CHARACTERIZATION

OF A SUBTIDAL GASTROPOD ASSEMBLAGE

IN THE STRAIT OF GEORGIA

BY

ERIC L. CABOT

B.A., Boston University, 1974

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in
THE FACULTY OF GRADUATE STUDIES
(Department of Botany)

We accept the thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April, 1979

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the Head of my Department or by his representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

ERIC L. CABOT

Department of BOTANY

The University of British Columbia
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

Date April 24, 1979

ABSTRACT

A subtidal site at Saturnina Island was sampled quantitatively to determine the seasonal and depth related trends of gastropod populations. The resulting density estimates were used to characterize the assemblage using diversity, niche-breadth, and cluster analyses. The relationship between gastropod abundance and diatom density, as estimated from colonization of glass microscope slides, was investigated. One experiment, which was conducted at the site, was designed to determine whether the macrophytic algae still attracted the numerically dominant snail after the algae had been either cleaned with hydrogen peroxide, or killed by immersion in 50° C. seawater.

Most species attained their maximum development after recruitment in spring or early summer. The greatest number of species was found at the shallowest station that was sampled, and abundances tended to decrease with depth with most species. Most of the snails had dispersion patterns that were similar to those of the two dominant species Margarites costalis and Lacuna marmorata. Ninety-five percent of all the individuals collected were found to belong to five species. This high degree of numerical dominance severely affected the results of the diversity and the cluster analyses. Analyses of

frequency vs. mean abundance, and niche-breadths revealed detailed information concerning the distributions of the gastropods that was not readily obtainable from graphs of mean density per quadrat.

Diversity, species richness, the total abundance of gastropods, and the densities of several species were correlated to the abundance of diatoms. Several species were also found to contain diatoms among their gut contents.

Several other factors, including parasitism, predation, low salinity-high temperature water, and competition are discussed as factors, which, in addition to diatom abundance, may have affected the gastropod dispersion patterns.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENT

I am grateful to many people who helped in the successful completion of this study, but, above all, to Dr. Ronald E. Foreman, who supervised the work and provided space, materials, and money, largely through a grant from the Fisheries Research Board of Canada. I am eternally indebted to Mr. Barry D. Smith who was my diving buddy for most of the study. Dr. R.E. DeWreede also helped with some of the diving and, along with Dr. P.A. Dehnel, reviewed the manuscript. Special thanks are due to Dr. Mary Jo Duncan who offered countless useful suggestions as well as moral support throughout the entire course of research and writing. Dr. H. Ching deserves mention for opening my eyes to the possible ecological effects of parasitic infestations. Mr. Tom Nicol assisted with computer programming, and Dr. Foreman supplied several of the FORTRAN programs.

INTRODUCTION

One approach to the study of organisms in relation to their environment is to characterize the biotic assemblage or community of a habitat in terms of species composition and, if possible, the patterns of abundance and resource utilization. This information is an invaluable aid in formulating the course of further experimental investigations into specific interactions between species and particular biotic and physical components of the environment (Shelford and Towler 1925, Elton 1927, Odum 1971, Whittaker 1975). In order to ascertain the ecological relationships between co-occurring species, detailed information regarding the number of individuals, their distributions, and their resources held in common must be obtained. It is also important to determine whether any shared resources are in short supply, for if not, then other factors must control the abundances of the species.

Taxonomic affinity provides a convenient and meaningful basis for partitioning assemblages into units of workable size when it is not feasible to consider all organisms at once. The greatest degree of overlap in the resource utilization by co-occurring species is expected for those organisms which have similar physiological and structural features, and, therefore, groups of taxonomically related organisms are of particular ecological interest (King 1964).

The gastropods, which are conspicuous upon rock and seaweed surfaces in coastal marine environments are an ecologically diverse group of organisms (Morton and Yonge 1964,

Yonge and Thompson 1977), making them well suited for initial studies of marine assemblages. Due to a wide range of morphological specialization, gastropods are able to utilize many consumer niches. Additionally, there are several known examples of habitat diversity (Kohn 1959, 1968, 1971, 1976, Test 1945, Hylleberg and Fenchel 1978), life-cycle diversity (Spight 1976, Grahame 1976), and physiological diversity (Kingston 1968, Test 1945, Fenchel 1975a, 1975b, Hylleberg 1975, Bertness and Schneider 1976) among gastropod congeners.

Early naturalists were aware of the diverse gastropod fauna of the West coast of North America (see e.g. Darwin 1860, Dall 1927, Olroyd 1928, 1935) but in America, the few dispersion patterns of marine gastropods that are actually known are for intertidal species. In other areas, such as Danish fjords (Fenchel 1975b, Hylleberg 1975), and tropical reefs (Kohn 1959, 1968, 1971, Leviten 1978, Kohn and Leviten 1976), studies of gastropod assemblages have revealed the phenomenon of resource partitioning, whereby related species utilize different foods, or different sizes of the same foods in order to reduce competition. Marine gastropod dispersions have also been studied upon the eastern continental shelf of North America (Franz 1977), the Atlantic Ocean floor (Rex 1977), and the fjords of Greenland (Thorson 1933).

The majority of studies of marine benthic assemblages have been conducted in the more easily accessible intertidal zone (see e.g. Southwood 1958, Nybakken 1978, Holland and Polgar 1976). Early subtidal studies were commonly restricted to areas

of relatively soft and flat substrata, since animals and plants dwelling on rocky substrata cannot be efficiently collected with grabs or similar equipment. Therefore, since the nineteenth century, studies of intertidal and soft-substrate communities have flourished, but detailed quantitative studies of rocky subtidal assemblages were rare until after the advent of SCUBA in 1943. With diving equipment, biologists are able to obtain accurate ecological data, as well as direct observations as to the distribution and behavior of marine organisms in situ. It is noteworthy that as early as 1930, Gislen utilized hard-hat diving equipment and quadrat frames to enumerate the flora and fauna of subtidal communities.

Most workers have emphasized the roles of subtidal invertebrates as grazers (Saito and Nakamura 1961, Carlisle et al. 1964, North 1971, Paine and Vadas 1969, Forster 1959, L. Jones 1971, Leighton 1971, Carefoot 1967, Powell 1964), prey of fish (Quast 1968), and other animals (Paine 1965, Robilliard 1971, Menge 1972), or as useful indicators of the severity of human-induced environmental perturbations such as oil spills (D. Jones 1971, North et al. 1964), kelp harvesting (Clendenning 1971) and sedimentation (Foreman 1975), but there have been few attempts to elucidate dispersion patterns of the animals as a means of understanding basic ecological interrelationships.

The objectives of this study are (1) to determine the seasonal and depth related dispersion patterns of shell-bearing gastropods in a subtidal seaweed-dominated habitat in the

Strait of Georgia, and (2) to characterize the entire assemblage by examining the distribution of individuals among species and by comparing the individual dispersion patterns. To clarify the dispersion pattern of the numerically dominant gastropod, Margarites costalis, the size-frequency distributions of this species were examined. The utilization and abundance of benthic diatoms were investigated under an initial hypothesis that they are a major determinant of gastropod dispersion patterns.

Typically, studies of animals on seaweed have been concerned with the number of species and individual organisms found on various plant parts (i.e., holdfasts, stipes and blades) and species (Bergh 1871, Andrews 1925, Warmke and Almodovar 1963, Duffas 1969, Gehlardi 1971, Wing and Clendenning 1971, Nassichuck 1974, Smith 1973). This approach presumes that there is some inherent substrate specificity for all organisms which reside on plants in the sea. In many cases this may not be so, especially for motile animals. Since gastropods are often motile it may be more desirable to measure their absolute densities and dispersion patterns through the use of quadrat collections.

MATERIALS AND METHODS

Site Description

All field work was conducted at a sheltered subtidal site adjacent to the southwestern shore of Saturnina Island in the central province of the Strait of Georgia, B.C., Canada, (49° 8.8' N, 123° 40.3' W) (Figure 1). Saturnina is one of the Flat Top Islands in the Gulf Islands archipelago. The Flat Tops are described more fully by Lindstrom and Foreman (1979). For a detailed account of the geological features of this portion of the Strait of Georgia, refer to Muller (1971). Appendix A lists the common and dominant algae at the site, most of which belong to a grouping that has been named the shallow red algal community by Lindstrom and Foreman (1979). The dense macrophytic cover harbors great numbers of minute gastropods.

The sites upper boundary is approximately at Canadian datum (Lowest Lower Low Water), above which is a narrow zone of barren rock. A substratum of sandstone bedrock overlain by large flat boulders (up to 4 sq. m in area and 1 m in height) extends into the subtidal to a depth of 3.5 m, at which point there is a change in slope with the boulders becoming more rounded and smaller (1 m or less in diameter). At 6.8 m below datum, the substratum abruptly changes to a gently sloping, broken-shell covered bottom, delimiting the lower boundary of

the site. This region contains rocks (0.5 m or less in diameter) spaced at 4 to 5 meter intervals. At the lower site boundary most algal species are replaced by a sparse eel-grass community.

Gastropod Collection And Treatment

Within the site, a permanent transect was placed perpendicular to the shore to a point 2.5 m past the change from boulder-covered bedrock slope to shell-covered flat bottom. Four permanent stations were located at 10 m intervals along the transect line (Figure 2) with the deepest station (no. 4) at the transect endpoint. Boundary effects and the influence of tides were minimized by placing station 1 at a depth of 1.5 m below datum. Quantitative collections were made at each station, in an area extending 3 m on either side of the transect.

Each month, for a period of one year beginning October, 1975, twenty 15 x 15 cm quadrat frames, five at each station, were collected with a SCUBA-operated airlift sampler (Foreman 1977) that was fitted with collection bags made from nylon stockings in order to retain minute gastropods (Fig. 3). A random numbers table was used to determine the placement of quadrat frames along imaginary lines extending perpendicularly from the transect at each station. No frame was placed at a

Figure 1. Location of Saturnina Island in the Strait of Georgia, B.C. The subtidal research site is denoted by an arrow.

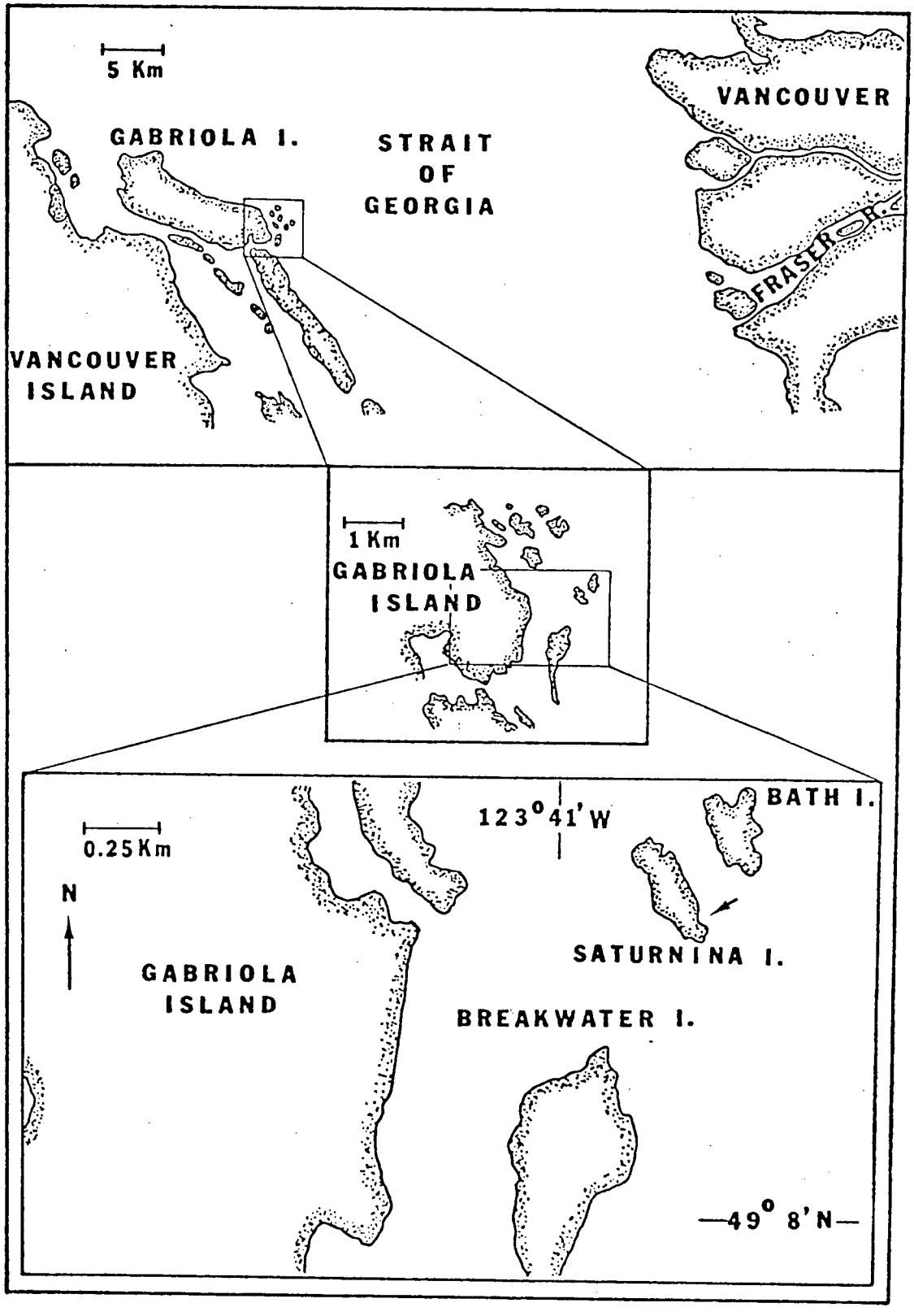

5 Km
GABRIOLA I.
STRAIT
OF
GEORGIA
VANCOUVER
FRASER R.
VANCOUVER
ISLAND
1 Km
GABRIOLA
ISLAND
0.25 Km
N
123°41'W
BATH I.
SATURNINA I.
GABRIOLA
ISLAND
BREAKWATER I.
49° 8'N

Figure 2. Cross-sectional perspective view of the research site. Depths are relative to Canadian datum (LLLW) as recorded by a SCUBA diver with a hand-held depth gauge. Rectangles illustrate sampling areas at each station. A-C correspond to substrate zones. A: gently-sloping bedrock overlain with flat boulders up to 4 m^2 in area, up to 1 m in height. B: more steeply sloped bedrock overlain by round boulders up to 1 m in diameter. C: relatively flat bottom of sand and broken shell with small rocks of up to 0.5 m in diameter.

