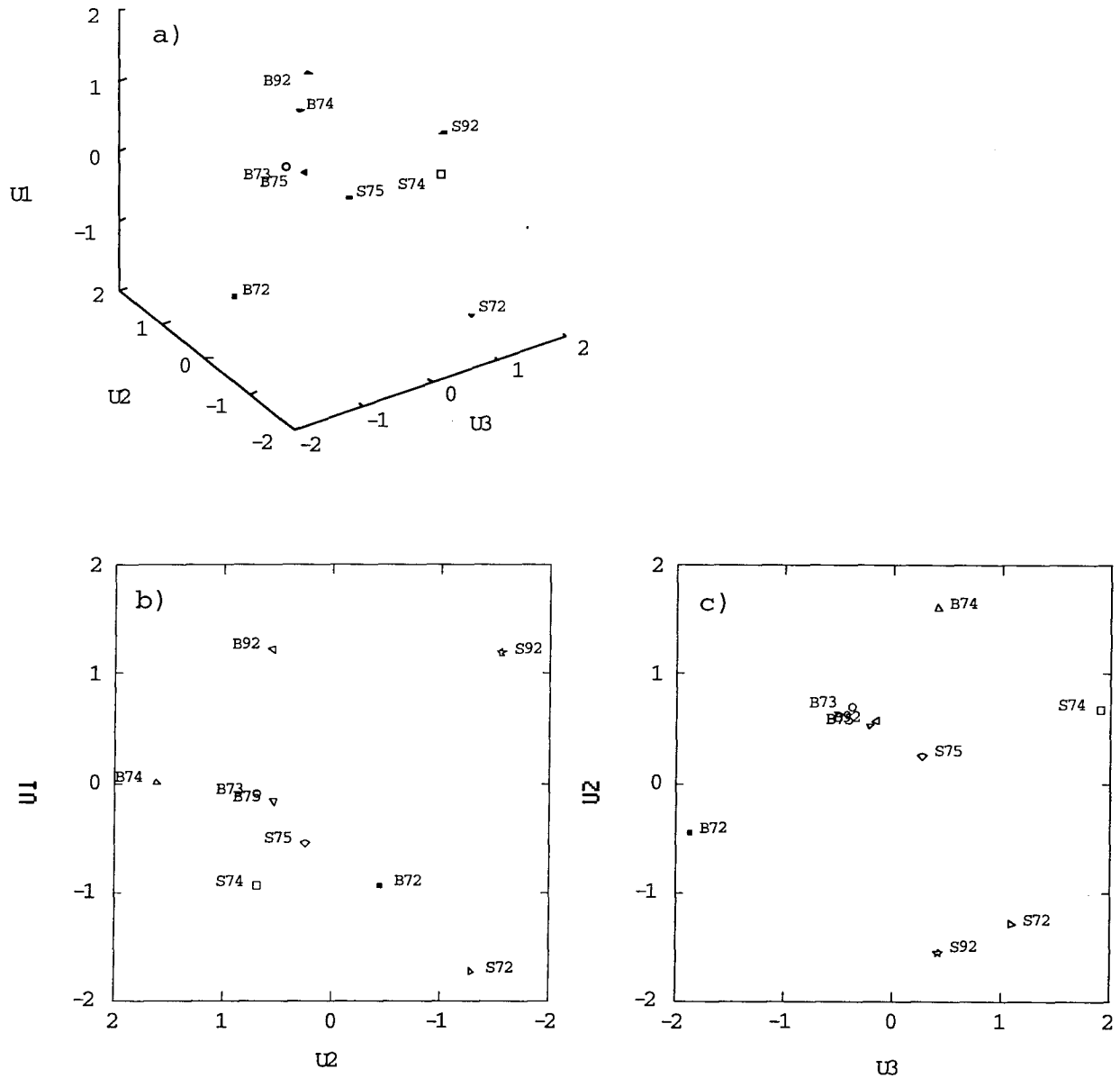
Figure 7. Scatter plots of quadrat scores on u_1, u_2 and u_3 from the CVA of log-transformed species data; a) three dimensional plot, b) u_1 vs u_2, c) u_2 vs u_3. b) and c) represent two dimensional views of a) along the u_3 axis and u_1 axis respectively (• B72, ○ B73, ▵ B74, ▿ B75, ⁊ B92, ▹ S72, □ S74, ◇ S75, ⋇ S92).

separation from the other sites along the first axis, but are very different on u_2 and u_3.

Canonical Correlations Analysis

This analysis correlates the same data sets as the CVA, but includes depth as an additional variable to the dummy variable set. The first three canonical correlations are shown in Table 6. The canonical loadings on the v_i variate from the strongest correlation (0.784), indicate that *Fucus* spp. (0.737), *Mastocarpus papillatus* (0.607), *Porphyra* spp.(0.315), and *Neorhodomela larix* (0.232) are strong positive contributors to that correlation, and *Laminaria* spp. (-0.525), *Gelidium* spp.(-0.476), *Agarum fimbriatum* (-0.461), and *Corallina officinalis* (-0.399), among others, are strong negative contributors. Figure 8 shows the strong effect that depth has on the quadrat scores, with shallow quadrats scoring much higher on v_1 (corresponding to the intertidal species *Fucus* spp., *M. papillatus*, *Porphyra* spp., and *N. larix*) than the deep quadrats. Figure 9a shows that most of the separation between quadrats on u_1 is due to depth, while very little separation between site/years is present.

The canonical loadings (Table 6) on v_2 show that *Callophyllis* spp.(0.649), *Cryptopleura ruprechtiana* (0.593), *Desmarestia viridis* (0.389), *Polyneura latissima* (0.373), and *Nereocystis luetkeana* (0.508) are

TABLE 6. Canonical correlation coefficients, redundancies, % variance extracted, and canonical loadings from the CCO of log-transformed species abundances.

Correlation Coefficient	.784	.704	.655
Canonical Variate	v1	v2	v3

Species		Canonical Loadings	
Laurencia spectablis	-0.324	0.133	0.136
Plocamium cartilagineum	-0.201	0.257	0.310
Odonthalia floccosa	-0.011	0.093	0.121
Corallina officinalis	-0.399	-0.068	0.447
Ceramium pacificum	0.010	0.039	0.194
Prionitis spp.	0.014	0.168	0.321
Iridaea splendens	-0.078	0.330	0.261
Constantinea subulifera	-0.190	0.342	0.339
Ulvaria obscura	0.107	0.263	-0.345
Laminaria spp.	-0.525	0.307	0.171
Ulva spp.	0.141	-0.446	0.359
Fucus spp.	0.737	-0.082	0.297
Gelidium spp.	-0.476	-0.078	0.485
Callophyllis spp.	-0.040	0.649	0.134
Calliarthron tuberculosum	-0.139	-0.130	-0.335
Cryptopleura ruprechtiana	0.024	0.593	0.072
Sargassum muticum	-0.183	-0.295	0.407
Mastocarpus papillatus	0.607	0.067	0.384
Desmarestia viridis	-0.093	0.389	0.054
Neorhodomela larix	0.232	-0.230	0.203
Polyneura latissima	-0.033	0.373	0.031
Gigartina exasperata	-0.354	-0.097	0.340
Lomentaria hakodatensis	-0.171	-0.152	0.373
Porphyra spp.	0.315	0.050	-0.004
Agarum fimbriatum	-0.461	0.077	-0.027
Costaria costata	-0.333	0.187	0.066
Nereocystis luetkeana	-0.208	0.508	-0.044
% Variance	9.370	8.470	7.440
Redundancy	5.760	4.200	3.190