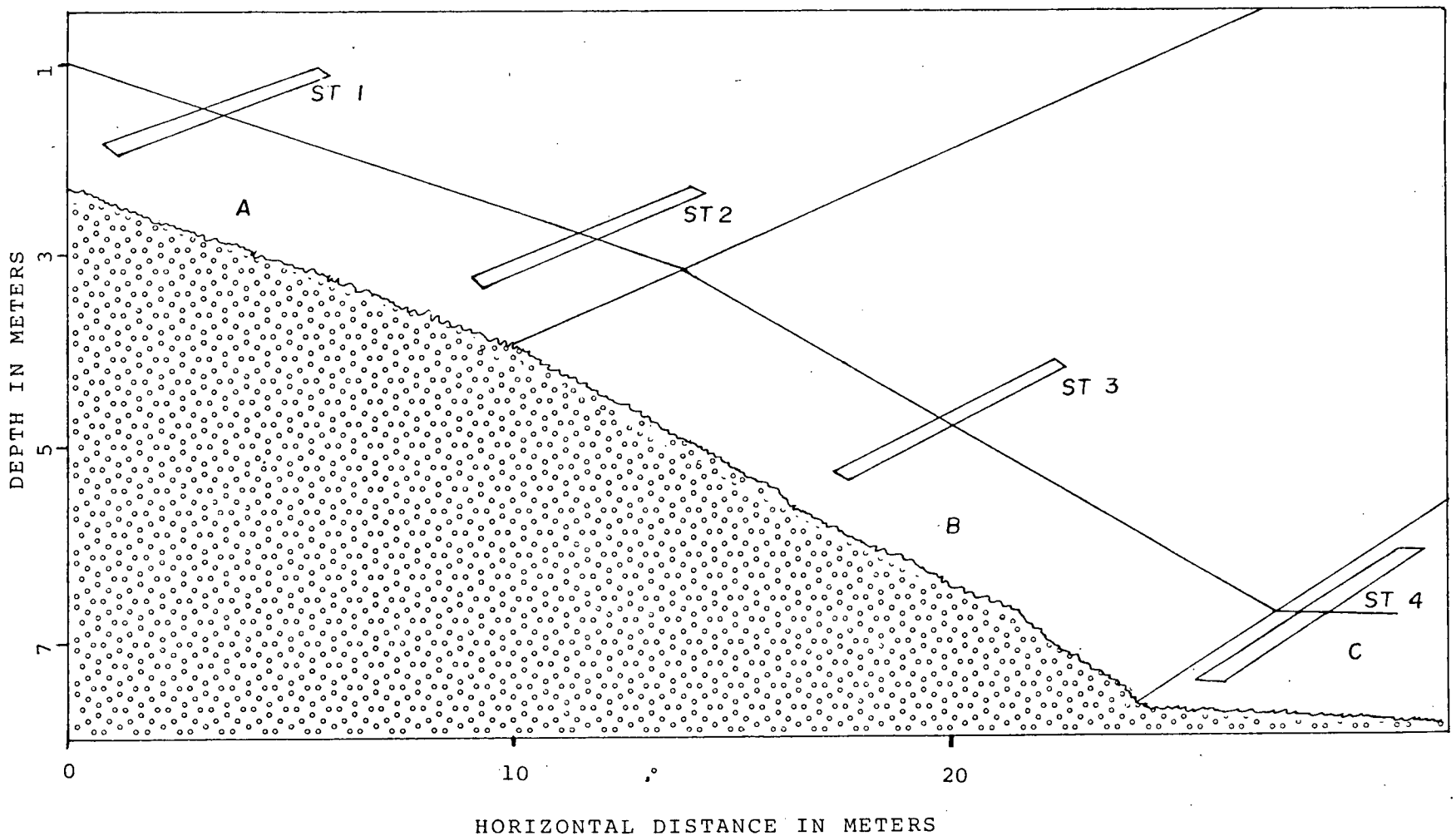
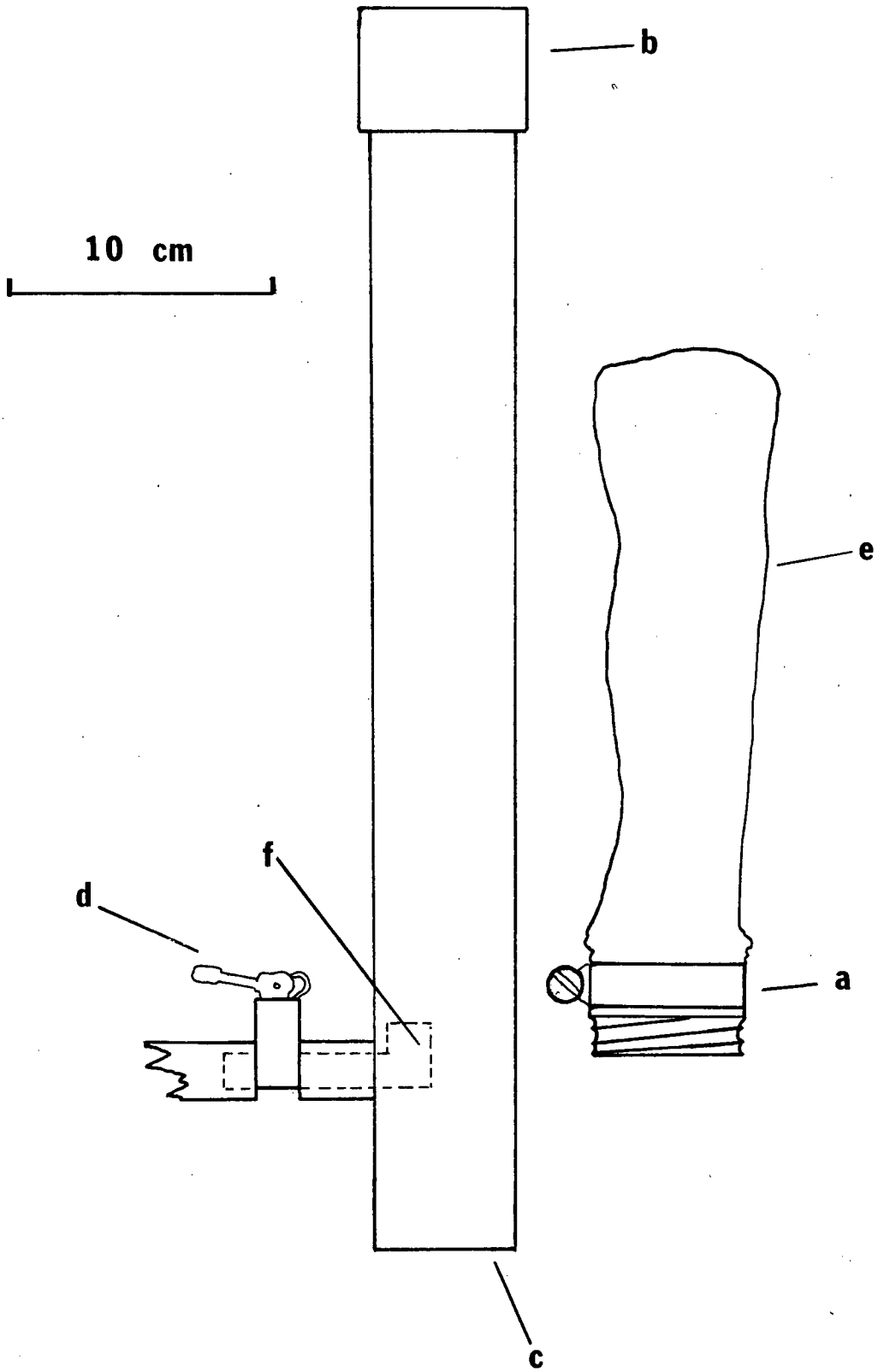

ST 1
ST 2
ST 3
ST 4
A
B
C
DEPTH IN METERS
1
3
5
7
0
10
20
HORIZONTAL DISTANCE IN METERS

Figure 3. Schematic representation of the airlift sampler developed by Foreman (1977). The device is constructed of PVC with brass fittings. A threaded male PVC fitting with a steel screw clamp (a) is easily connected to the ailift which is fitted with a threaded female PVC joint (b). Specimens enter the airlift at c, propelled by compressed air from the first stage of a SCUBA regulator. A valve (d) controls the release of air. Specimens are retained in a nylon stocking (e). A j-shaped brass fitting (f) directs the air upwards.


b
10 cm
e
f
d
a
c

previously sampled point. All animal and plant material lying within a quadrat was collected.

A group of replicate quadrats from a particular station and month is referred to, in this study, as a station-month sampling unit, or an SMU. Each monthly sample of twenty quadrats, therefore, represents four SMU's.

After two to three weeks of drying in the open air, the contents of the airlift bags were carefully brushed into separate plastic bags for storage. Each sample was later passed through metal sieves (U.S. Standard sizes: 0.84 mm, 0.46 mm, and 0.25 mm) and shell-bearing gastropods were removed from the resultant fractions using a pair of fine forceps under a dissecting microcope. The presence of tissue or an operculum was used as a sign that a specimen had been alive at the time of collection.

Margarites costalis retained upon the largest size sieve were sized by measuring the longest shell axis with a pair of vernier calipers. These lengths were recorded to the nearest 0.5 mm. Smaller individuals were sized according to which sieve they came to rest upon. Snails passing through a 0.25 mm sieve, for instance, were expected to have shell lengths that were less than 0.25 mm. Careful examinations of the sieve-sorted fractions occasionally revealed the presence of individuals that were too small for the given size-category. These individuals were then properly sized with the calipers.

All gastropod identifications were substantiated by Dr. I. Mc Taggart Cowan and the taxonomic nomenclature follows Abbott

(1974) and Carlton and Roth (1975). Exact identification of some species (i.e. Cerithiopsis sp., Odostomia sp., and an unidentified rissoid gastropod) was impossible, owing to inadequacies of the taxonomic literature.

GUT ANALYSIS

Snails were collected for gut analysis on two occasions, June 10, and October 7, 1976, at points 5 to 10 m north of, and at the same depth as, station 1. Seaweed with snails on it was placed into plastic bags which were sealed in situ.

The snails were removed from the seaweed and fixed in 50% EtOH within 10 minutes of collection. Shells were softened by a 12 hour rinse in Bouin's Picro-Formol fixative (75 parts picric acid, 25 parts formalin, 5 parts glacial acetic acid) which was cleared with three 30 minute rinses in 50% EtOH. Specimens were stored in 100% EtOH until dissection.

Soft tissues were exposed for dissection by gentle flaking of shell material with forceps. A scalpel was used to excise head and foot regions, and the remainder of the tissue was streched out upon a microscope slide. Stomach contents were teased out of the snail bodies under a dissection microscope at 40x magnification. After teasing, large pieces of snail remains were removed from the slide, coverglass and distilled water were added, and the gut material was viewed at magnifications of 400x and 970x.

Diatom Collection And Treatment

On eight occasions from July, 1976 through March, 1977, concrete bricks, upon which were fastened three glass microscope slides, were submerged at stations 1, 2, and 3 for 14 days (+- 4 hours). Slides were set in place and retrieved by SCUBA divers. Within minutes of retrieval, a drop of mounting medium and a coverslip were placed upon the exposed face of each slide. The mounting medium consisted of a 50% solution of corn syrup and 10% formalin.

The number of diatom cells was recorded for fifteen 0.177 sq. mm fields of each slide at 400x magnification. Diatoms lacking pigmentation were not counted. The mean number of cells per field was computed for each slide and then for each set of triplicates. Individual field counts were transformed to cells per sq. mm before data analysis.

Margarites costalis Feeding Experiment

An experiment was performed to determine if the presence of epiphytic microflora had any effect on the affinity of *M. costalis* to seaweed.

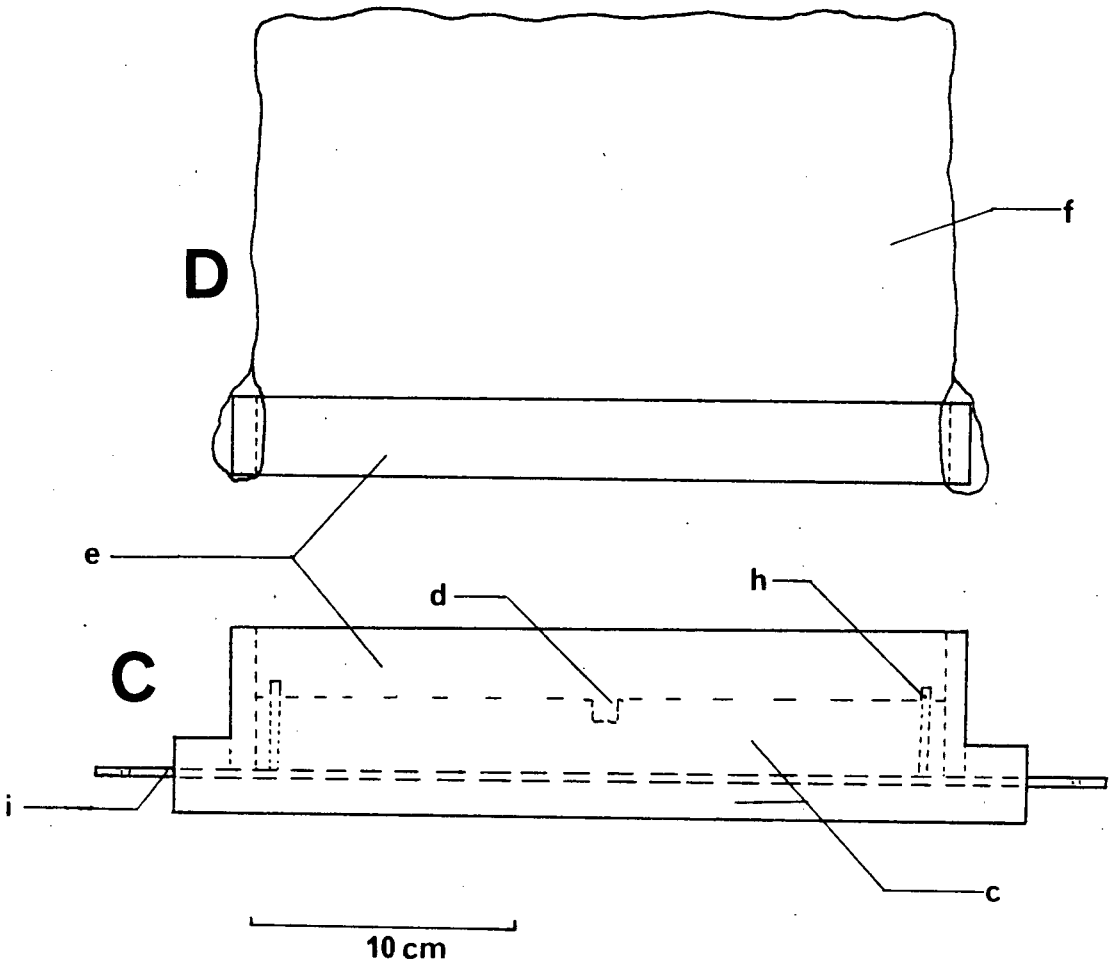
The experiment was conducted using three artificial enclosures held underwater at Saturnina Island during August and September, 1976. Twenty freshly collected adult *M. costalis*

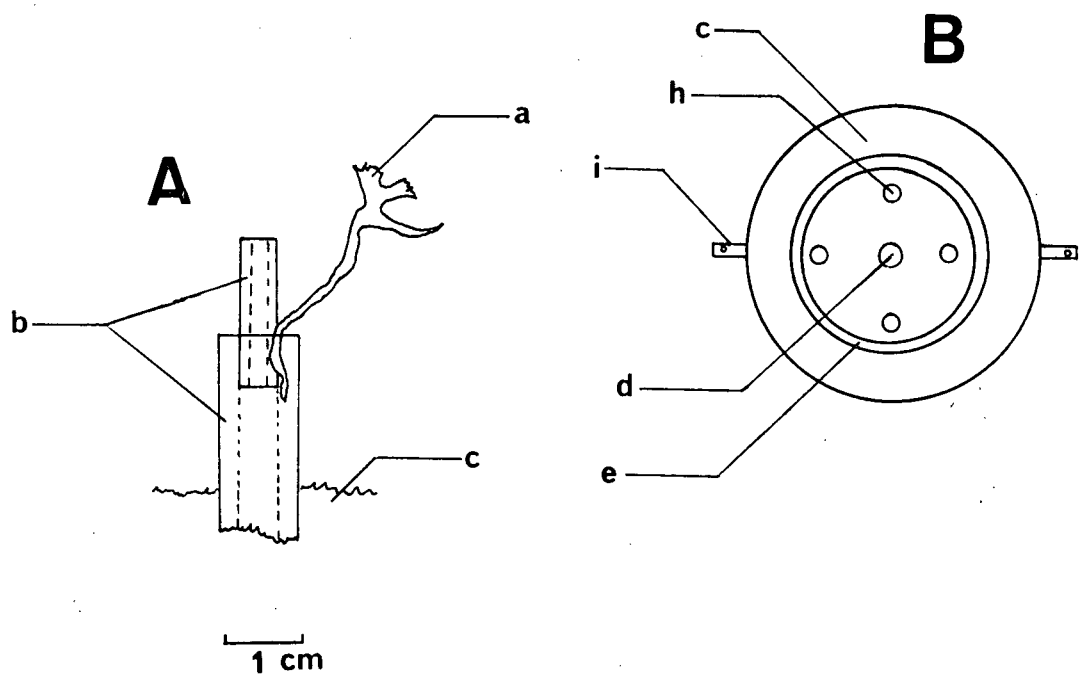
were placed in each of the enclosures with fronds of Plocamium cartilagineum that were either dead, surface-cleaned, or in the natural state. Plocamium was selected because it was highly abundant and easy to separate into approximately equal sized clumps. Algae for the experiment were treated within five minutes of collection and immediately taken to the enclosures. Fronds 10 cm in length and with approximately the same order of branching and thickness were used throughout. The P. cartilagineum were all collected from a single patch that was 10 m from, but at the same depth as, station 2 on the transect.