Canonical Variate	u1	u2	u3
		Canonical Loadings	
B73	0.161	0.032	0.242
B74	0.227	0.095	0.518
B75	-0.036	-0.044	0.220
B92	0.109	0.576	0.133
S72	0.114	-0.549	-0.398
S74	0.115	-0.305	0.072
S75	-0.050	-0.151	0.076
S92	-0.451	0.449	-0.619
Depth	-0.866	-0.209	0.356
% Variance	11.920	11.180	11.910
Redundancy	7.320	5.540	5.110

Figure 8. Quadrat scores on v_1 from the canonical
correlations analysis of log-transformed species abundances,
site/year dummy variables and depth vs. quadrat depth (m).
Negative values for depth indicate depths below zero tide
level.

positively correlated, whereas *Sargassum muticum* (-0.249), *Calliarthron tuberculosum* (-0.130), *Ulva* spp. (-0.446), and *Neorhodomela larix* (-0.230) are negatively correlated. Figure 9b shows that B92 and S92 score higher than the other site/years on u_2. The relationship between v_2 and u_2 (Figs. 10a, 10b) indicates that low scores on v_2 account for the high scores of B92 and S92 on u_2. The separation of B92 and S92 from the other sites is apparently due to higher abundances of *S. muticum*, *C. tuberculosum*, *Ulva* spp., and *N. larix*.

The relationships between v_3 and *Constantinea subulifera* (0.339), *Gelidium* spp. (0.485), *Plocamium cartilagineum* (0.310), and *Corallina officinalis* (0.447) are among the many that are strong and positive, whereas negatively correlated species include *Ulvaria obscura* (-0.345), and *Calliarthron tuberculosum* (-0.335) (Table 6). The scores on u_3 indicate a separation between low scoring site/years such as S92, S72 and B72 (none of which were grazed by sea urchins), and higher scoring site/years such as B92, B73 and B74 (all of which were grazed by sea urchins) (Fig. 9c). Figure 11a and 11b indicate that the low scores of S92, S72, and B72 on u_3 are mainly accounted for by high scores on v_3, or high abundances of such species as *C. subulifera*, *Gelidium* spp., *P. cartilagineum*, and *C. officinalis*. The high scoring site/years on u_3 likewise appear to have more *U. obscura* and *C. tuberculosum*. These site/year groupings are similar to those that were indicated by the second canonical correlation

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of the CVA analysis.

a)

b)

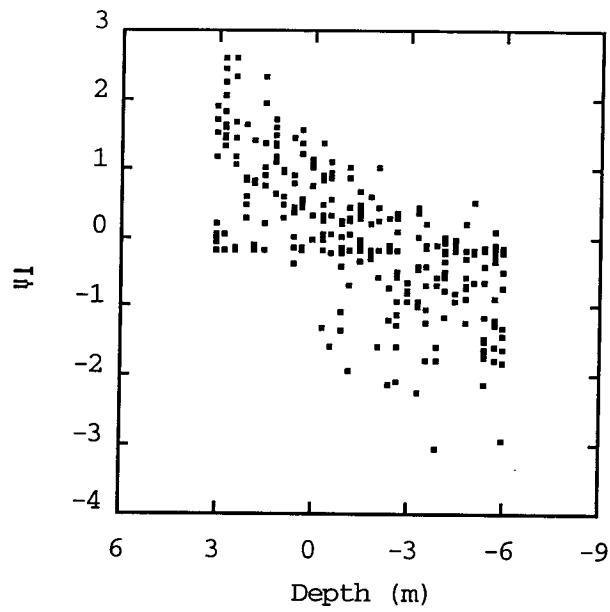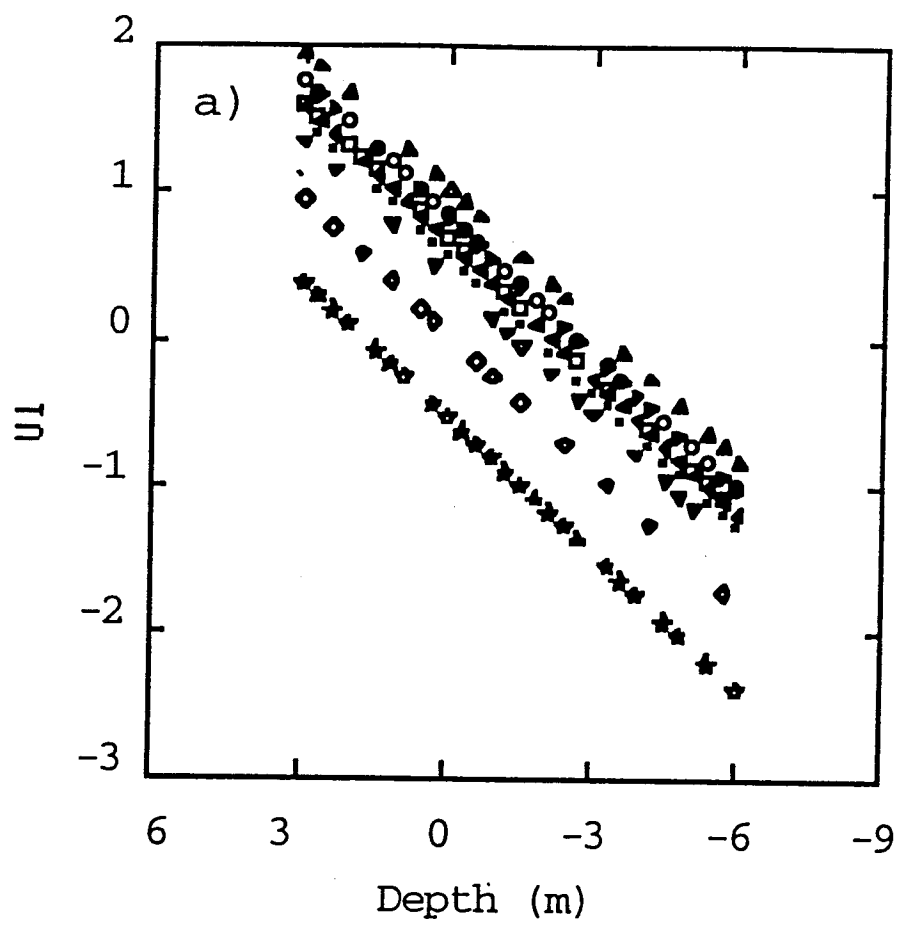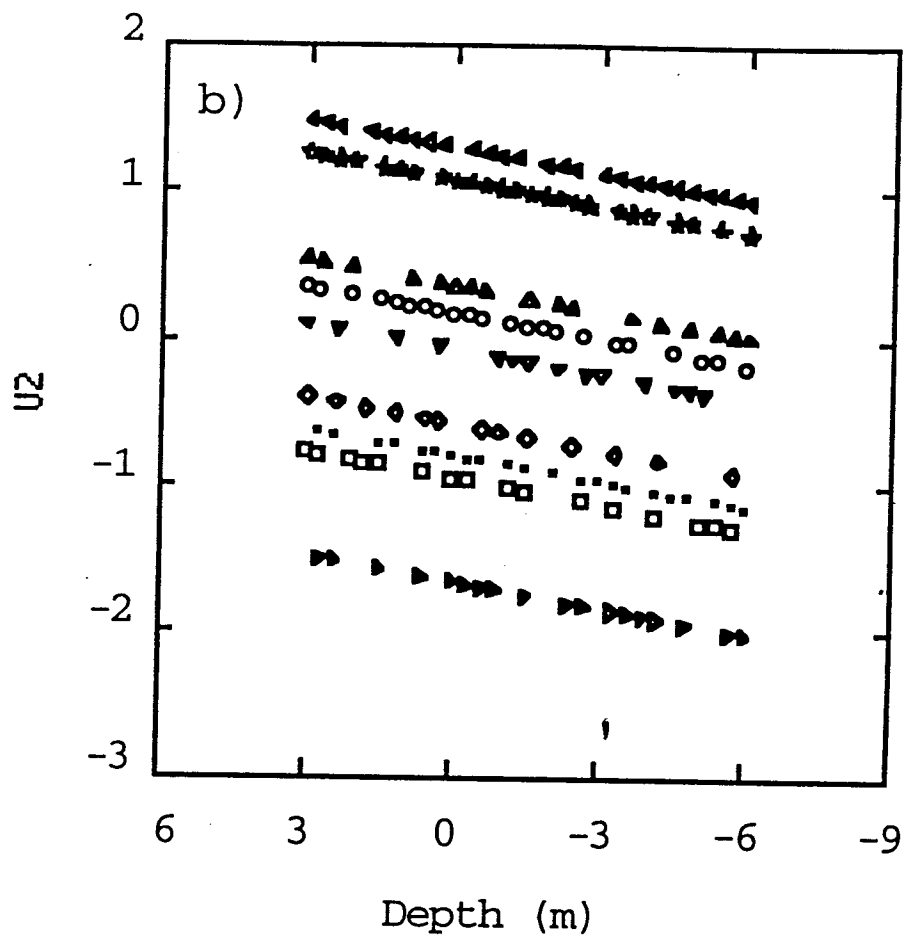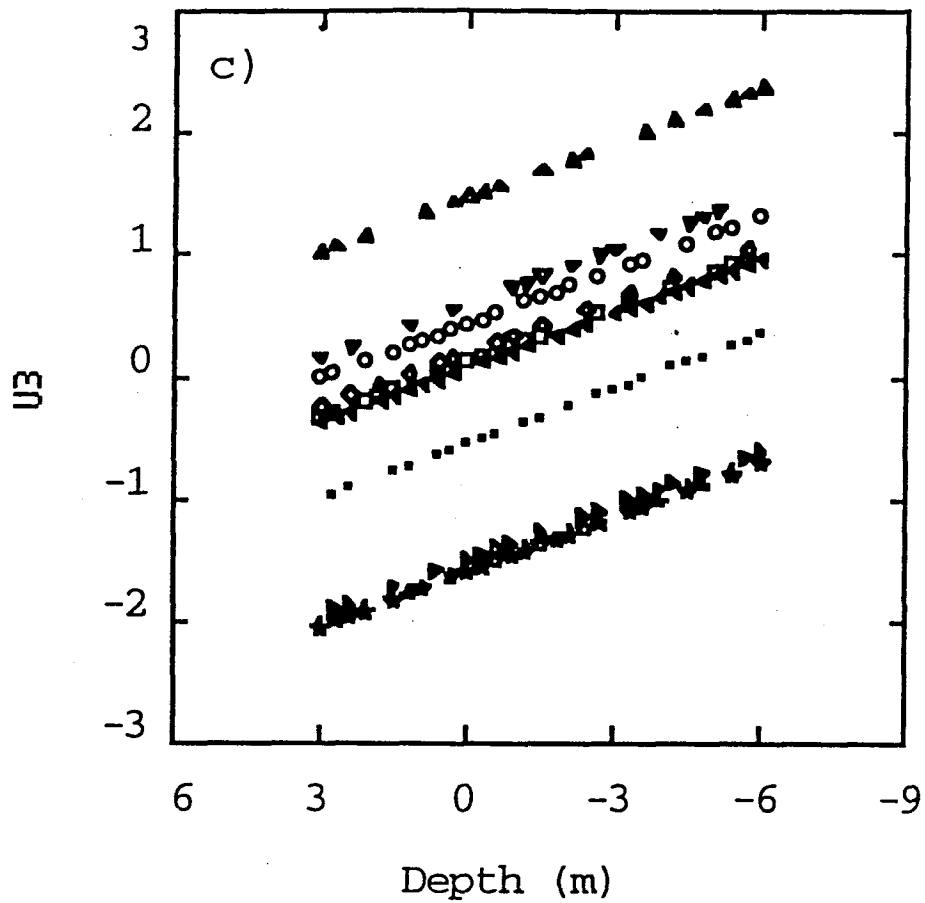Figure 9. Quadrat scores on u_i from the canonical
correlations analysis of log-transformed species abundances,
site/year dummy variables and depth vs. quadrat depth (m); a)
u_1 from first correlation, b) u_2 from second correlation, c)
u_3 from third correlation (· B72, ∘ B73, ▲ B74, ▼ B75, ◀ B92,
▶ S72, ▫ S74, ● S75, ✦ S92). Negative values for depth
indicate depth below zero tide level.