A five minute bath in 50° C seawater was used to kill the Plocamium and its epibionts. Cleaning was accomplished by five minutes of immersion in 10% hydrogen peroxide. Microscopic examinations revealed that the surfaces of the heat killed algae still bore the remains of microrganisms but displayed severe cellular damage. The cells of the peroxide-treated algae remained intact, but the plant surfaces had become devoid of epibionts. The untreated Plocamium, which was brought to the surface and kept in covered trays of seawater, was found to support a dense cover of microorganisms, mostly diatoms.

Each enclosure (Figure 4) consisted of a flat, round concrete base (27 cm in diameter) with a removable cover of 0.85 mm plastic mesh. Artificial holdfasts were constructed with two sizes of Nalgene tubing, one inside the other, with the outer segments vertically embedded into the concrete. P. cartilagineum fronds were held by lodging the stipes firmly

Figure 4. Schematic representation of submersible enclosure used in the feeding experiment. A, articial holdfast; B, top view of enclosure base (not to scale); C, side view of enclosure base; D side view of enclosure covering. Labels: a, Plocamium cartilagineum stipe; b, Nalgene tubing; c, concrete; d, depression for vial; e, polyethylene rims cut from a bucket; f, plastic screen with 0.85 mm pores; h, artificial holdfast; i, flat iron bar handle.


D
f
e
d
h
C
i
c
10 cm


A
a
b
c
1 cm
B
c
h
i
d
e

between both pieces of tubing. The holdfasts were positioned 1 cm from the base rim, in four locations corresponding to the major points of a compass. Although the enclosures were themselves maintained in level positions, the general direction of slope at the site was from west to east, and, therefore, to confound any fixed directional bias in the movement of M. costalis, the choice of holdfast in each trial (N-S vs E-W) was determined by a coin toss. The allocation of algae to the various treatments was randomized by a lottery.

Snails were carried to the enclosures in 16 dram plastic medicine vials, each with four equally spaced 1x1 cm ports cut in the side. The ports were sealed with cloth strips until the vials were in place in the centers of the bases with the ports facing the holdfasts. Silastic (patented) silicone adhesive was used to hold the vials in shallow depressions and to form a continuous seal with the concrete surface. In order to reduce any toxicity of the silicone or concrete, the enclosures and fittings were seasoned by immersion, in situ, for three months prior to the experiment.

After 24 hours, the number of snails in contact with P. cartilagineum of different treatments was recorded, all snails removed, the enclosures cleaned by vigorous hand-generated water movement and a new experimental trial begun. A one-way ANOVA was used to test whether the seaweed in all three conditions was contacted by the same number of snails.

Analytical Methods Used To Characterize The Gastropod Assemblage

DENSITY

The basic abundance measure used, density, is the mean number of individuals of a given species per quadrat in samples of several quadrats. Mean density (n) refers to the mean of 5 quadrats comprising each SMU, while total density refers to samples containing all the quadrats of the study.

Density is the product of two components, the percentage of quadrats in the sample which contain the species, or the occurrence, and the mean number of individuals per occurrence.

TOTAL ABUNDANCE

Total abundance (N) is the sum of all of the species densities in a sample.

SPECIES RICHNESS

The number of species found in a sample is the species richness (S). This is the simplest measure of species diversity (Peet 1974).

SIMPSONS' INDEX

Simpson's index of concentration, or dominance, contains components related to both the species richness and the evenness of the distribution of individuals among species, and is an index of the apparent diversity or compositional heterogeneity of a sample (Simpson 1949). This index was originally borrowed from the field of linguistics (Gini 1912) and in an ecological context is used as a measure of the probability that two randomly selected individuals from a sample will belong to the same species. A sample that is either species poor, or has most individuals concentrated among a few species, has little "apparent diversity" since there is a large chance of two individuals of the same species being obtained by a random draw.

Pielou (1967) modified the original form of Simpson's index to derive the following unbiased estimator of sample heterogeneity:

$$D=1-\sum_{i=1}^{s}\{[n_i(n_i-1)]/[N(N-1)]\}$$

The value of D varies from zero, when all individuals belong to a single species, to unity, when each species is represented by one individual.

THE SHANNON-WIENER INDEX

The Shannon-Weiner index, H', is mathematically related to D, but has its origins in the information theory of communications (Shannon and Weaver 1949). Like D, H' is used to estimate the degree of compositional heterogeneity of a population from the relative abundances of species in a representative sample. Stated formally, H' is the average amount of uncertainty involved in predicting the identity of a species in a sample, and it is measured in bits of information per individual as (Patten 1962):

$$H' = -\sum_{i=1}^{s} \{(n_i/N) \log_2 (n_i/N)\}$$

An increase in either the number of species or the evenness of their proportional representations will increase the uncertainty in prediction, and thus H' is related to heterogeneity in the same manner as D. Unlike D, however, H' ranges from 0 to infinity.

CONSIDERATIONS APPLYING TO BOTH D AND H

The Evenness And Richness Components Of Heterogeneity

There are significant positive correlations of the values of D and H' to both of their respective components of richness and evenness (De Jong 1975). However in each case, it is impossible to resolve which component has the greater influence over the heterogeneity index without independent measurement. Although several evenness indices have been proposed (Pielou 1977), all are mathematically dependent upon species richness, and, therefore, can only be used for comparisons of the evenness of samples with the same number of species (Peet 1974). However, differences in evenness between a group of samples can be qualitatively assessed by comparisons of the concomittant behavior of S, N, and the heterogeneity indices.

Sample Size

The evenness component of D depends entirely on the most abundant species of sample (Peet 1974), while the intermediate species (species whose densities approach N/2) contribute the most information to the H' evenness component (Farger 1972). H' is also more severely affected by equal changes in the abundance of rare species than of dominants, although dominant species are not completely ignored (Peet 1974). Thus, comparisons of D and H' may reveal, in some cases, whether evenness changes are due to rare or common species.

Because the exclusion of rare species has a large effect upon the relative magnitude of H' (Peet 1974, Whittaker 1972), the H' index is susceptible to severe sampling errors when too small an area is sampled (Pielou 1977). To counter this effect and yet permit comparisons between other statistical techniques used, the five replicate quadrats of each SMU are pooled for the calculation of heterogeneity, richness, and total abundance. The use of a larger sample size also increases the chance of obtaining a more representative accounting of the true species proportions within an assemblage.

There are two reasons why it is better to lump the quadrats first and then to derive heterogeneity and richness, rather than to average indices calculated from the individual replicates. Firstly, heterogeneity indices are rarely additive since each of the pooled samples would have to have completely unique species compositions, but the same degree of heterogeneity. Furthermore, species richness can only be additive when replicates have no species in common. Calculation either before or after averaging produces the same results for total abundance.

NICHE BREADTH

According to Levins (1968), the breadth of a species' niche can be assessed in terms of the extent or evenness of its distribution through a range of habitats, or degrees of the availability of an important resource. Allan (1975), Pielou (1972), and Colwell and Futayama (1971), further elaborated Levins' mathematical model, and extended it to permit simultaneous comparisons of the heterogeneity of species abundances through several habitats or resources.

Habitat can be partitioned into two dimensions in this study, time and depth. In terms of these two habitat dimensions, the total niche breadth of ith species is (Allan 1975):

$$B(t)_i = -\sum_{j=1}^{q} \sum_{k=1}^{u} \{(n_{ijk}/n_{i..}) \log_2 (n_{ijk}/n_{i..})\}$$

where i, j, and k, and, s, q, and u are subscripts for species, time, and depth, respectively. A dot in place of a subscript indicates summation for all values of that subscript, as is standard notation.

In the same fashion as the partitioning of the squares in an ANOVA model, the total niche breadth is separated into two components whose magnitudes reflect the relative contributions of a species' distribution through depth and time.

The time-related niche breadth of the ith species is (Allan 1975):

$$B(m)_i = -\sum_{j=1}^{q} \{(n_{ij}./n_{i}..)\log_2(n_{ij}./n_{i}..)\}$$

The niche breadth of the ith species at the jth time (the term in brackets) is weighted by the proportion of individuals occurring at that time to produce the average depth-related niche breadth (Allan 1975):

$$B(d)_i = B(t)_i - B(m)_i$$

$$= \sum_{j=1} (n_{ij}./n_{i}..) - \sum_{k=1}\{[(n_{ijk}/n_{ij}..)\log_2(n_{ijk}/n_{ij}.)]\}$$

Note that since the depth component of B(t) is nested within the component for time, the niche breadth model requires that the same number of depths be sampled each month.

The ratio of B(m) to B(t) provides an index (INB) of the degree of vertical restriction that exists in a species range. When a species is relatively restricted in depth, most of the breadth of its total niche, is due to the heterogeneity of its dispersion through time, and it will have a value of INB that is close to unity. When the indivduals of a species are approximately evenly apportioned between depth and time, the value of INB is nearly equal to (t)/(t+d), where t and d represent the respective number of time and depth units in use.

CLUSTER AND INVERSE CLUSTER ANALYSES

The Pair-group Method

Cluster analysis is a method of classifying entities into successively larger hierarchical groupings based upon multivariate information contained in each entity. Originally applied to behavioral sciences, clustering techniques have been adapted and greatly elaborated by numerical taxonomists who use lists of morphometric attributes to classify taxa of organisms (Sneath and Sokal 1976). The same methods are used to order ecological data, except sites or samples are compared instead of taxonomic units, and the attributes consist of the abundance values of the species that are in the samples.

The data matrix of species in samples is used to generate a hemi-matrix of similarity values for every possible pair of samples. This similarity matrix is utilized in the clustering procedure to produce groups of samples with the highest possible internal similarity. The outcome of a cluster analysis is highly dependent upon the choice of both the clustering strategy and the similarity index. The Bray-Curtis similarity index is used in this study, and is presented in detail in the next section.

The unweighted pair-group method (Sokal and Michner 1958) used in this study is among the most straightforward and widely used clustering procedures. In what is known as the first clustering cycle, the pair of samples with the highest

similarity is fused as a cluster and the similarity index is saved as the clustering level of the first group. The two rows of the similarity matrix which correspond to the pair are replaced by one row which contains the arithmetic average of the two rows, for every column. The same basic procedure is carried out in successive cycles, with clusters being treated in the same fashion as individual samples, until all of the samples have been fused into a single group. A dendrogram is used to illustrate the hierarchical amalgamation of the samples. Inversion of the entire site-species data matrix permits the clustering of species on the basis of some measure of abundance in the various samples by the same procedure. This technique is referred to a inverse cluster analysis (Sneath and Sokal 1976).

The Bray-Curtis Similarity Index

The Bray-Curtis similarity index is used in this study not only because it has been employed in a large number of ecological studies, but also because it is relatively simple and, thus, produces easily understood results. In general terms, a simple index of the minimum abundance shared between the hypothetical samples A and B is expressed as (Motyka et al. 1950):

$$I_s = 2\left(\sum_{i=1}^{s} c_i\right)/N_A + N_B$$

where c_i is the minimum abundance of the ith species that is common to both sites and N is the total abundance in each sample.

Mean density is the abundance measure used to calculate the similarity matrix for the gastropods of this study. A double-standardization is performed upon the matrix in order to reduce values of density for all species to scales of comparable range, and to prevent a small number of species of wide-ranging abundance from automatically dominating the remainder (Williams 1971). The maximum abundance value of each species is reset to 100, and the remaining values scaled accordingly. Then the values in every sample are adjusted so that the total abundance in each sample is 1.0.

With double standardization the similarity index reduces to (Bray and Curtis 1957):

$$I_{BC} = \sum_{i=1}^{s} c_i$$

This index ranges from 0 to unity when there is 100% similarity between samples.

The Bray-Curtis index is insensitive to unique species and zero-zero matches. Because of the standardization and the use of minimum, rather than average, shared abundance, the index reduces the numerical dominance of one site over another.

RESULTS

The Gastropod Assemblage

Most of the analytical methods employed in the characterization of the gastropod assemblage require that the same number of depths be sampled in each month. Samples from October, Station 4 and November, Station 1 were wet-sorted and yielded suspiciously low mean densities for most species, presumably because the presence of large amounts of seaweed in the collections made it difficult to find the small gastropods. These two samples were, therefore, omitted, and this precluded the use of October and November samples in most analyses. Unless explicitly indicated, all analytical results given below pertain only to the 200 quadrats (40 SMUS) collected over a 10 month period from December, 1975 through September, 1976.

ABUNDANCE

The mean densities of 16 species of high abundance are plotted as a functions of station and month in Appendix C. The time-depth dispersion patterns of the remaining 10 species are cited in tabular form in Appendix D.

Table I lists the total densities of all 26 species found in 200 pooled quadrats. The most abundant species, Margarites costalis had a total density of approximately 3000 per square

Table I. Densities of twenty-six gastropod species in two hundred quadrats collected from December, 1975 through September, 1976.

SPECIES	DENSITY		
	RANK	no./QUADRAT	CUMULATIVE %
Margarites costalis	1	130.316	48.0
Lacuna marmorata	2	83.800	78.8
Alvania compacta	3	36.455	92.3
Lacuna carinata	4	8.768	95.5
Granulina margaritula	5	6.065	97.8
Odostomia sp.	6	1.543	98.3
Lirularia lirulata	7	0.865	98.6
Cerithiopsis sp.	8	0.790	98.9
Mitrella gouldii	9	0.670	99.2
Admete circumcincta	10	0.536	99.4
Margarites olivaceus	11	0.480	99.7
Notoacmea scutum	12	0.250	99.7
Diaphana californica	13	0.185	99.8
Alvania carpenteri	14	0.150	99.8
Amphissa columbiana	15	0.135	99.8
Balcis micans	16	0.115	99.9
Collisella pelta	17	0.075	99.9
Bittium eschrichtii	18	0.055	99.9
Cerithiopsis stejnegeri	19	0.050	99.9
Ocenebra interfossa	20	0.040	99.9
Nassarius mendicus	21	0.030	99.9
Velutina laevigata	22	0.030	99.9
Crepipatella lingulata	23	0.020	99.9
Acmaea mitra	24	0.015	99.9
unidentified sp.	25	0.010	99.9
Turbonilla vancouverensis	26	0.005	100.

meter. Margarites costalis, Lacuna marmorata, and Alvania compacta comprised 92% of the individuals taken from December, 1975 through September, 1976, while Lacuna carinata and Granulina margaritula contributed another 5%.