a)
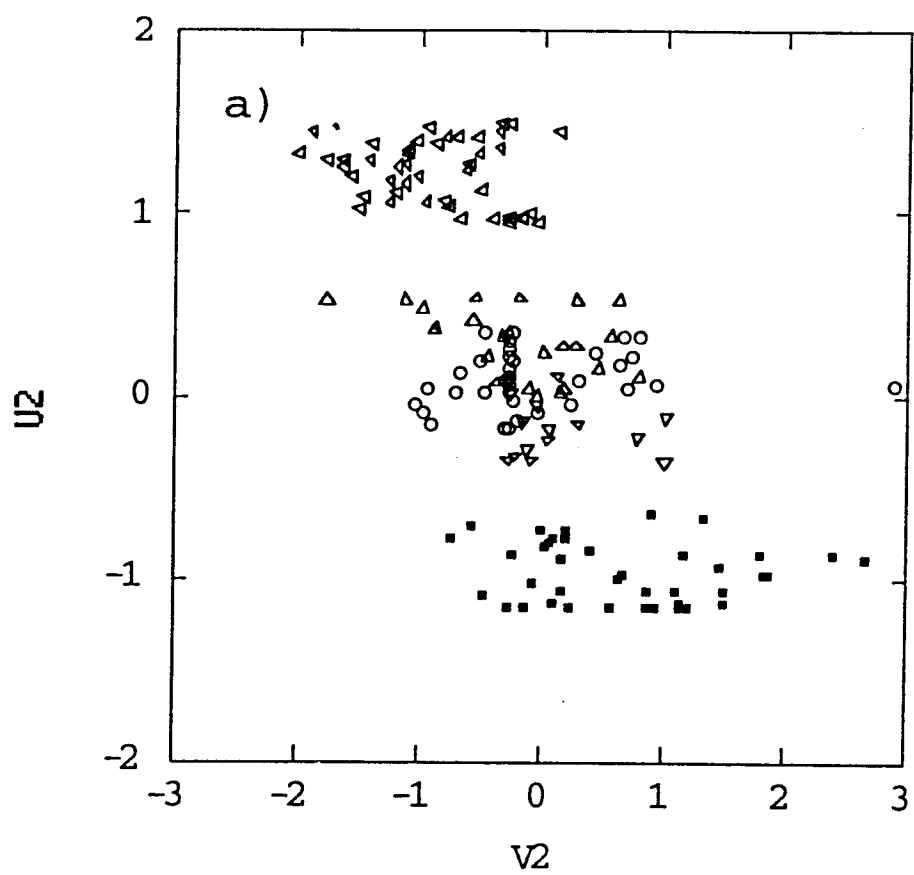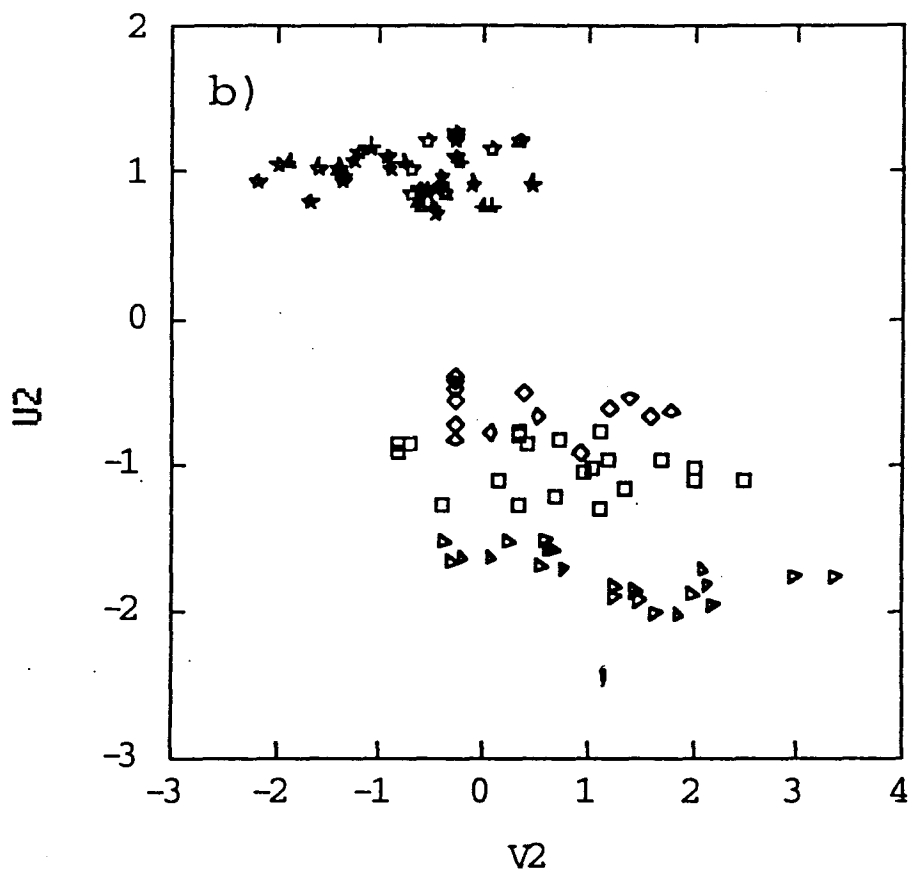
Figure 10. Quadrat scores on u_2 and v_2 from the canonical
correlations analysis of the log-transformed species
abundances, site/year dummy variables and depth. Bath Island
quadrats (a) and Sear Island quadrats (b) are shown on
separate graphs to minimize distortion caused by overlapping
points (• B72, ○ B73, ▲ B74, ▽ B75, ◁ B92, ▸ S72, □ S74,
○ S75, ✶ S92).

a)
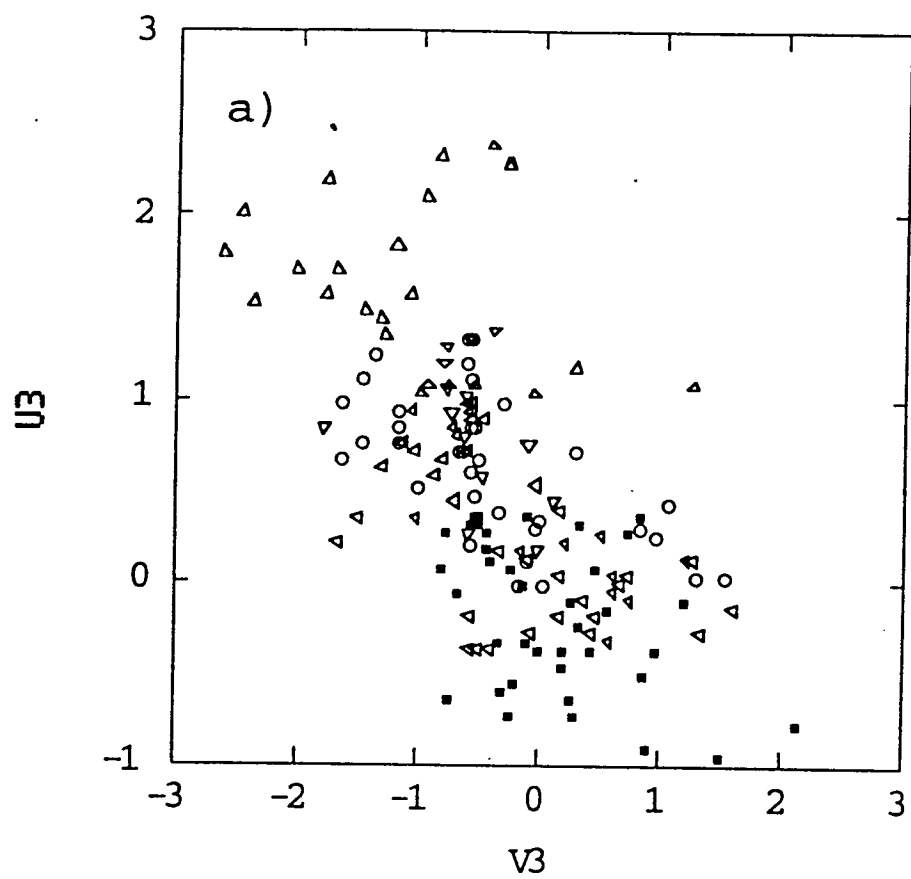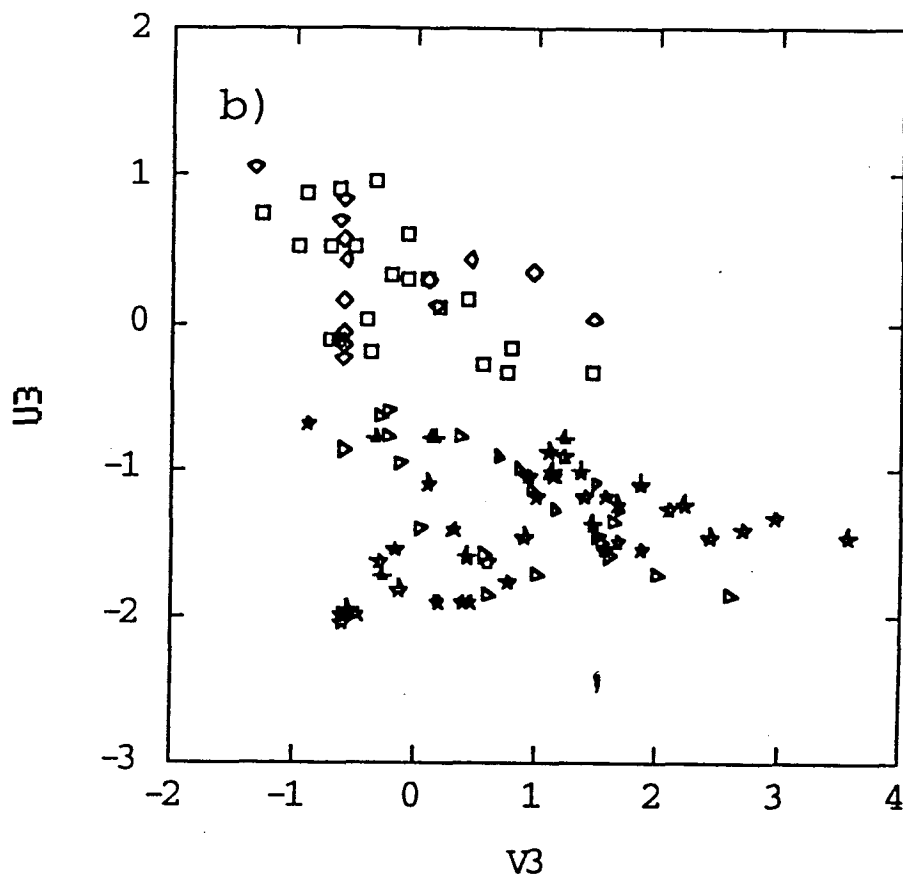
Figure 11. Quadrat scores on u_3 and v_3 from the canonical correlations analysis of the log-transformed species abundances, site/year dummy variables and depth. Bath Island quadrats (a) and Sear Island quadrats (b) are shown on separate graphs to minimize distortion caused by overlapping points (• B72, ○ B73, ▲ B74, ▼ B75, ◄ B92, ► S72, □ S74, ◇ S75, ✦ S92).

DISCUSSION

The objectives of this study have been to show changes
in macrophyte community structure 1) along the depth
gradient, 2) in response to grazing, 3) after removal of
grazing pressure, and 4) over the long term from the 1970's
to 1992. Although formal tests of hypotheses were not
possible based on the failure of the data to meet the
assumption of multinormality, much information regarding
community change has been learned from the analyses. For
each objective, various aspects of the analyses combine to
identify macrophyte associations which are indicative of
community change.

Community Change Along the Depth Gradient

The PCA and CCO included the effects of depth on the
species associations, and in both analyses, the first axes
revealed a separation between intertidal and subtidal
associations. In fact, the component loadings on the first
principal component axis and the v_1 axis from the CCO are
highly similar, (the sign of the correlation is arbitrary)
showing the same trends for virtually all of the species.
The species identified with the intertidal association are
Fucus spp., *Mastocarpus papillatus*, *Neorhodomela larix*, and
Porphyra spp. *Ulva* spp. may also be associated with these
species, as it has a somewhat similar loading on the v_1 axis

from the CCO. Further, *Ulva* spp. appears to correlate with the second principal component analysis in a similar manner as *N. larix*, and based on the relationship between depth and the second principal component axis, *Ulva* spp. is probably contributing to the high scores of the intertidal quadrats on this axis. *Fucus* spp., *M. papillatus*, and *N. larix* were previously identified as characteristic species of an intertidal algal community at the same sites (Lindstrom and Foreman 1978), using a species-quadrat coincidence table based on the 1972 data only.

The other species on the first axes of the PCA and CCO seem to comprise a widely distributed subtidal association of foliose red algae and kelp species. Most of these species were included as characteristic species of either the foliose red algal community (i.e. *Plocamium cartilagineum*, *Constantinea subulifera*, *Prionitis* spp.) or the kelp community (i.e. *Laurencia spectablis*, *Corallina officinalis*, *Laminaria* spp., *Costaria costata*) described by Lindstrom and Foreman (1978). Although there was no separation along the depth gradient evident between these communities on the first axes, the third axis of the PCA may indicate a separation between quadrats in the foliose red algal community and the kelp community, which would be more consistent with the findings of Lindstrom and Foreman (1978).

The subtidal association evident from the first axes of the PCA and CCO analyses also yielded information on the effects of grazing on community structure. The kelp/foliose red association was apparently that which was most strongly impacted by the grazing activity of the urchins. The low scores of the Bath Island site (Figs. 5a through 5e) at the positive end of the first principal component axis in.1973 and 1992, years in which urchins were present at the site, and 1974 and 1975, the two years directly following the urchin removal, indicate a low abundance of species comprising this association. The high scores of the Sear Island quadrats, free of urchins during all years of sampling, at the positive end of the axis (Fig. 5f through 5i) contrasts with these Bath Island site/years. Further, the decrease in area of the ellipses at Bath Island from 1972 to 1973 (Fig. 5a, 5b; Table 4) indicates an overall decrease in the variability of species assemblages in 1973.

This decrease in species variability is consistent with other observations of decreased macroalgal abundance in response to heavy urchin grazing (Foreman 1977, Duggins 1980, Dean *et al.* 1984, Ebeling *et al.* 1985) and with traditional views of intensive herbivory in terrestrial plant communities (Crawley 1983).

Elements of the kelp/foliose red subtidal association were also apparent in the canonical loadings of v_2 from the

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CVA, and v_3 from the CCO. These axes were highly similar, and seemed to separate quadrats of the kelp/foliose red association from those which contained a large amount of *Calliarthron tuberculosum* and *Ulvaria obscura*. Quadrats that were sampled at Bath Island following the arrival of the urchins scored low on these axes relative to those that were not (Fig. 9b). This suggests that the *C. tuberculosum* association exists as a grazed form of the subtidal kelp/foliose red association. Coralline algae such as *C. tuberculosum* have consistently been found to persist in heavily grazed "barrens" areas described in other studies of sea urchin grazing (Pearse and Hines 1979, Harrold and Reed 1985). Further, Paine and Vadas (1969) found *Ulva-Gayralia* species were the only foliose algae to consistently tolerate grazing in enclosed cages with sea urchins.

This evidence suggests that the grazing activity by sea urchins effectively reduced the overall variability of the macroalgal assemblages by removing various foliose red and kelp species. Grazing resistant species such as *Calliarthron tuberculosum* and *Ulvaria obscura* were not affected by the sea urchins and so remained in disproportionate abundance following grazing. These findings are in accordance with those described by Foreman (1977), who found, based on a species importance measure (frequency x mean biomass), that the most important species during 1973 were members of the Chlorophyceae and encrusting or articulated coralline species. Foreman (1977) postulated that the persistence of

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the Chlorophyceae may result from their weedy nature. The removal of individuals by grazing would have little influence on the population which would quickly re-establish, and perhaps benefit by the reduced abundance of potential competitors.