Table II reveals the variability in the relative contributions of mean abundance and occurrence to density. Margarites costalis was usually the most abundant species in a quadrat. Lacuna marmorata was, on the average, three times more abundant, per occurrence, than Alvania compacta yet L. marmorata occurred less frequently than either A. compacta or M. costalis.

All but the five dominant species occurred in less than half of the samples. Three species had extremely low abundances. Acmaea mitra, an unidentified rissoid and Turbonilla vancouverensis were represented by one, two, and three individuals, respectively.

A classification scheme based upon the relative values of mean occurrence and abundance is shown in the fourth column of Table II. Species of the first group occurred frequently in high numbers. Those which are placed into the second category had relatively high frequencies yet low mean abundances. The third type of species were numerous within rare clumps. The fourth grouping is a catch-all for species of low density which are either truly rare, or could be included in either the second or third categories, but with little confidence.

For most of the species, density decreased through the winter to minimal values in April, followed by recruitment in

Table II. Occurrence and mean abundance of twenty-six gastropod species found in two hundred quadrats collected from December, 1975 through September, 1976. See text for an explanation of species groupings based upon occurrence and abundance.

SPECIES	OCCURRENCE		MEAN ABUNDANCE	GROUP
	RANK	no. of QUADRATS		
Margarites costalis	1	189	137.90	I
Alvania compacta	2	185	39.40	I
Lacuna marmorata	3	161	104.10	I
Granulina margaritula	4	131	9.26	I
Lacuna carinata	5	128	13.70	I
Odostomia sp.	6	98	3.15	III
Mitrella gouldii	7	57	2.35	II
Lirularia lirulata	8	56	3.09	III
Admete circumcincta	9	47	2.28	II
Cerithiopsis sp.	10	35	4.51	III
Margarites olivaceus	11	30	3.20	III
Notoacmea scutum	12	23	2.17	II
Diaphana californica	13	23	1.61	II
Balcis micans	14	20	1.15	II
Amphissa columbiana	15	16	1.69	IV
Alvania carpenteri	16	10	3.00	III
Cerithiopsis stejnegeri	17	10	1.00	IV
Collisella pelta	18	7	2.14	III
Bittium eschrichtii	19	5	2.20	III
Ocenebra interfossa	20	5	1.60	IV
Velutina laevigata	21	5	1.20	IV
Nassarius mendicus	22	4	1.50	IV
Crepipatella lingulata	23	3	1.33	IV
Acmaea mitra	24	2	1.00	IV
unidentified sp.	25	2	1.00	IV
Turbonilla vancouverensis	26	1	1.00	IV

May and June and peak densities through September. Nassarius mendicus was the only species not found during the summer. Five species, Collisella pelta, Velutina laevigata, Acmaea mitra, Turbonilla vancouverensis, and the unidentified rissoid were absent from the winter collections. Another seven, Lirularia lirulata, Admete circumcincta, Diaphana californica, Amphissa columbiana, Notoacmea scutum, Balcis micans, and Cerithiopsis sp. were rarely encountered in the winter.

Twelve species were found at all depths. They were: Margarites costalis, Lacuna marmorata, Alvania compacta, Lacuna carinata, Granulina margaritula, Odostomia sp., Lirularia lirulata, Admete circumcincta, Margarites olivaceus marginatus, Balcis micans, and Cerithiopsis stejnegeri.

The dispersion patterns of the 11 most important species are briefly described below. Species of lesser abundance were too sporadically distributed for meaningful descriptions. Time-blocked analyses of variance were performed on M. costalis, L. marmorata, A. compacta, L. carinata, and G. margaritula using data from the 200 quadrats (Table III). The other six species described occurred in less than half of the quadrats and so ANOVA could not be used.

Margarites costalis and Lacuna marmorata had similar dispersion patterns (Appendix C). Both species generally showed a decrease in numbers with depth but no significant differences between stations 1 and 2 (Duncan's New Multiple Range Test $p=0.01$, Table III). L. marmorata had its maximum density at station 2 in July and M. costalis peaked at station 2 in July,

Table III. Time-blocked analyses of variance of mean density at four stations using ten monthly blocks. Each station was sampled with five replicate quadrats. Density was transformed as: $Y=\log_{10}(n+1)$.

SPECIES	p[1]		HOMOGENEOUS GROUPS OF STATIONS WITH DUNCAN'S NMR TEST[2]
	DEPTH	TIME	
Margarites costalis	<.001	<.001	(1 2) (3) (4)
Lacuna marmorata	<.001	<.001	(1 2) (3) (4)
Alvania compacta	NS	NS	
Lacuna carinata	<.001	<.01	(1) (2 3) (4)
Granulina margaritula	<.01	NS	(1) (2) (3 4)

[1] Probability of the difference between mean densities being due to chance.

[2] $\alpha=0.01$

August, and September.

The mean density of Alvania compacta varied little between stations 2 and 3. During most of the winter, most A. compacta were found at station 2, but the maximum abundance occurred at station 1 in July (Table III, Appendix C).

Lacuna carinata was most abundant at station 1 in the spring and summer (Table II, Appendix C) but had a winter peak at station 2 in February. Few L. carinata were found at station 4 or during samples from October through January.

There is a noteworthy dissimilarity between the dispersion pattern of L. carinata and those of L. marmorata and M. costalis. Recruitment of Lacuna carinata occurred earlier and at a shallower depth than the other two species.

The abundance of Granulina margaritula decreased continuously with depth although the difference between stations was greater in the summertime. There was relatively little month-to-month variation at stations 1 and 2 (Appendix C).

Except for a slight peak at station 3 in December, the density of Odostomia was greatest at station 2, throughout the year. The differences between stations 1, 2, and 3 were slight except during September when the species attained its maximum abundance of 11 per quadrat at station 2. The late summer peak was the only major seasonal change observed for Odostomia sp.

Lirularia lirulata was mostly limited to stations 1, 2 and 3 between June and August, with a definite peak at station 2 in July (Appendix C).

Cerithiopsis sp. was restricted to stations 1 and 2, and was rarely found in the fall samples (Appendix C). The density peak was at station 2 in April, but after June, cerithiopsis sp. was only observed a station 1.

Mitrella gouldii was more frequently encountered than Cerithiopsis sp. but usually at a lower density (Table II). There was a fall peak for M. gouldii at station 2 and a summer peak of slightly greater magnitude at station 1. M. gouldii was rare at stations 3 and never found at 4.

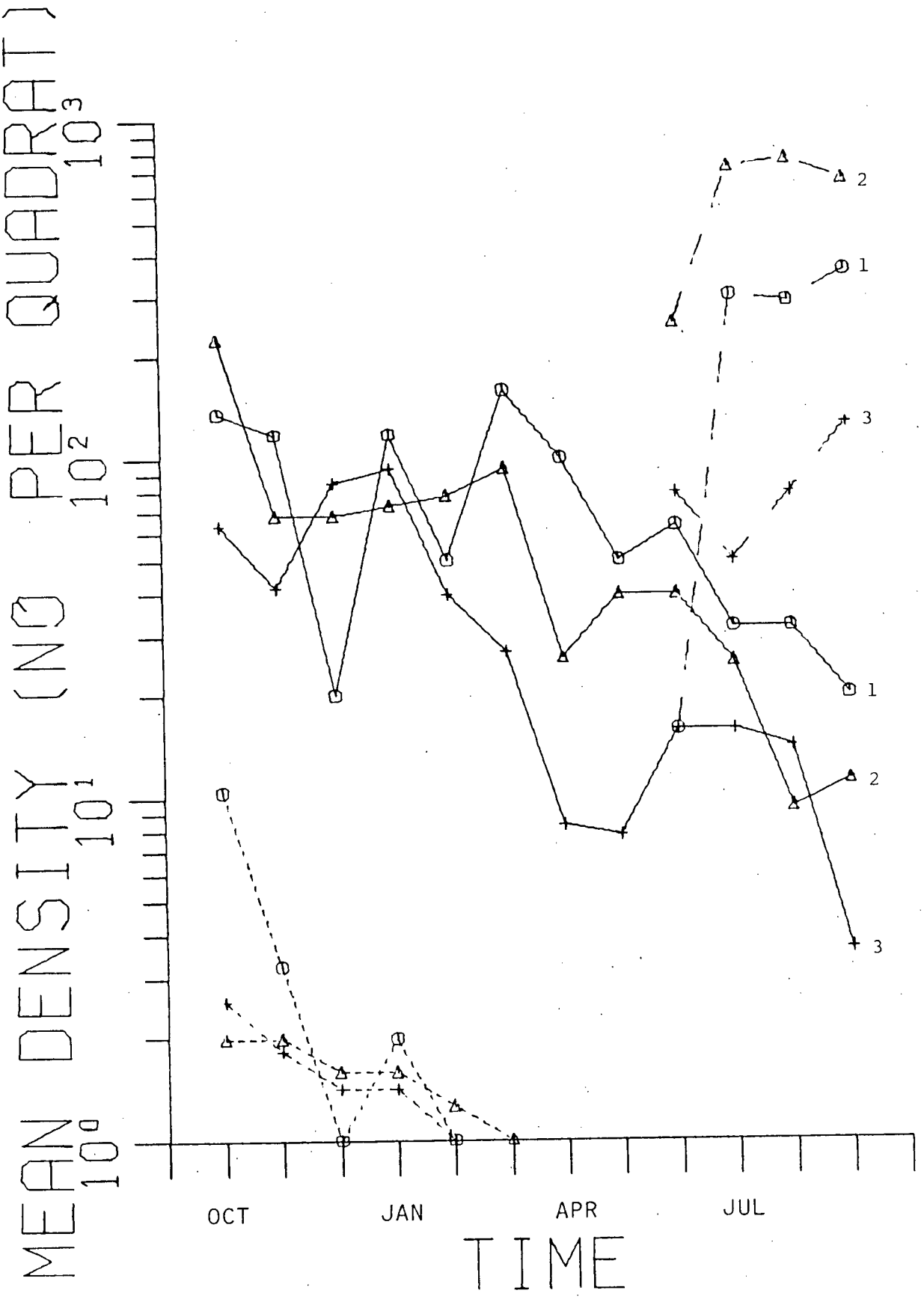
Admete circumcincta was found at station 3 in December, but only had appreciable abundance from April through September. Most of the A. circumcincta were at station 2.

Margarites olivaceus was the only species which had greater abundance at stations 3 and 4 than the shallower stations. This species was only numerous in July, August, and September.

The Margarites costalis population was partitioned into three generations on the basis of shell length. There were only slight depth-related differences in importance for the oldest (first) generation (Figure 5). No first generation snails were collected after February, 1976, so the maximum age of M. costalis at Saturnina Island is apparently 22 months.

Margarites costalis was consistently less abundant at station 3 than at stations 1 and 2, for all three generations. Values of abundance were so low at station 4 that they are not included in Figure 5.

Figure 5. Mean density versus time for Margarites costalis of three generations at stations 1, 2, and 3. Numerals on the graph relate the stations at which snails were collected. Small dashes, first generation; solid lines, second generation; large dashes, third generation.


MEAN DENSITY (NO PER QUADRAT)
10^3
10^2
10^1
10^0
OCT
JAN
APR
JUL
TIME
1
2
3
1
2
3

Most of the M. costalis collected from October, 1975, through May, 1976, belonged to the second generation. During the fall and winter months, there was little difference in the number of second generation M. costalis at station 1,2, and 3. From March through September, however, there was a greater decrease in numbers with depth for the second generation.

Third generation M. costalis were most numerous at station 2 during the summer. This caused species abundance to be maximal at station 2 at times when the greatest numbers of adult snails were found at station 1.

There were no differences between the mean shell lengths of second generation M. costalis from stations 1 and 2, but shells were slightly smaller (Figure 6), and the rate of length increase was significantly slower at station 3 (Table IV). Size differences between stations were not significant for the other two generations of Margarites costalis.

NICHE-BREADTH

Niche-breadth indices, which were computed for all species occurring in the 10 month collection of 200 quadrats, are presented as functions of species rank in Figure 7.

Alvania compacta had the largest total niche-breadth indicating that this species was the most evenly dispersed. Some species, such as Bacis micans, Alvania carpenteri, and Cerithiopsis steinegeri, occurred frequently yet possessed relatively broad niches because of constant, though slight

Figure 6. Shell length versus time for Margarites costalis of three generations at stations 1, 2, and 3. Lengths were recorded in millimeters with a vernier caliper. Numerals on the graph relate to the stations at which snails were collected. Small dashes, first generation; solid lines, second generation; large dashes, third generation.

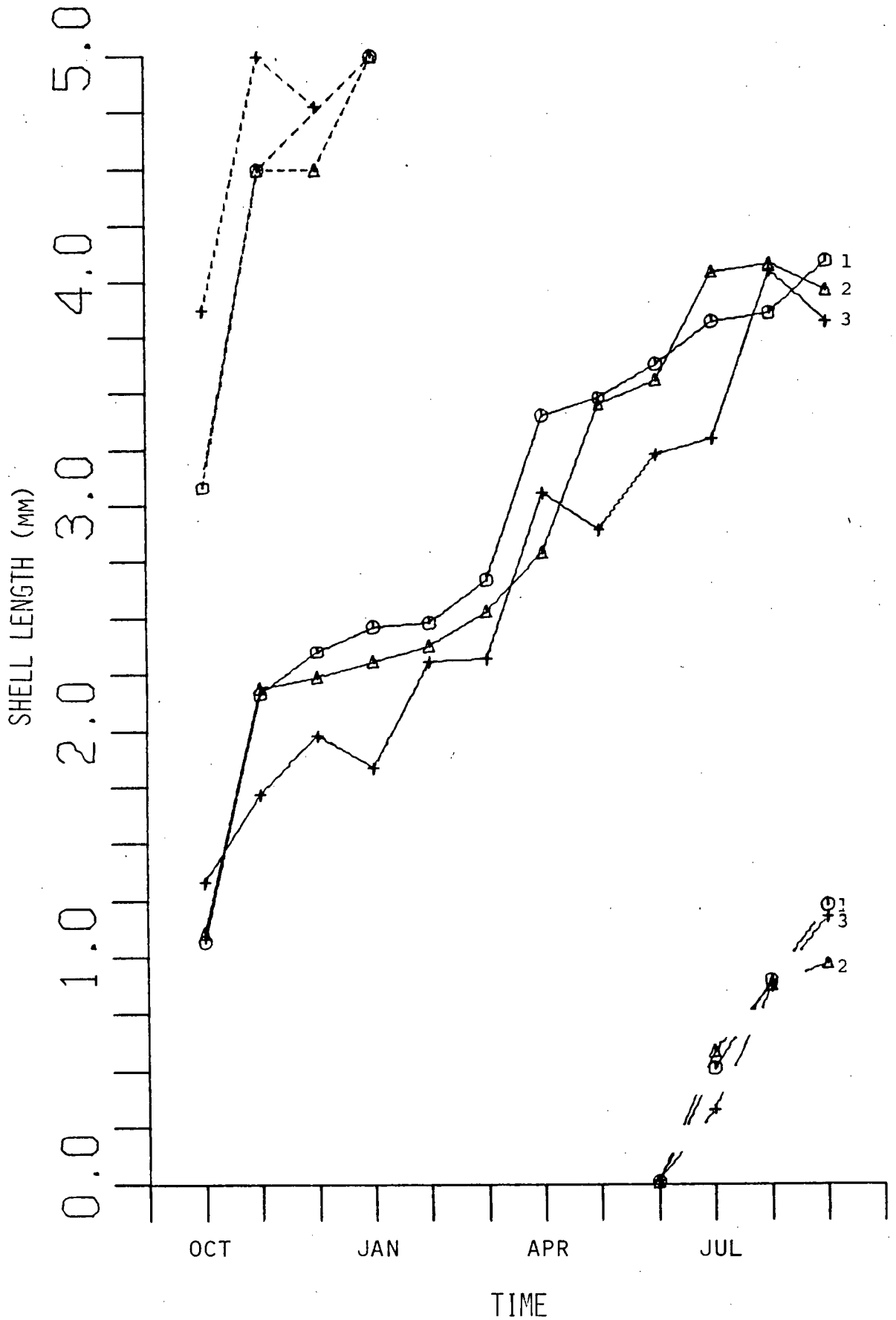

SHELL LENGTH (MM)
0.0
1.0
2.0
3.0
4.0
5.0
OCT
JAN
APR
JUL
TIME
1
2
3
1
3
2

Table IV. Differences in shell length increase in mm as a function of time for *M. costalis* at stations 1, 2, and 3.