Community Change After Sea Urchin Removal

The extent of recovery of the macrophyte communities at Bath Island after removal of the sea urchins in 1973 was summarized by the PCA, evident in Figures 5b through 5d. There is an increasing trend in the ellipse areas from 1973 through 1975, corresponding to increased variability among quadrats of each site/year. The trend contrasts that which is evident at Sear Island over the same time period (Fig. 5g, 5h), which lends to the supposition that community enrichment is occurring. The change in area occurs with a decrease in the value for θ in 1974 (Fig. 5c), reflecting the higher quadrat scores at the positive end of PC2. This corresponds to small increases in *Ulva* spp., *Sargassum muticum*, *Lomentaria hakodatensis*, *Gigartina exasperata*, and *Gelidium* spp. *S. muticum* has been shown to colonize experimentally denuded surfaces at Bath Island, particularly in summer months (DeWreede 1983). As *S. muticum* is the strongest contributor to PC2, the higher scores of B74 on this axis probably reflect the recruitment of *S. muticum* in the free space created by the sea urchins in 1973. A further

contributor to the higher scores of B74 on PC2 is *Ulva* spp.,
which was also observed to colonize experimentally created
free space by DeWreede (1983).

The increase in abundance of these species did not
continue in 1975 where θ has increased (Table 4),
corresponding to decreased scores at the positive end of PC2
(Fig. 5d). This is consistent with the findings of DeWreede
(1983), who found poor over-winter survival of *Sargassum
muticum* that had colonized free space in the summer of 1976
and 1978. Concurrent with the decrease in the species
indicated by PC2, the slight increase in the scores of B75 at
the positive end of PC1 indicates increased abundances of
foliose red and kelp species in the second year after
disturbance.

At Bath Island from 1973 through 1975, the trends in
community structure indicated by the positive end of PC1 and
PC2 would suggest a change from the low variability and heavy
impact described for 1973, towards an increased abundance of
space colonizing species such as *Sargassum muticum* and *Ulva*
spp. in 1974. By 1975, increasing trends in ellipse area, as
well as decreased scores at the positive end of PC2 and
increased scores at the positive end of PC1 suggest a trend
in overall macrophyte composition of B75 towards that of B72.
However, the sample size of B75 is small and conclusions
should be viewed with caution.

The descriptive methods of interpretation employed by
Foreman (1977), based on measures of species diversity,

abundance of 10 arbitrary growth form/taxonomic macrophyte groups, and a species importance measure (frequency x mean biomass), indicated similar trends in community regeneration. In 1974, foliose reds and annual kelps (i.e. *Nereocystis luetkeana*) increased in importance and relative abundance. Also noted was a maximum importance value for *Sargassum muticum*, which was postulated to represent the early foliose red community. The return of pre-disturbance importance levels for *Constantinea subulifera, Plocamium cartilagineum* and *Iridaea splendens* was apparent in 1975. Although an increase in 1975 for these species was suggested by the multivariate analyses, there was no indication that they had reached their 1972 pre-grazing abundance. This suggests that if detailed information on the response of particular species was required in a study, univariate analyses by individual species would be more appropriate. The same conclusion has been reached by other researchers using a combination of multivariate and univariate approaches to successional change in plant communities (Gibson and Brown 1992).

Community Change from the 1970's to 1992

Another association that appeared consistently in all three of the analyses was a shallow subtidal association of *Sargassum muticum, Gigartina exasperata, Lomentaria hakodatensis, Corallina officinalis, Gelidium* spp., and *Ulva*

spp. High scores on axis 2 from the second PCA, low scores on v_1 from the CVA, and low scores on v_2 from the CCO all indicated this association. The relationship between this association and the 1992 quadrats from both Bath and Sear Island (Figs. 4, 5i, 7b, 9b, 10a, and 10b) suggests that these species have increased in abundance at the two sites from the 1970's through 1992. Of these species, only *Gelidium* spp. was identified as characteristic of one of the communities discussed by Lindstrom and Foreman (1978), further indicating that a redistribution of species has occurred at the sites since the 1970's.

The 1992 shallow subtidal association contrasts with another association of species including *Callophyllis* spp., *Cryptopleura ruprechtiana*, *Nereocystis luetkeana*, *Polyneura latissima*, and *Desmarestia viridis*. These species were correlated positively with v_1 from the CVA and v_2 from the CCO, and negatively with the second principal component axis. The relationship between the quadrats sampled during the 1970's and these species is apparent from the same evidence as that which identified the 1992 shallow subtidal association (Figs. 4, 5i, 7b, 9b, 10a, and 10b). It appears that sites sampled during the 1970's accounted for virtually all of the negatively scoring quadrats on the second principal component axis (Fig. 4), particularly during 1972 at Bath and Sear Island (Figs. 5a, 5f). Because of the overlapping depth distribution of positively and negatively scoring quadrats on this axis (Fig. 4), *Callophyllis* spp.,

C. ruprechtiana, *P. latissima*, and *D. viridis* represent an association that has been replaced by the 1992 shallow subtidal association. The differences in upper subtidal macrophyte community structure between the early 1970's and 1992 seems to be summarized by increases in abundance of *Sargassum muticum*, *Gigartina exasperata*, *Lomentaria hakodatensis*, *Corallina officinalis*, *Gelidium* spp., and *Ulva* spp., and decreases in *Callophyllis* spp., *C. ruprechtiana*, *N. luetkeana*, *P. latissima*, and *D. viridis*.

Sargassum muticum was introduced to the northeast Pacific from Japanese oyster spat in the 1930's or 1940's (Scagel 1956), and has since spread as far south as Baja California and as far north as Southeast Alaska (Lindstrom 1977). A similar origin in the northeast Pacific is postulated for *Lomentaria hakodatensis*, which has also since spread south in its distribution (Hawkes and Scagel 1986). The increases of these two species apparent in this study is indicative of further success of these introduced species in the northeast Pacific.

Studies of community change or constancy in benthic marine communities have primarily dealt with changes in small patches, involving recolonization after a disturbance event, or the question of succession (Connell 1987). This focus, emphasized during the investigation of the community responses to grazing in the first part of this study, contrasts with the more long-term changes that are suggested here. The strongest evidence that these changes represent

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long-term changes in community structure as opposed to yearly random variation in species abundances is as follows. Were the differences in community structure between the 1992 site/years and the 1970's site/years a result of annual variation in recruitment, it is likely that other site/years would have shown similar community structures, high in abundance of *Sargassum muticum*, *Gigartina exasperata*, and *Ulva* spp. and low in abundance of *Callophyllis* spp., *Nereocystis luetkeana*, *Polyneura latissima*, and *Desmarestia viridis*. As it was, only the 1992 site/years showed this trend. However, continuous sampling efforts would be mandatory to distinguish between annual variation in community structure and long-term changes. Further, to determine if the changes were widespread throughout the Strait of Georgia, more sites at random locations throughout the strait would need to be sampled. A continuous data set for these sites could have provided more information on the causes of community change, and suggested more specific areas in which to concentrate further experimental studies.