GENERATION	STATION	LINEAR REGRESSION[1]	p[2]	HOMOGENEOUS GROUPS OF STATIONS WITH SHEFFE'S TEST[3]
1	1	Y=2.835+.291X	NS	(1 2 3)
	2	Y=2.875+.285X		
	3	Y=2.866+.218X		
2	1	Y=1.609+.226X	.0003	(1 2) (3)
	2	Y=1.439+.213X		
	3	Y=1.315+.244X		
3	1	Y=-3.51+.405X	NS	(1 2 3)
	2	Y=-2.43+.397X		
	3	Y=-3.62+.402X		

[1] (SHELL LENGTH)=b+a(MONTH) with October, 1975 considered month 1.

[2] F-TEST for equality of slopes.

[3] Subsets are based upon slopes of regressions.

average abundances per occurrence (Table II, Appendix C). These species are relatively evenly dispersed (Figure 7b).

The values of INB are plotted for all 26 species (Figure 7a). There are 10 time categories and 4 for depth, so therefore INB should approach 0.71 (=10/10+4) when a species is as evenly distributed among the time as the depth dimension.

On the basis of INB values, six species groupings can be distinguished (Table V). The members of group I were the seven most important species and were found in most of the SMUs although niche-sizes and dispersion patterns varied considerably. The five species of group II had INB values slightly below 0.71, indicating that the small depth and time restrictions in the dispersion of these species were of approximately equivalent magnitudes. The species of group III occurred in less than four stations but the relative restrictions of these species through time were less severe than for depth and thus the INB values were slightly greater than 0.71. Group IV consists of six species which were found in several monthly collections but at only one depth per month. Turbonilla vancouverensis occurred in a single SMU and had the narrowest possible niche (B(t)=B(d)=B(m)=0). The only species which displayed a value of B(d) that was greater than B(m) was Collisella pelta. This species was present for only three months (33% of the time categories considered in the calculation of niche-breadth) but occurred at three different stations (75% of the sampled vertical range). Because of the severe relative time restriction in its range through time,

Figure 7. INB (A) and total niche breadth (B) for the gastropod species. The gastropods were collected in 200 quadrats in 10 monthly samples. See text for explanations of the niche breadth indices.

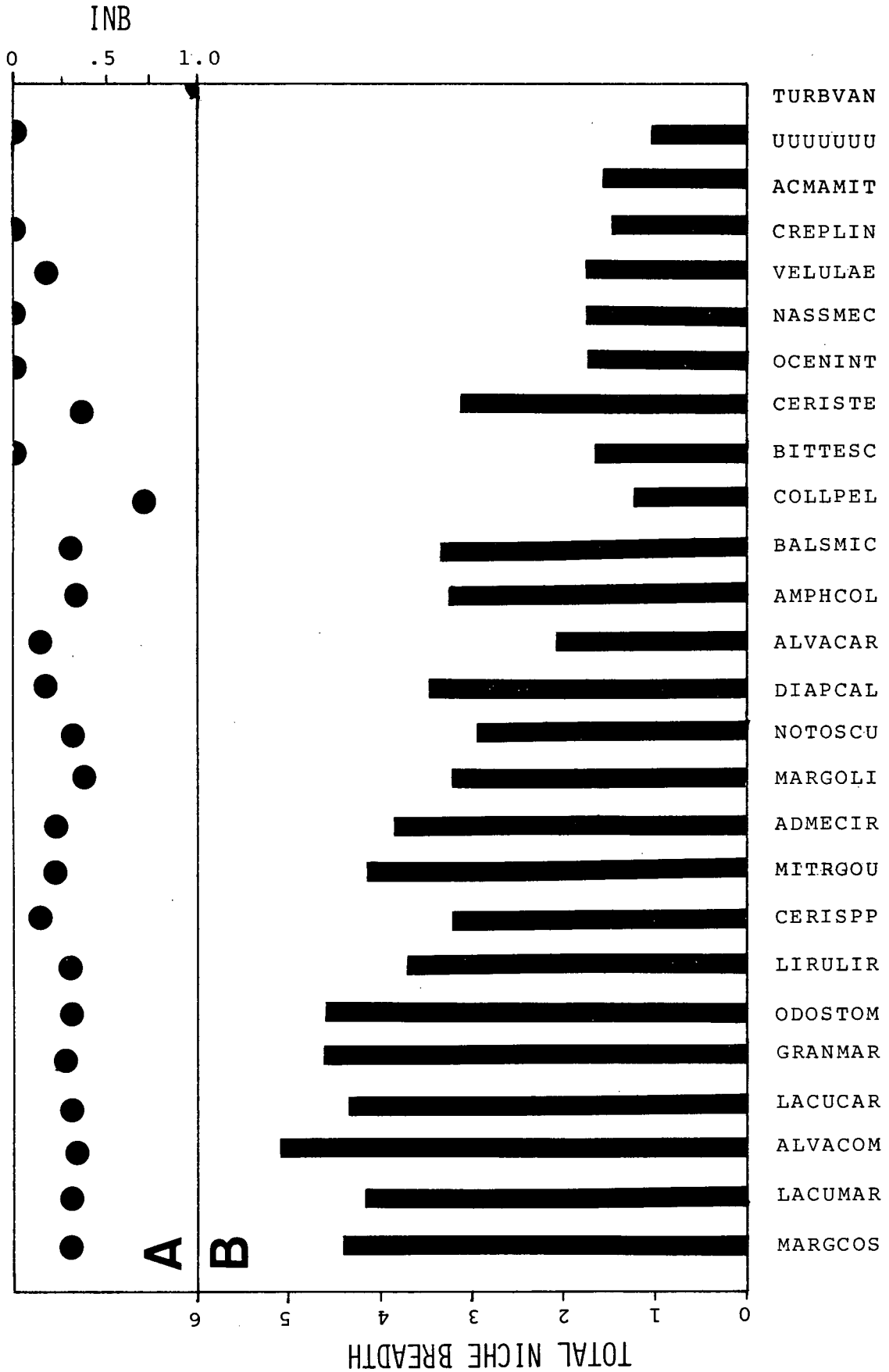

INB
0
.5
1.0
TURBVAN
UUUUUUU
ACMAMIT
CREPLIN
VELULAE
NASSMEC
OCENINT
CERISTE
BITTESC
COLLPEL
BALSMIC
AMPHCOL
ALVACAR
DIAPCAL
NOTOSCU
MARGOLI
ADMECIR
MITRGOU
CERISPP
LIRULIR
ODOSTOM
GRANMAR
LACUCAR
ALVACOM
LACUMAR
MARGCOS
A
B
0
1
2
3
4
5
6
TOTAL NICHE BREADTH

Table V. Classification of gastropod species by the ratio B(m)/B(t)=INB, which is explained in text.

GROUP I	INB≃.7 Species which span all depths at most times	
	Margarites costalis	*Alvania compacta*
	Lacuna marmorata	*Granulina margaritula*
	Lacuna carinata	*Odostomia* sp.
	Lirularia lirulata	
GROUP II	INB<.7 Species as restricted in depth as time	
	Notoacmea scutum	*Cerithiopsis stejnegeri*
	Margarites olivaceus	*Amphissa columbiana*
	Balcis micans	
GROUP III	INB>.7 Species more depth than time restricted	
	Cerithiopsis sp.	*Admete circumcincta*
	Mitrella gouldii	*Diaphana californica*
	Alvania carpenteri	*Velutina laevigata*
GROUP IV	INB=1. Species restricted to one depth per month	
	Bittium eschrichtii	unidentified sp.
	Nassarius mendicus	*Acmaea mitra*
	Ocenebra interfossa	*Crepipatella lingulata*
GROUP V	INB<.5 Species more time than depth restricted	
	Collisella pelta	
GROUP VI	INB=0. Species restricted to one depth and time	
	Turbonilla vancouverensis	

Table VI. Spearman rank correlations and linear regressions of total niche breadth, B(t), to total density and occurrence for twenty-six gastropod species.

INDEPENDENT VARIABLE	γ_s	t for γ [1]	t for regression [2]
TOTAL DENSITY	0.89	9.68[3]	4.61[3]
OCCURRENCE	0.94	13.64[3]	8.41[3]

[1] $t=\gamma_s[(25)/(1-\gamma_s^2)]^{\frac{1}{2}}$

[2] The regression equation is:

$$B(t)=b+a[\log_{10}(X+1)]$$

[3] Probability of the observed correlation or slope of the regression line being due to chance $\leq$ .001.

C pelta ranks 24th in total niche-breadth compared to a density rank of 17.

Total niche-breadth was more strongly correlated to frequency of occurrence than to species density (Table VI). Ranked by decreasing values of B(t), the first seven species are A. compacta, G. margaritula, Odostomia sp., M. costalis, L. carinata, L. marmorata, and M. gouldii, which is different from the order by frequency of occurrence (Table II). This discrepancy can be attributed to the fact that B(t) is dependent upon both the number of encounters and the evenness in the abundance of a species among the encounters (Levins 1968).

SPECIES RICHNESS, TOTAL ABUNDANCE AND SAMPLE HETEROGENEITY

The mean densities of gastropods from all 46 SMUs were used to calculate S, N, D, and H'. These results are shown as contour maps in Figures 8 and 9.

Species richness (Figure 8a) and total abundance (Figure 8b) were greater in the summer than in the winter, at all depths. The highest values of S and N were found at stations 1 and 2. Time-blocked ANOVAS and Duncan New Multiple Range tests (Table VII) showed that values of S and N at station 1, 2, and 3 were significantly different ($p=0.01$) from values at station 4.

The contour maps of D (Figure 9a) and H' (Figure 9b) are similar, and can be treated together. Although analyses of

Figure 8. Species richness and the total abundance of the gastropod assemblage. Contoured against the station and month of collection. Total abundance transformed by:

$$Y=\log_{10}(N+1)$$

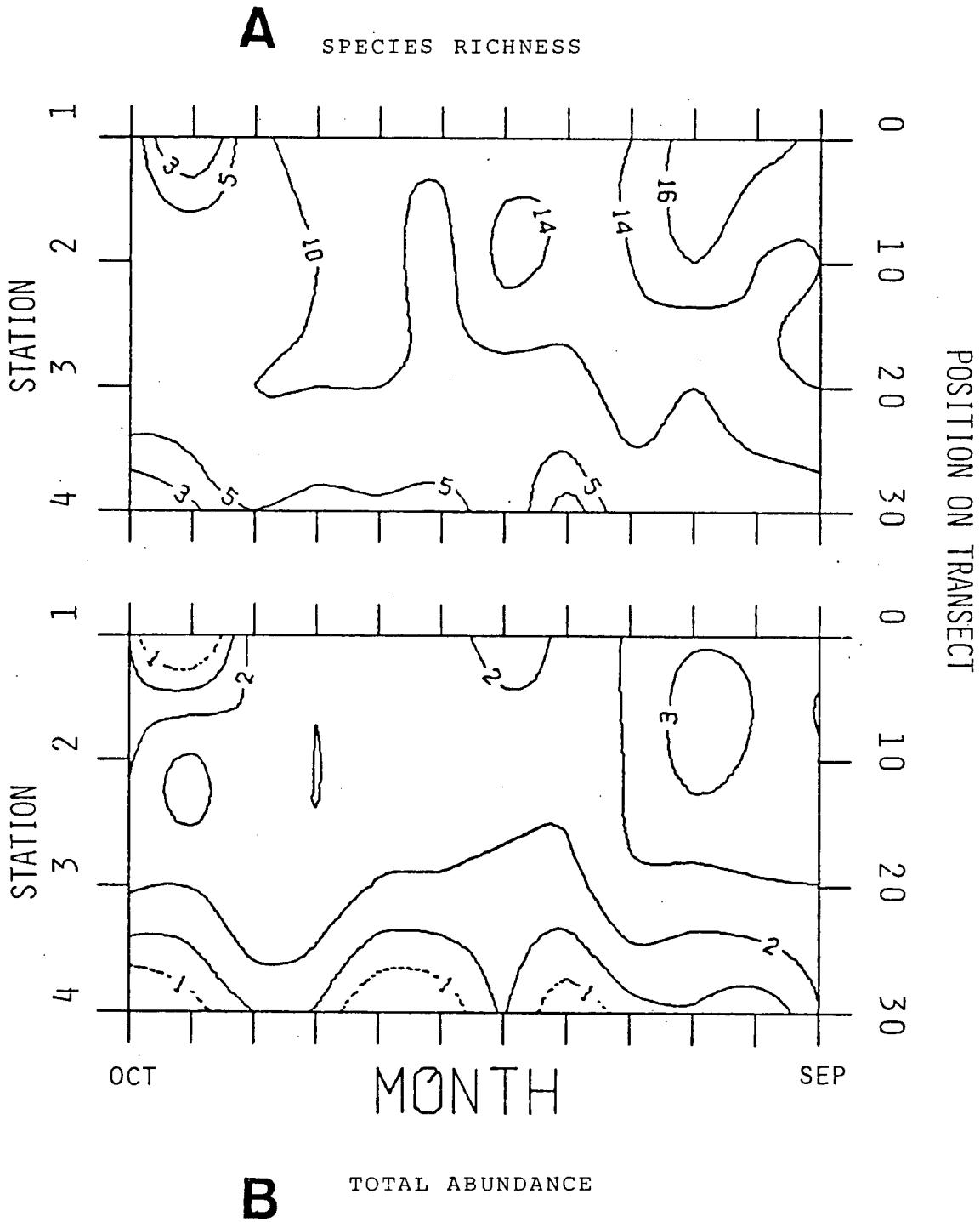

A
SPECIES RICHNESS
STATION
1
2
3
4
0
10
20
30
POSITION ON TRANSECT
3
5
10
14
16
B
TOTAL ABUNDANCE
1
2
3
OCT
MONTH
SEP

Figure 9. Gastropod species diversity expressed at Simpson's D (A) and H (B). Values are contoured against the station and month of collection.

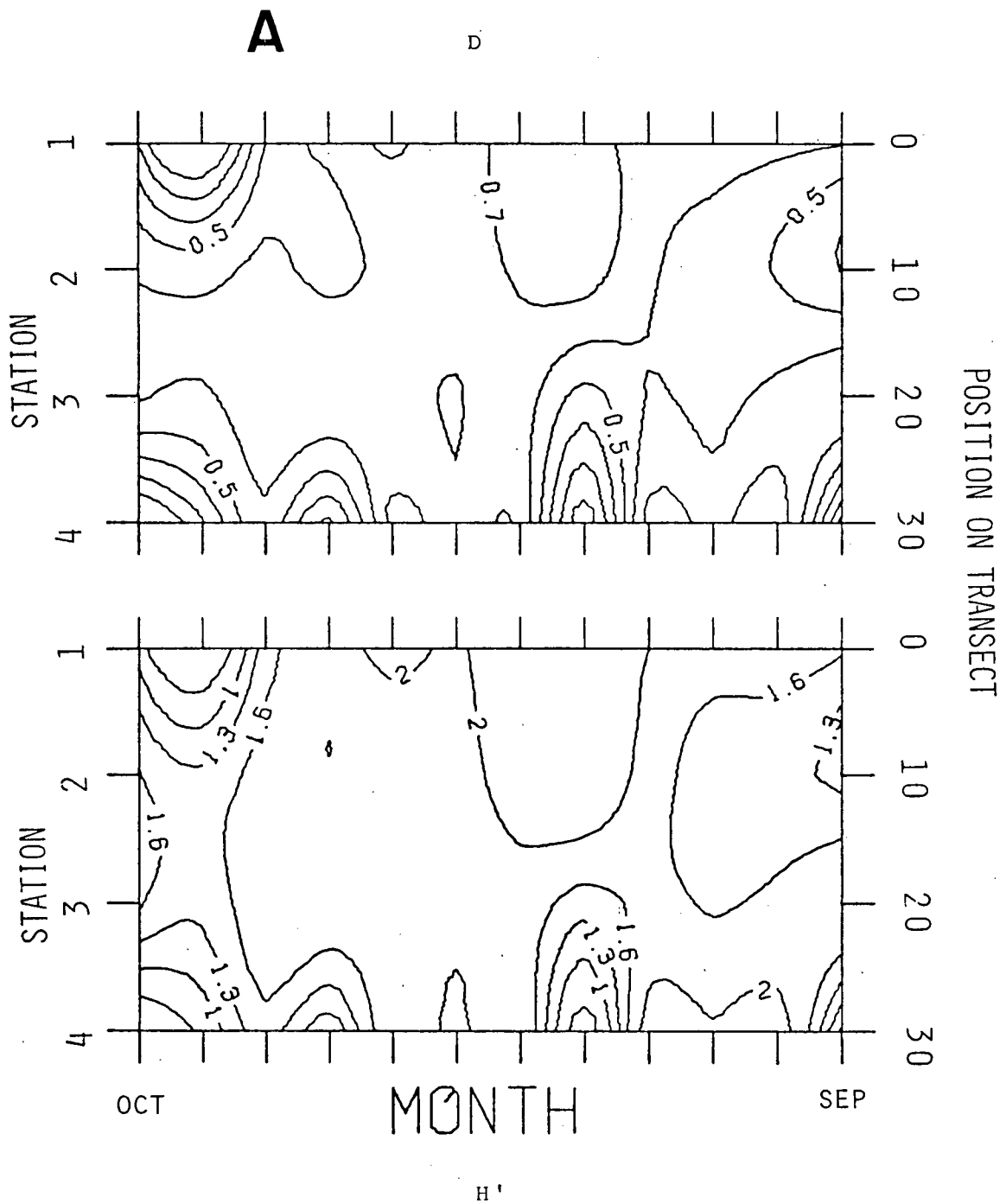

A
D
STATION
1
2
3
4
0.5
0.7
0.5
0.5
0.5
0
10
20
30
POSITION ON TRANSECT
STATION
1
2
3
4
1.6
1.3
1
1.6
2
2
1.6
1.3
1.6
1.3
1
1.6
2
0
10
20
30
OCT
MONTH
SEP
H'
B

Table VII. Time blocked analyses of variance for assemblage parameters in four stations using ten monthly blocks. Replicate quadrats were pooled as discussed in text.

DEPENDENT VARIABLE	MEAN	p[1]		HOMOGENEOUS GROUPS OF STATIONS WITH DUNCAN'S NMR TEST[2]
		DEPTH	TIME	
S	9.35(1.01)[3]	.001	.0035	(1 2 3) (4)
N	248(2.40)[3]	.001	NS	(1 2 3) (4)
D	.601	NS	NS	
H'	3.09	NS	NS	

[1] Probability of the difference between sample means being due to chance.

[2] $\alpha=0.01$

[3] Parentheses for transformed means where $Y=\log_{10}(Y+1)$ were used.

variance for these indices indicate no significant changes with station and month (Table VII), definite trends are visible. Sample heterogeneity was minimal in the fall at all depths, at station 4 in the winter and spring, and at station 2 in the late summer. High values of D and H' were found in the spring at station 1, and in the summer at station 4. The remainder of the SMUs possesed roughly the same intermediate degree of heterogeneity in the apportionment of individuals among species.

CLUSTER ANALYSIS OF THE SAMPLES

Cluster analysis of the SMUs using the Bray-Curtis index was performed upon 21 of the gastropod species in all 46 SMUs. Four of the species collected, *Crepipatella lingulata*, *T. vancouverensis*, *A. mitra*, and the unidentified rissoid occurred in fewer than four SMUs, and were excluded from the analysis. *C. pelta*, was also eliminated because of its narrow niche (Figure 7b).

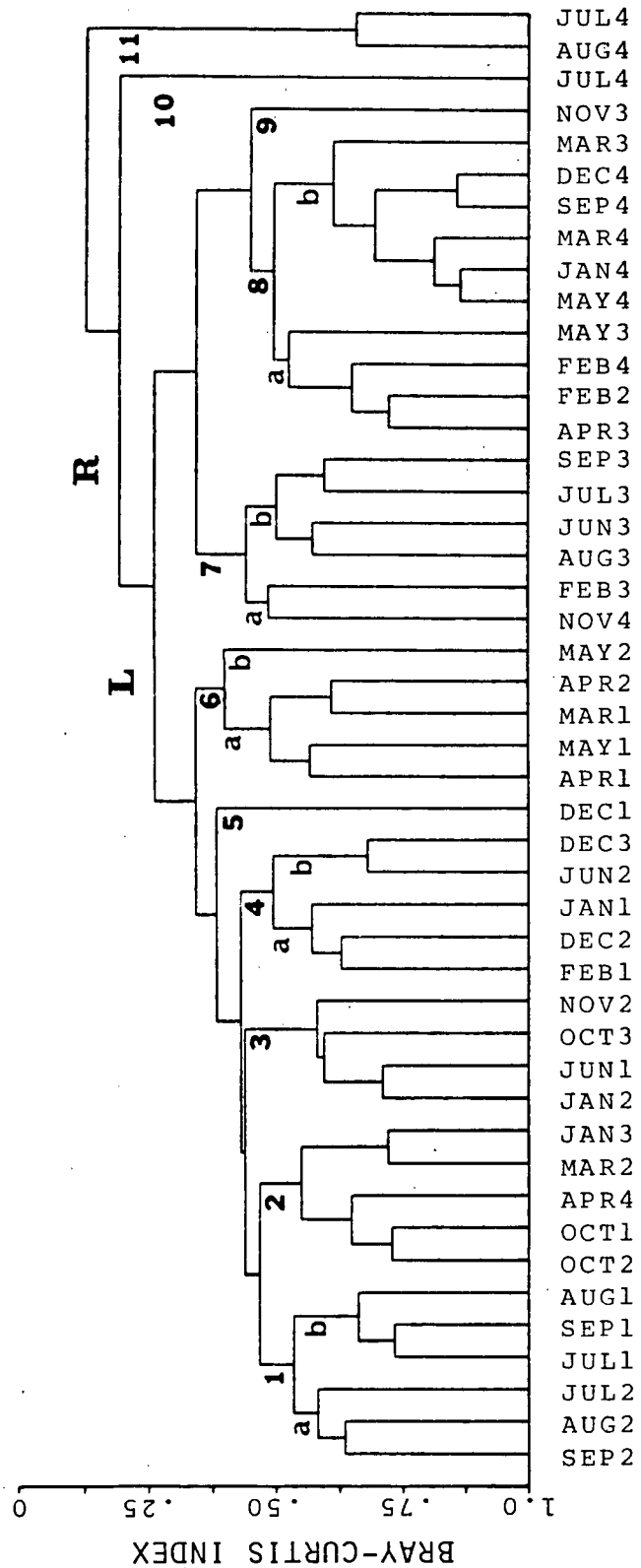
All but three SMUs on the dendrogram (Figure 10) are grouped into either a shallow or a deep super-cluster. 22 SMUs from stations 1 and 2 are included in the left-hand supercluster (L), which consolidates at a similarity level of 0.33. All but one of the 17 samples grouped into the right-hand supercluster (R) at 0.45 are from stations 3 and 4. The 0.25 similarity between R and L suggests that there was a large degree of overlap in the species present in shallow and deep

sampling units. Seasonal trends are less apparent, but at every depth, summertime SMUs are placed within distinct clusters.

Within L, the summer samples from stations 1 and 2 are separated into two sub-groups of cluster 1. These SMUs had greater numbers of individuals and species than any other samples, but differed most in the relative abundance of Margarites costalis, which was most numerous at station 2 in the summer. The remainder of L is comprised of six clusters which are chained together in order of decreasing similarity with the shallow summer samples. The SMUs in cluster 4 (December, stations 2 and 3, January and February station 1, and June station 2) had about half the number of M. costalis, L. marmorata, and A. compacta that were encountered in the cluster 1 samples. The December SMU from station 1, which is alone in cluster 5, was low in M. costalis, but was otherwise similar to the samples in cluster 4, to which it is linked. Most of the samples of cluster 6 (March, April, May at station 1 and May at station 2) are high in M. costalis, L. marmorata, and L. carinata, but are low in A. compacta. The May station 2 sample had fewer L. carinata, but more L. marmorata than the other samples in cluster 6, and therefore joins the group at a lower level of similarity.

The samples included in R have few species and low values of total abundance. Within cluster 8b, samples from station 4 in March, May, and June contained species with very low abundances. The remainder of cluster 8b are SMUs that also had few snails, but on the average more than ten A. compacta per

Figure 10. Dendrogram of cluster analysis of SMUs on the basis of species abundance. Each of the 46 SMUs that were considered consisted of five pooled quadrats. Numerals on the dendrogram correspond to groupings which are described in the text.


JUL4
AUG4
JUL4
NOV3
MAR3
DEC4
SEP4
MAR4
JAN4
MAY4
MAY3
FEB4
FEB2
APR3
SEP3
JUL3
JUN3
AUG3
FEB3
NOV4
MAY2
APR2
MAR1
MAY1
APR1
DEC1
DEC3
JUN2
JAN1
DEC2
FEB1
NOV2
OCT3
JUN1
JAN2
JAN3
MAR2
APR4
OCT1
OCT2
AUG1
SEP1
JUL1
JUL2
AUG2
SEP2
R
L
11
10
9
8
7
6
5
4
3
2
1
a
b
1.0
.75
.50
.25
0
BRAY-CURTIS INDEX

quadrat. Cluster 8a contains all of the summertime samples from station 3, as well as SMUs from station 4 in November and station 3 in February. The principal species in these samples are A. compacta, L. marmorata, and M. costalis, but the total abundance values that were recorded were low, and so cluster 8a joins cluster 8b, before the other clusters located in L.

Station 4 sites from June, July, and August are classified separately on the dendrogram and fuse with all other samples at a level of less than 0.20.

INVERSE CLUSTER ANALYSIS OF THE SPECIES

Inverse cluster analysis was performed with the same data as were used for the regular cluster analysis. As a means of interpreting the relationships between the gastropod species expressed in the inverse-cluster dendrogram (Figure 11), a Spearman rank correlation coefficient was computed for every possible pair of the 21 species (Figure 12), and comparisons were made between the contour maps of species density vs. station and month (Appendix C). Correlation coefficients were calculated with species abundance values from individual quadrats rather than from means of replicates. The increase in sample size and degrees of freedom allows the Spearman coefficient to become more critical of interspecific correlations (Siegel, 1956).

There are 13 species-clusters shown on the dendrogram in Figure 11. The five species of lowest and most sporadic

Figure 11. Dendrogram of inverse cluster analysis. Analysis was performed on 21 gastropod species in 46 SMUs. Numerals on the dendrogram correspond to groupings which are described in the text.