Community changes that have occurred over long periods of time may result from gradual shifts in local physical conditions (Connell 1987). One possible explanation for the observed shift in community composition from the 1970's to 1992 may be related to the temperature tolerance of the various species involved in the changes. In a study of temperature tolerance among northeast Pacific macroalgae, *Sargassum muticum*, *Gigartina exasperata*, and *Ulva fenestrata*

were among the most tolerant species tested for survival at high temperatures whereas *Callophyllis* spp., *Nereocystis luetkeana*, *Polyneura latissima*, and *Desmarestia viridis* all appeared in lower temperature tolerant groups (Lüning and Freshwater 1988). By inspection of monthly mean surface temperatures at Active Pass, near the study sites (Fig. 12), it appears that a gradual increase of perhaps 2 °C in average temperature at the study sites has occured. There is thus the possibility that temperature changes in the strait have created an environment in 1992 that is favourable to a different pool of species (*S. muticum*, *G. exasperata*, and *Ulva* spp.) from that in the 1970's (favourable to *Callophyllis* spp., *N. luetkeana*, *P. latissima*, and *D. viridis*).

The above postulation is suggested with much reserve, as other explanations may well describe the differences in abundance of the above species. For example, the low abundance of *Nereocystis luetkeana* in the 1992 quadrats may reflect the state of recovery of the sites from grazing at the time of sampling. *N. luetkeana* has been shown to behave as a "fugitive species", establishing itself at grazed sites soon after removal of the urchins, and gradually being replaced by perennial kelp species over the next 4 to 6 years (Paine and Vadas 1969, Foreman 1977). Thus *N. luetkeana* may be in low abundance at Bath Island due to the active grazing of the sea urchins, and absent from Sear Island due to its replacement by other kelp species.

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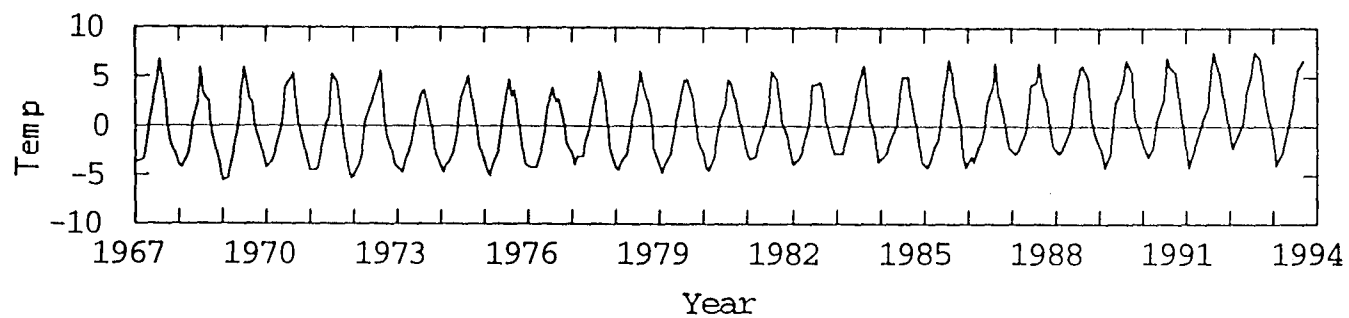
Figure 12. Time-series of seawater surface temperatures at Active Pass, British Columbia, near the study sites. Temperatures are shown as the difference between the monthly mean surface temperature (°C) and the mean surface temperature over the total time interval (10.8 °C).

Regardless of the cause, it is clear from these results that there has been a shift in community structure at Bath and Sear Island since the 1970's. Although not specifically ascertained by this study, it is likely that similar changes in community structure have occurred elsewhere in the Strait of Georgia. The implications of a long-term shift in macrophyte community structure in the Strait of Georgia are several fold. If an accurate assessment of environmental impact were needed at some location in the strait, this study has shown that the baseline to which the post-disturbance data would be compared must be recent. Changes in community structure may have been occurring at the disturbed site in the interim between the last sampling session and the time of disturbance. Comparisons to an outdated data set could result in an over or under-estimation of the costs of the disturbance or in a misinterpretation the success of clean-up efforts.

The possibility remains that these changes are indicative of long-term changes in environmental conditions (not necessarily restricted to temperature) in the Strait of Georgia, which may be of concern to parties with financial or other interest in the biota of the strait. Although the species observed to be changing in abundance during this study are not currently of particular economic importance, other more valuable species are subject to the same conditions, and may be experiencing changes of their own. In this case, the potential effects on related industries should

be anticipated, and appropriate measures taken to deal with them. Changing conditions in the Strait of Georgia also suggest that more power should be granted to environmental protection agencies, and decisions regarding the use of the strait should be made to err on the conservative side.

One final implication of this study is the potential for the use of biomonitoring to indicate changing conditions in ecological systems. Information of the sort collected in this study could be collected in a systematic manner, with the purpose of indicating when and where important changes may be occurring. Time and money invested in long-term studies aimed at monitoring and preserving the natural resources of the Strait of Georgia would certainly pay dividends by ensuring the success of industries that rely on its ecological integrity.

CONCLUSIONS

The multivariate approach of this research has

demonstrated community level changes in benthic marine

macrophyte abundances. Given the limitations imposed on true

hypothesis testing by the nature of the data set, an

exploratory approach to data interpretation has been most

appropriate; it has revealed the following changes in

community structure. 1) Along the depth gradient from 3 m

above to 6 m below zero tide level, quadrats above zero tide

level are characterized by high abundances of *Fucus* spp.,

Mastocarpus papillatus, *Neorhodomela larix*, *Porphyra* spp.,

and *Ulva* spp., whereas deeper quadrats are characterized by a

foliose red association (i.e. *Plocamium cartilagineum*,

Constantinea subulifera, *Prionitis* spp.) and a kelp

association (i.e. *Laurencia spectablis*, *Corallina*

officinalis, *Laminaria* spp., *Costaria costata*). 2) Intensive

urchin grazing activity results in an overall decrease in

macrophyte variability, primarily resulting from removal of

the foliose red and kelp species, and increases in

Calliarthron tuberculosum and *Ulvaria obscura*. 3) After

removal of grazing pressure, site recovery is characterized

by an initial slight increase in *Ulva* spp. and *Sargassum*

muticum during the first year, and further increases in

abundance of the foliose red and kelp species in the

following year. 4) Long-term change in community structure

has occurred with increases in introduced species such as *S.*

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muticum and *Lomentaria hakodatensis*, as well as *Gigartina exasperata*, *C. officinalis*, and *Gelidium* spp., and decreases in species such as *Callophyllis* spp., *Cryptopleura ruprechtiana*, *Polyneura latissima*, and *Desmarestia viridis*. This study has underlined the importance of long-term studies of biotic communities in environmentally sensitive areas. Data collected during these studies, which contains recent quantitative information of the composition of local biota, is indispensable to monitor possible changes in valuable natural resources, and to ensure that an accurate impact assessment can be carried out after a disturbance event.

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Appendix 1. Macrophyte species collected during the five
years of sampling.