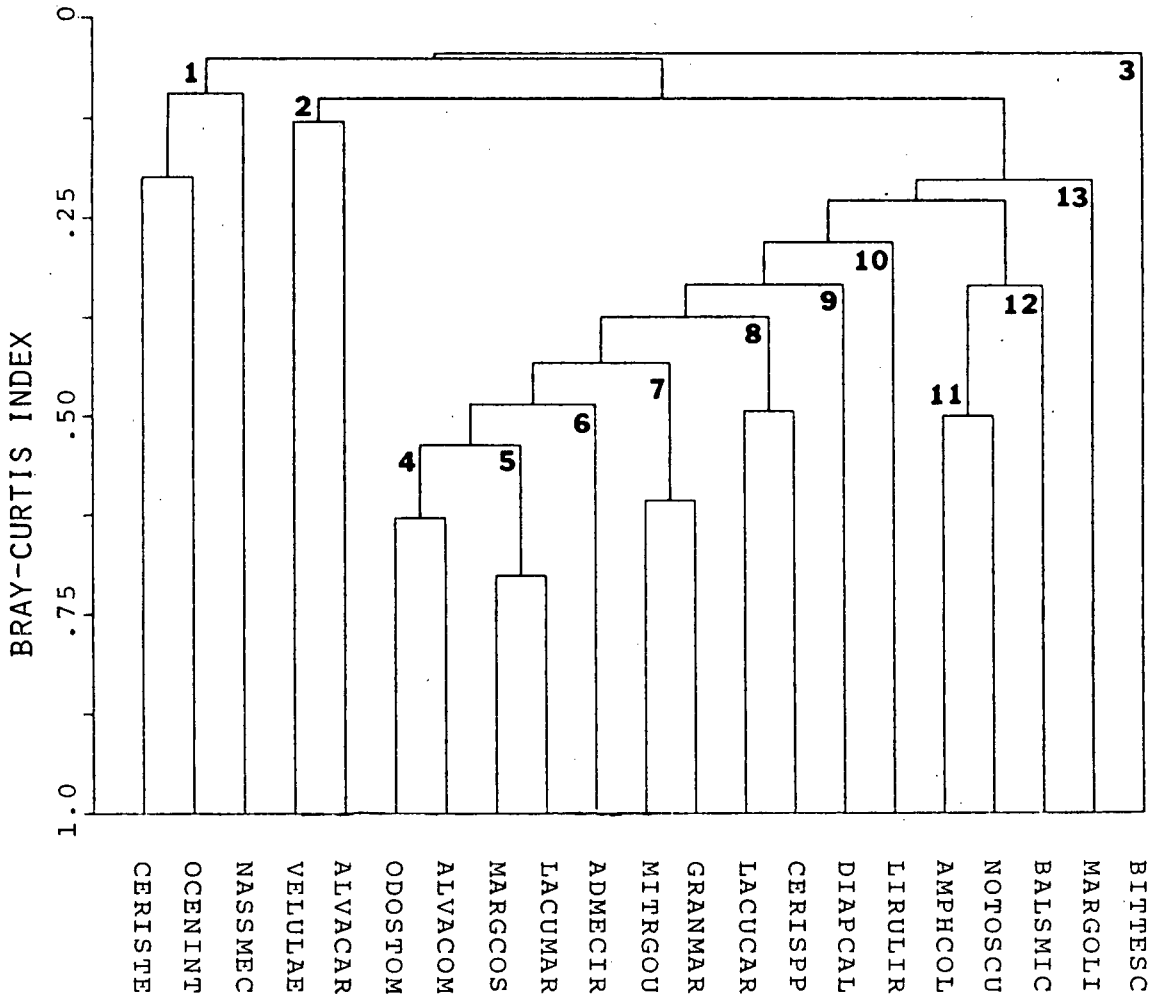
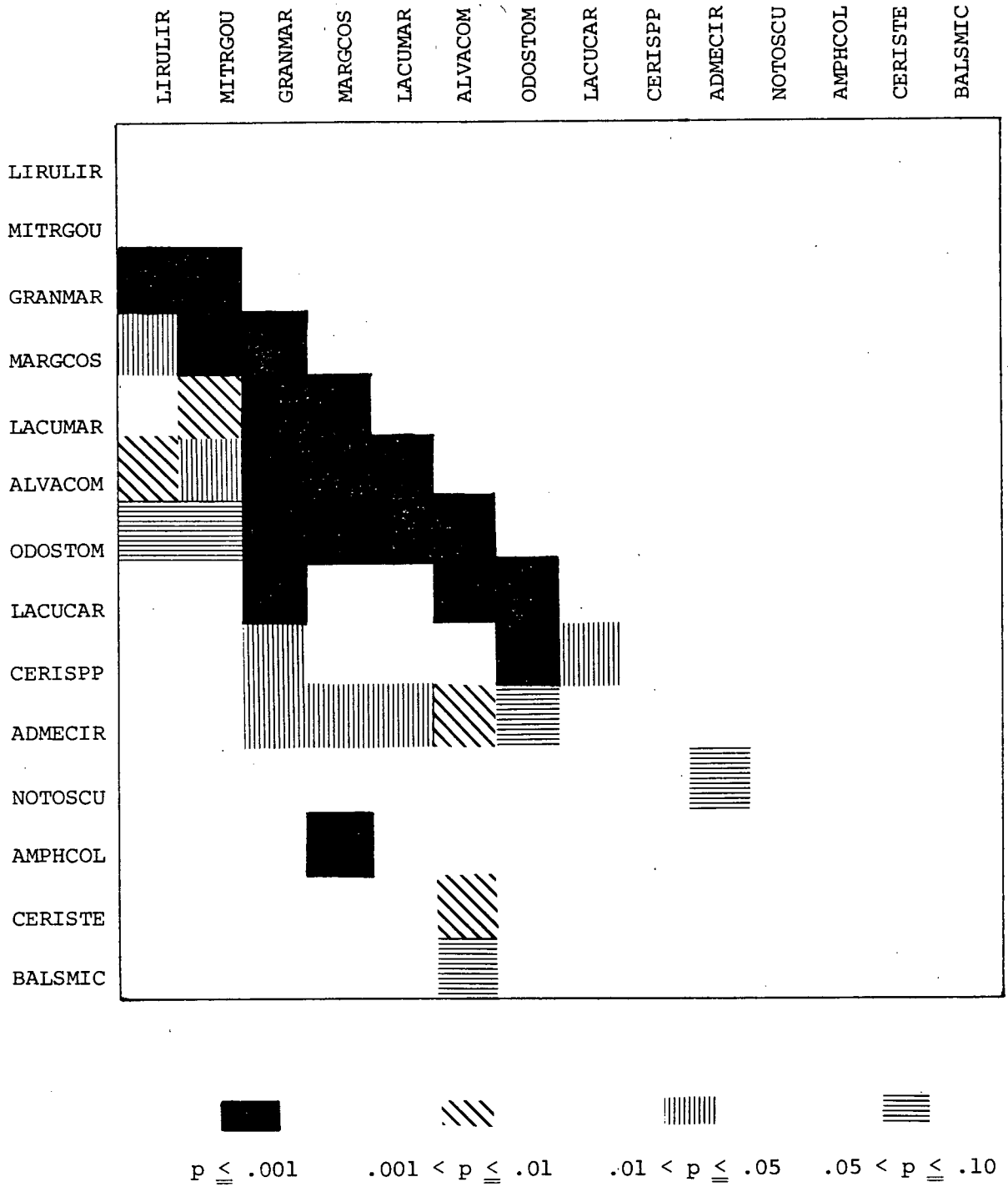

BRAY-CURTIS INDEX
0
.25
.50
.75
1.0
1
2
3
4
5
6
7
8
9
10
11
12
13
CERISTE
OCENINT
NASSMEC
VELULAE
ALVACAR
ODOSTOM
ALVACOM
MARGCOS
LACUMAR
ADMECIR
MITRGOU
GRANMAR
LACUCAR
CERISPP
DIAPCAL
LIRULIR
AMPHCOL
NOTOSCU
BALSMIC
MARGOLI
BITTESC

Figure 12. Spearman rank correlation matrix of gastropod species. Correlations were based upon values of abundance in 200 quadrats, and were performed for a total of 21 species, but only 14 which showed significant correlations were included in the matrix. Probability was determined from the one-tailed probability of *t* (see Table X).


LIRULIR
MITRGOU
GRANMAR
MARGCOS
LACUMAR
ALVACOM
ODOSTOM
LACUCAR
CERISPP
ADMECIR
NOTOSCU
AMPHCOL
CERISTE
BALSMIC
p ≤ .001
.001 < p ≤ .01
.01 < p ≤ .05
.05 < p ≤ .10

importance, Cerithiopsis steinegeri, Ocenebra interfossa, Nassarius mendicus, Velutina laevigata, and Bittium eschrichtii, clustered seperately from all of the other species, except Alvania carpenteri. Since there are no greater than two joint occurrences for any pair of these five species (table in Appendix B), the calculated similarities are of questionable validity. Alvania carpenteri is grouped with Velutina laevigta, but the two species only occurred together in two samples.

The remaining 15 species are grouped into 10 clusters which are joined in a stepwise--or "chained"-- fashion, indicating a large amount of overlap in dispersion patterns. This result agrees favorably with the interspecific correlations and the contour maps. Five of the 10 clusters contain pairs of species while the other five contain one species each.

The pairing of A. compacta with Odostomia sp., M. costalis with L. marmorata, and L. carinata with Cerithiopsis sp. are reasonable, considering the correlation and contour map information. There is a highly significant correlation between M. gouldii and G. margaritula, and the two species have coincident peaks of importance at station 1 throughout the year, but M. gouldii was seldom found deeper than station 2, while G. margaritula, which appears to be more similar to A. compacta and Odostomia sp., occurred in all four stations. In contrast, the contour maps of Notoacmea scutum and Amphissa columbiana which are grouped together on the dendrogram, are

quite similar, but there is no significant correlation between the two species.

Admete circumcinta occurs in a separate cluster which is fused to a group containing both clusters 4 and 5. This species correlates significantly with all four species that are in the group, as well as to Granulina margaritula and Notoacmea scutum, but the highest correlations and the greatest amount of contour map overlap are with Alvania compacta and Odostomia sp.

Lirularia lirulata is also clustered solitarily, but correlates to Margarites costalis, Odostomia sp., Alvania compacta, and most strongly, to Granulina margaritula. The contour map of L. lirulatus bears partial resemblance to all of the above-mentioned species, as well as to that of Diaphana californica. Although it is restricted almost entirely to stations 1 and 2, and displays no interspecific correlations, the contour map of D. californica has some similarities to those of M. costalis and L. marmorata, as well.

Balcis micans of cluster 12 is grouped to Amphissa columbiana and Notoacmea scutum on the dendrogram. But B. micans is correlated only with A. compacta, and at a low level of significance.

Margarites olivaceus, which was the only species in cluster 13, showed no correlations with other species, and had a unique distributional pattern.

Alvania carpenteri was only found at station 1, and had a time-depth dispersion which was similar to Lacuna carinata and Cerithiopsis sp. of cluster 8.

Gut Analyses

Qualitative observations of the gut contents of all nine species that were examined revealed the presence of great numbers of diatoms with few cells which could definitely be attributed to other organisms (Table VIII). The size of ingested diatoms ranged from under 10 um (e.g. Cocconeis scutellum) to over 150 um in length (Synedra fasciculata). Easily digested organisms and organic debris were probably ingested to some degree by all diatom-grazing species, but could not be identified. It is particularly difficult to separate ingested bacteria from the resident micro-flora of the gastropod gut (Calow 1975, Galli and Giese 1959).

Some specimens of L. marmorata also contained portions of cyanophyte and rhodophyte filaments as well as bryozoan fragments. Two large adult M. gouldii were found that had consumed an encapsulated mass of veligers belonging to the opisthobranch Styliger fuscovittata in addition to diatoms.

Table VIII. Gut content summary. The presence of a type of food is denoted by an X.

SPECIES	N	MATERIAL FOUND AS GUT CONTENTS			
		DIATOM	RHODOPHYTE	CYANOPYHTE	OTHER
Margarites costalis	30	X			
Lacuna marmorata	30	X	X	X	X[1]
Alvania compacta	10	X			
Lacuna carinata	10	X			
Granulina margaritula	10	X			
Cerithiopsis sp.	2	X			X[2]
Mitrella gouldii	2	X			
Lirularia lirulata	10	X			
Margarites olivaceus	10	X			

[1] Bryozoan fragments in two individuals

[2] Encapsulated opisthobranch veligers.

Diatom Abundance

Figure 13 shows the densities of diatoms on slides retrieved from July 22, 1976, through March 14, 1977, after two week immersion periods at either station 1,2, or 3. The average number of cells per square mm decreased significantly with depth (Table IX). At all times, except in July, the relative trends in density were similar at all three stations (Figure 13). In July, densities were high at station 1 and relatively low at station 2 and 3. Diatom abundance fluctuated during the late summer with peaks on August 5 and September 9, and a depression in between on August 19. The lowest diatom densities occurred in December followed by an increase to March 1 at all three stations on June 18, 1976, abundances were so great as to render counting impossible. Therefore, diatom abundance was probably continuously high throughout the recruitment periods of most of the gastrods.

Diatom abundance was compared to the mean densities of eight gastropod species, N, S, and H', using the Spearman rank correlation coefficient with portions of the previously described data (Table X). Since the gastropods from the fall were collected in 1975, and the diatoms were from the fall of 1976, these correlations might have limited applicability.

Diatom density was strongly correlated to N, S, H', and the densities of A. compacta, L. carinata, and L. lirularia. The relationships between the densities of diatoms and the two

Figure 13. Diatom density in mm^2 versus date of collection at stations 1,2, and 3. Numerals on the graph correspond to station numbers. Diatom densities in June were too great to be ennumerated at all three stations.

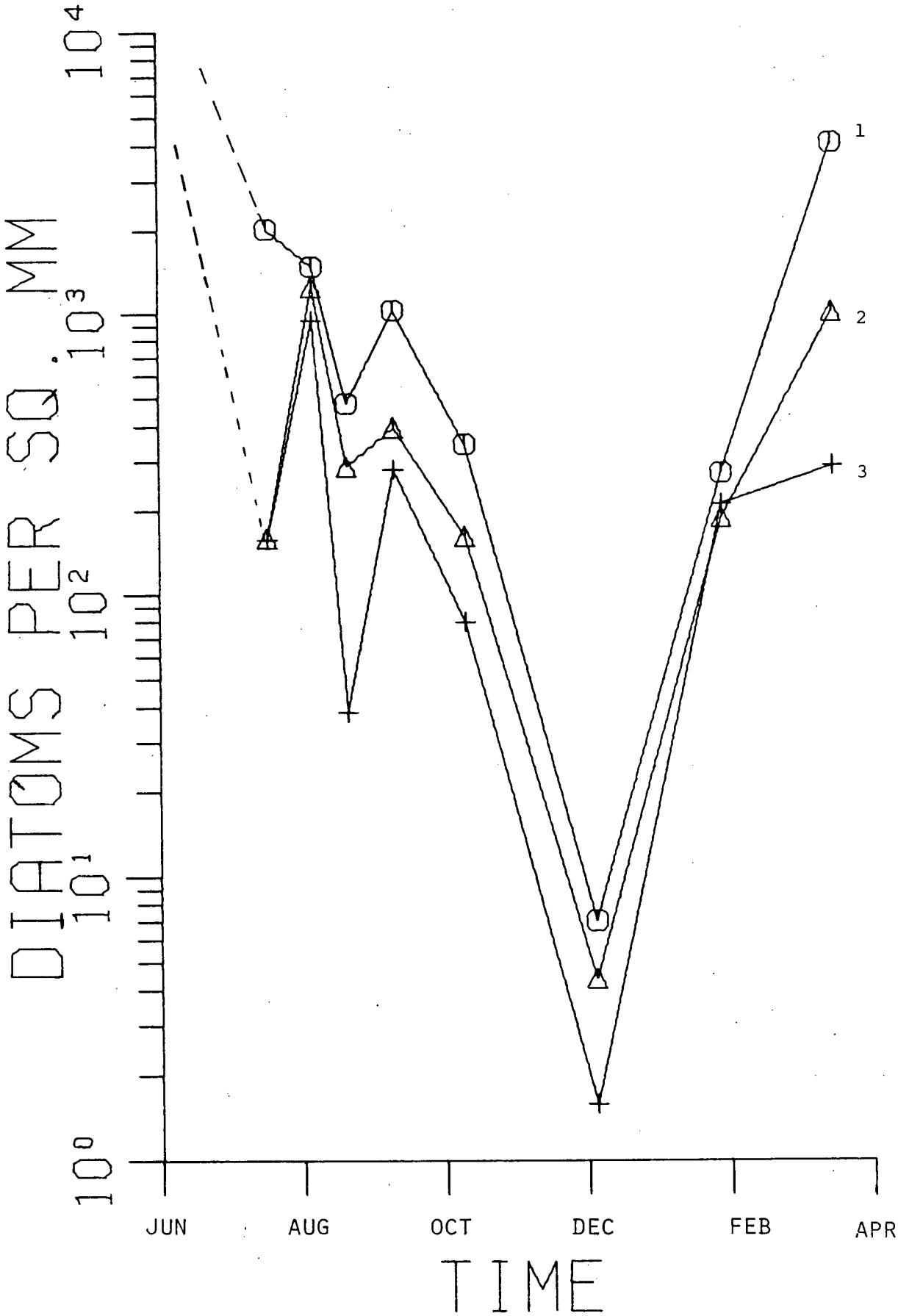

DIATOMS PER SQ. MM
10^0
10^1
10^2
10^3
10^4
1
2
3
JUN
AUG
OCT
DEC
FEB
APR
TIME

Table IX. Time-blocked analysis of variance for diatom density on glass slides at three stations in eight monthly blocks.

SOURCE	p[1]	HOMOGENEOUS GROUPS OF STATIONS WITH DUNCAN'S NMR TEST[2]
STATION	<.001	(1) (2) (3)
MONTH	<.001	

[1] Probability of the difference between mean densities being due to chance.