<hr>

<div align="center">Species</div>

<hr>

Acrochaetium spp.
Acrosiphonia saxatilis (Ruprecht) Vinogradova
Agarum fimbriatum Harvey
Ahnfeltia fastigiata (P.&R.) Makienko
Ahnfeltiopsis leptophylla (J. Agardh) Silva and DeCew
Alaria tenuifolia Setchell *in* Collins, Holden and Setchell
Amplisiphonia pacifica Hollenberg
Analipus japonicus (Harvey) Wynne
Antithamnion defectum Kylin
Antithamnionella pacifica (Harvey) Wollaston
Antithamnionella spirographidis (Schiffer) Wollaston
Blidingia minima var. *minima* (Nageli and Kutzing) Kylin
Bonnemaisonia nootkana (Esper) Silva
Bossiella orbigniana (Descaine) Silva
Bossiella californica (Descaine) Silva
Bossiella chiloensis (Descaine) Johansen
Bossiella cretacea (Postels and Ruprecht) Johansen
Bossiella plumosa (Manza) Silva
Botryocladia pseudodichotoma (Farlow) Kylin
Branchioglossum bipinnatifidum (Montagne) Wynne
Bryopsis plumosa (Hudson) C.A. Agardh
Callophyllis flabellulata Harvey
Callophyllis heanophylla Setchell
C. firma (Kylin) Norris
Callithamnion spp.
Calliarthron tuberculosum (P.&R.) Dawson
Callophyllis violacea J. Agardh
Caulocanthus ustulatus (Mertens *ex* Turner) Kutzing
Ceramium californicum J. Agardh
Ceramium strictum Harvey
Ceramium pacificum (Collins) Kylin
Chaetomorpha californica Collins *in* Collins,Holden and Setchell
Cladophora microcladioides Collins
C. seriacea (Hudson) Kutzing
Colonial diatoms
Colpomenia peregrina (Sauvageau) Hamel
C. bullosa (Saunders) Yamada
Constantinea subulifera (Setchell)
Corallina frondescens Postels and Ruprecht
Corallina officinalis var. *chilensis* (Descaine *in* Harvey) Kutzing
Costaria costata (Turner) Saunders

<div align="center">75</div>

Cryptonemia borealis Kylin
Cryptonemia obovata J. Agardh
Cryptopleura ruprechtiana (J. Ag.) Kylin
C. lobulifera (J. Ag.) Kylin
Cryptosiphonia woodii J. Agardh
Delessericeae
Derbesia marina (Lyngbye) Solier
Desmarestia ligulata (Lightfoot) Lamouroux
Desmarestia viridis (Muller) Lamouroux
Dictyota binghamiae J. Agardh
Ectocarpus spp.
Endocladia muricata (Postels and Ruprecht) J. Agardh
Enteromorpha intestinalis (Linnaeus) Link *in* Nees von Esenbeck
Erythrotrichia carnea (Dillwyn) J. Agardh
Erythrocladia irregularis f. *subingtegra* (Rosenvinge) Garbary,
Hansen and Scagel
Farlowia mollis (Harvey *et* Bailey)Farlow *et* Setchell *in* Collins
Fauchea spp.
Fryeella gardneri (Setchell) Kylin
Fucus spp.
Fucus gardneri Silva
Fucus spiralis Linnaeus
Gastroclonium subarticulatum (Turner) Kutzing
Gelidium coulteri Harvey
G. purpurescens Gardner
Gigartina exasperata Harvey and Bailey
Gomontia polyrhiza (Lagerheim) Bornet and Flahault
Gonimophyllum skottsbergii Setchell
Goniotrichopsis sublittoralis Smith *in* Smith and Hollenberg
Gracilariopsis lemaneiformis (Bory) Dawson, Acleto and Foldvik
Gracilaria pacifica Abbott
Grateloupia doryphora (Montagne) Howe
Grateloupia pinnata (Postels and Ruprecht) Setchell *in* Collins,
Holden and Setchell
Grateloupia setchellii Kylin
Griffithsia pacifica Kylin
Gymnogrongus chiton (Howe) Silva and DeCew *in* Silva
Halosaccion glandiforme (Gmelin) Ruprecht
Halymenia gardneri (Kylin) Parkinson
Haraldiophyllum mirable (Kylin) Zinova
Herposiphonia plumula (J. Ag.) Hollenberg
Heterosiphonia densuiscula Kylin
Hildenbrandia spp.
Hincksia ovata (Kjellman) Silva
Hollenbergia subulata (Harvey) Wollaston
Hymenena spp.
Iridaea heterocarpa Postels and Ruprecht
Iridaea splendens (Setchell and Gardner) Papenfuss
Janczewskia gardneri Setchell and Guernsey *in* Setchell
Kallymenia oblongifructa (Setchell) Setchell

Laminaria spp.
Laminaria farlowii Setchell
Laminaria bongardiana Postels and Ruprecht
Laminaria saccharina (Linnaeus) Lamouroux
Laurencia spectablis Postels and Ruprecht
Leachiella pacifica Kugrens
Leathesia difformis (Linnaeus) Areschoug
Lithothamnion spp.
Lithothrix aspergillum Gray
Lomentaria hakodatensis Yendo
Mastocarpus papillatus (C.A. Agardh) Kylin
Membranoptera tenuis Kylin
Microcladia borealis Ruprecht
Microcladia coulteri Harvey
Neodilsea borealis (Abbott) Lindstrom
Neorhodomela larix (Turner) Masuda
Nereocystis luetkeana (Mertens) Postels and Ruprecht
Nienburgia andersoniana (J. Ag.) Kylin
Odonthalia floccosa (Esper) Falkenberg
Opuntiella californica (Farlow) Kylin
Palmaria mollis (Setchell and Gardner) van der Meer and Bird
Petelonia fascia (Muller) Kuntze
Peyssonelia pacifica Kylin
Phycodrys spp.
Pikea californica Harvey
Platysiphonia clevelandii (Farlow) Papenfuss
Platythamnion pectinatum Kylin
Platythamnion reversum (Setchell and Gardner) Kylin
Platythamnion villosum Kylin
Pleonosporium vancouverianum J. Agardh
Plocamium cartilagineum (L.) Dix.
Polyneura latissima (Harvey) Kylin
Polysiphonia scopulorum var. villum (J. Agardh) Hollenberg
Polysiphonia spp.
Porphyra spp.
Prionitis spp.
Pterosiphonia dendroidea (Montagne) Falkenberg
P. bipinnata (P.&R.) Falkenberg
Pterosiphonia gracilis Kylin
Pterosiphonia hamata Sinova
Pugetia fragilissima Kylin
Punctaria spp.
Pilayella tenella Setchell and Gardner
P. littoralis (Linnaeus) Kjellman
Ralfsia fungiformis (Gunner) Setchell and Gardner
Rhizoclonium riparium (Roth) Harvey
Rhodoglossum affine (Harvey) Kylin
Rhodymenia californica Kylin
Rhodymenia pertusa (P.&R.) J. Agardh
Rhodoptilum plumosum (Harvey and Bailey) Kylin

Rhodoglossum roseum (Kylin) Smith
Sarcodiotheca furcata (Setchell and Gardner) Kylin
Sarcodiotheca gaudichaudii (Montagne) Gabrielson
Sargassum muticum (Yendo) Fensholt
Schizymenia pacifica Kylin
Scytosiphon lomentaria (Lyngbye) J. Agardh
Sphacelaria rigidula Kutzing
S. racemosa Greville
S. norrisii Hollenberg
Stenogramma interrupta (C. Ag.) Montagne
Stylonema cornu-cervi Reinsch
Syringoderma phinneyi Henry and Muller
Tiffaniella snyderae (Farlow) Abbott
Ulva spp.
Ulvaria obscura (Kutzing) Gayral var. *blyttii* (Areschoug)
Bliding
Urospora spp.
Weeksia coccinea (Harvey) Lindstrom