[2] α=.01

Table X. Spearman rank correlations of gastropod species and assemblage parameters to diatom density. All data from gastropod samples collected at the same stations and months as the diatoms were used regardless of the year of collection.

VARIABLE	df	p[1]
N	19	<.005
S	19	<.05
H'	19	<.005
M. costalis (all generations)	19	<.025
M. costalis (excluding juveniles)	19	NS
L. marmorata	19	<.05
L. carinata	19	<.0005
A. compacta	19	<.0005
G. margaritula	16	NS
M. gouldii	15	NS
L. lirulata	14	<.025
M. olivaceus	8	NS

[1] The one-tailed probability of positive correlation being due to chance where p is derived from *t* and:

$$t=\gamma_s[(df)/(1-\gamma_s^2)]^{\frac{1}{2}}$$

dominant gastropods, M. costalis, and L. marmorata were also significant, but to a lesser degree. When juvenile M. costalis were excluded from the analysis, the relationship no longer existed. The dispersions of M. gouldii and M. olivaceus were not correlated to diatom abundance.

Feeding Experiment

In eight experimental trials, more Margarites costalis were found in contact with live Plocamium cartilagineum than with either heat or hydrogen peroxide treated fronds (Table XI). The dead material averaged the least number of contacts. M. costalis may be attracted to the live algae because it contained higher surface concentrations of diatoms. This view is supported by the fact that an average of 10 snails per cage per trial were found upon the plastic mesh cage covers which developed dense diatom growths during each experimental period of 24 hours.

Table XI. One-way classification analysis of variance for the number of *M. costalis* in contact with *Plocamium cartilagineum* of three treatments. See text for an explanation of the three treatments and the experimental design.

SOURCE	MEAN[2]	df	F	p	HOMOGENEOUS GROUPS OF TREATMENTS WITH DUNCAN'S NMR TEST[1]
TREATMENT					
A (live)	2.0				
B (clean)	0.5	2	5.91	<.01	(A) (B C)
C (dead)	0.25				
ERROR		21			
TOTAL		23			

[1] $\alpha=0.01$

[2] Mean number of contacts in eight trials.

DISCUSSION

Characterization Of The Gastropod Assemblage

Maximum development of the gastropod assemblage occurred in the summertime. Large numbers of small, post-larval individuals, seen in the period between April to June for most species, caused increases in population densities and species richness. Only one species was found in the winter that was not also present in the summer, although a few were restricted entirely to the summer collections. The species which were encountered only seasonally were probably present year round but at such low densities that they could be detected only after recruitment, when densities were high.

Species richness and the abundance of most species decreased with depth. Thorson (1933) noted the same trend for M. costalis and other animals inhabiting seaweed in two fjords of northeastern Greenland. The epifauna rarely extended as deeply as the host macrophytes, Desmarestia and filamentous red algae. In this study, however, the absolute depth to which the fauna could reach was not determined since the the red-algal zone at Saturnina Island is interrupted by a bed of eelgrass at an approximate depth of 6.5 m. The few gastropods collected at station 4, on the fringe of the eelgrass community (Figure 2), were entirely restricted to the relatively small boulders and

blades of Agarum cribosum.

The assemblage was dominated year-round by five species which ranged to all depths, but were more numerous at the shallower stations. Most other species were more restricted vertically. This extreme numerical dominance had a heavy influence upon values of N, D, H', and the Bray-Curtis similarity index.

Although S and N showed similar trends through depth and time, the contour map of N bears even stronger resemblance to those of M. costalis and L. marmorata, due to these species' high densities. Total importance, therefore, yielded little information concerning the overall assemblage.

Cluster analysis with the unweighted pair-group method and the Bray-Curtis index grouped samples principally by depth, but summer samples were separated from all others within each station. Closer consideration of the contents of the SMU clusters revealed that the analysis was based almost completely upon the dominant three gastropods, and ignored any information concerning the time-depth dispersions of the remaining species. A similar problem was encountered by Rex (1977), who found that cluster analysis with a related index of similarity (a quantified version of the Jaccard index, Sepkoski 1974) fused deep-sea samples by order of the abundance of the numerically dominant gastropod, Alvania pelagica.

The cluster analysis was successful in the sense that a large (242 x 20) data matrix was reduced to groupings of samples that were based upon more than 80% of the individual

snails collected. This is the primary purpose for using a multivariate approach to data analysis (Sneath and Sokal 1976, Green and Vascotto 1978). Superficially, the analysis seemed to represent the entire assemblage because many species had dispersion patterns which were similar to the the dominants. Had the lesser species displayed more varied vertical or temporal distributions, it is doubtful that the cluster analysis would have provided any indication.

The inverse cluster analysis was reasonably sensitive to similarities in the distributions of species with high densities, but those with intermediate to low frequency of occurrence tended to be joined when no real similarities existed. This sort of error is common to hierarchical schemes which are designed to classify all of the units that are included in an analysis (Pielou 1977, Williams 1971). The process of interpreting the inverse analysis led to direct comparisons of species dispersions, which ultimately proved to be more useful. The co-dominants, M. costalis and L. marmorata, had the greatest similarity in dispersions, a fact reflected by inverse analysis, the Spearman correlation coefficients and the superimposition of the contour maps. No other species had distributions which even remotely approached this degree of overlap.

The relative abundance of the species, i.e. the evenness, did not fluctuate greatly and most SMUs had equivalent values of the two heterogeneity indices, H' and D. Most changes in heterogeneity were caused by fluctuations in the numbers of

species encountered. The only exception occurred in the summer samples from stations 1 and 2, when both heterogeneity indices were insensitive to the large number of species that were present. This was because of a severe drop in evenness associated with the large increases in L. marmorata and Margarites costalis.

Both the depth and time components of niche-breadth were partially dependent upon abundance, in that values were generally slight for species of low density. Some species (e.g. Balcis micans and Diaphana californica) had relatively large values for the niche-breadth indices despite low mean density. These species had relatively constant, though low, densities through the resource dimensions of time and/or space. The relationship between abundance and niche-breadth was more pronounced for the depth component, B(d), that is, species of low density were usually more evenly dispersed through time than depth, and characteristically displayed high INB values.

The classification schemes using frequency, mean abundance and niche-breadth provided information that was not as easily attainable from the contour maps of mean density. Species groupings based upon INB (Table V), however, showed only partial agreement with those utilizing the relative values of occurrence and abundance (Table II). This indicates that within a given group with a certain amount of time or depth zonation, there were species displaying varying degrees of clumping. For example, cerithiopsis sp. and M. gouldii were both restricted to 3 depths, but the first species was infrequently

encountered, though in relatively high numbers, while the other, M. gouldii, was present in many samples yet usually at a low density.

Very little confidence can be placed upon any findings regarding species of low density. The sampling method was adequate for species with high densities, whose representations varied little between replicate quadrats, but as the abundances of species dropped they tended to become increasingly sporadic in occurrence. This could well be an artifact, since there are decreased probabilities of encounter when species have low densities or are distributed into rare clumps, as could have been the case for species only observed during or just after periods of recruitment. Nonetheless, it is impossible to determine if a "rare" species was genuinely uncommon or had simply been undersampled without additional, more intensive sampling. In addition, rarely encountered species may have been localized into non-sampled areas between the stations or into micro-habitats such as crevices or the undersides of rocks.

It is likely that the limpets Acmaea mitra, Collisella pelta, Notoacmea scutum, and the snails Velutina laevigata, Crepipatella lingulata, which were low in abundance, are space competitors of macrophytic algae. These five gastropods were usually observed upon bare rock at Saturnina Island. Within a kelp-bed at Bath Island, 150 m distant (Figure 1), there is more rock than algal surface available at the bottom and limpets are relatively common.

The Potential Of Diatoms As A Gastropod Food Resource

Diatoms comprised a major portion of the gut contents for the nine species that were examined. Foods which are are eaten on an intermittent basis, or during non-sampled periods, may have been overlooked, since samples for gut analyses were obtained on only two occasions. Most of the diatom species observed on the microscope slides were found in the gut preparations.

Proportionately few of the diatom cells found contained cytoplasmic material, indicating that the gastropods which ingest diatoms are able to digest them as well. This agrees with Nicotri's (1977) finding that most diatom digestion by Collisella pelta and Notoacmea scutum was accomplished by chemical digestion through pores in the cell walls rather than by mechanical degradation. Cell damage could also be caused by the action of the radula during feeding. Measurements of the proportional representation of empty cells among the gut contents, while possible, were not attempted because digestive capabilities would have been overestimated for any species which consumed proportionately large amounts of empty frustules. In addition, the ratio of full to empty diatom cells should vary during the progression of a bolus from mouth to anus, but the dissection technique used did not allow determinations of the exact locations of observed materials in the snails' alimentary tracts. Using radiotracers, Calow (1975)

has successfully quantified digestion by microphagous prosobranchs.

Enzymes capable of degrading the algal constituents amylose and cellulose are widespread among the gastropoda (Owen 1966b) and have even been found among such species as the detritivore Nassarius reticulatus and the predator Nucella lapillus. There is not necessarily any correspondence between enzymatic complement and diet (Owen 1966b), but presumably any ingested material that is dissolved or mechanically reduced to particles in the foregut and stomach is available for digestion if suitable enzymes are present.

An experiment run by Powell (1964) showed that Lacuna sp. ingested Constantinea subulifera but Margarites sp. did not. The same design was used by Roland and Druehl (personal communication) who found definite circular lesions on discs cut from blades of Nereocystis luetkeana corresponded to weight losses over 72 hour periods in which L. marmorata were present in the jars. These findings are in keeping with the results of the gut analyses performed upon L. marmorata and M. costalis in this study. That is, L. marmorata guts were found to contain a variety of material such as bits of bryozoan skeleton and polysiphonous red algae as well as diatoms, while only diatoms were ever found within M. costalis.

Apparently, the feeding niches of the two dominant snails only partially overlap. Several species of Lacuna reportedly eat macrophytic algae (Fralick et al 1974, Fretter and Graham 1962, Ankel 1936) but published lists of the foods known to be

utilized by Margarites spp. do not include macrophytes (Fretter and Graham 1962). Two explanations for dietary divergence are the differences in radular morphology and mode of operation exhibited by the two genera. The rhipidioglossan radulae of Margarites, and all other Trochidae have fan-like arrays of marginal teeth which sweep small particles of food into the paths of the short and flattened rhachidial and lateral teeth which then carry the food into the mouth (Markel 1966, Fretter and Graham 1962). Lacuna has a taenioglossan radula with fewer marginals for brushing and longer and sharper lateral and central teeth that can rasp either small encrusting organisms or the surfaces of macrophytes (Yonge and Thompson 1977, Fretter and Graham 1962).

Some members of the genus Alvania can consume red algae, including Corallina, and detritus. The taenioglossan Cerithiopsis tubercularis is an eater of sponges and detritus (Fretter and Graham 1962), but Cerithiopsis sp. of this study ingested mainly diatoms and had a well developed crystalline style, which is an organ known to produce amalytic enzymes (Owen 1966b).

Diets were not determined for 17 of the 26 gastropod species encountered at Saturnina Island and must be inferred from published accounts. For many species there are no dietary records and the feeding habits of congeners must be used. The foods consumed by the limpets Acmaea mitra, Collisella pelta, and Notoacmea scutum have been reported elsewhere and include a wide variety of both micro- and macro-algae (Craig 1968, Test

1945, Castenholz 1961, Nicotri 1977). Velutina laevigata is known as a predator of solitary ascidians (Diehl 1956). Bittium reticulatum and Nassarius spp. are generally considered detritivores but Nassarius eat carrion as well. Ocenebra species are carnivores that bore through the shells of adult barnacles, bivalves and snails or eat juveniles entire. Three species, Odostomia sp., Balcis micans, and Turbonilla vancouverensis are members of the opisthobranch order Pyramidellidae which are probably all suctivorous ectoparasites of bivalves, snails, sessile polychaetes and coelenterates with various degrees of host-specificity (Fretter and Graham 1949, Clark 1971, Thompson 1976). The actual hosts of these species are unknown.

The Influence Of Diatom Abundance On Gastropod Distributions

A major feature of the diatom dispersion pattern, one held in common with the gastropods, was a decrease in numbers with depth. Aleem (1949) and Castenholz (1963) have reported the reverse trend for benthic diatoms in a temperate intertidal zone, where chances of desiccation increase with height on the shore. Because of sampling difficulties, there have been few quantitative studies of epiphytic and epilithic diatoms in the subtidal habitats (Round 1971). Montgomery et al. (1977) found evidence of depth-zonation on one of three coral reefs that

were investigated.

The decrease in incident illumination with depth is usually cited as the factor responsible for the characteristic depth-profiles of diatoms (Chandler 1944, Lund 1949, Gruendling 1971). The rate of photosynthesis is directly proportional to the intensity of light, but only when light is limiting (Rabinowitch and Govindjee 1969). It is, therefore, possible that the rate of production of benthic diatoms at Saturnina Island is being influenced by temperature (Patrick 1969, Round 1968, Hutchinson 1967, Wallace 1955), turbulence (Patrick 1969, Gruendling 1971), salinity (Williams 1964, Kain and Fogg 1958, Mc Intire and Overton 1971, Curl and Mc Leod 1961, Guillard and Ryther 1962, Simmons 1957), and nutrient availability (Lee et al. 1975, Round 1971), as well as other physical and chemical parameters which may vary with depth (Parsons, Takahashi, and Hargrave 1977).

Glass slides were used to estimate diatom abundance, but the densities actually relate to the rates of colonization over two-week periods, rather than to standing crop on the natural substrata, rock and seaweed. Presumably, rate differences on slides at the various depths and times are representative of the proportional differences in colonization upon the natural substrata. This assumption is, in part, justified by Castenholz's (1961) finding that little difference existed in the intertidal diatom assemblages upon various types of glass and the surfaces of wood and rocks that were in close proximity.

Little is known regarding the rates of colonization on rocks versus macro-algae, although Round (1971) indicated that epiphytic diatoms probably exhibited some degree of host-specificity. De Felice and Lynts (1978) noted that characteristic and separate associations of diatoms occurred on Thalassia testudinum and the mud substratum of Upper Florida Bay. Montgomery et al. (1977) reported similar differences in the flora of coral, coral sand and T. testudinum in the Florida Keys. Attachment problems vary greatly between soft and hard substrata (Round 1971). Since rocks and macrophytes are both relatively hard, there may be considerable similarity between the diatom floras of these two substrata. Main et al. (1974) found this to be the case when epilithic assemblages were compared to those on nearby Zostera marina and Ulva sp. growing intertidally in an Oregon estuary.

Lee et al. (1975) have described a general successional sequence for benthic diatoms, beginning with solitary and closely adhering forms such as Cocconeis and Achnanthes, and proceeding to a vertically layered micro-community with an overstory of chain-forming diatoms such as Melosira. The rate of productivity determined the degree of micro-floral development on the glass slides, since only the slides from station 1, and occasionally station 2, during the bloom periods, were able to attain the multi-layered stage. Nicotri (1977) found that the morphology and means of attachment of various benthic diatoms greatly affected availability to the

grazers Collisella pelta and Notoacmea scutum which showed strong preferences towards chain-formers. The diatoms at the upper station in this study were, therefore, not only more numerous, but possibly more easily consumed, although the gut analyses revealed no such selectivity. Melosira, according to Nicotri (1977), was the least digestable of eight diatoms considered, probably owing to the fact that this species has relatively few pores in its cell wall. Thus greater consumption of chain-forming species does not necessarily imply greater nutritional yield.

The diatom and gastropod assemblages also displayed similar patterns through time. The youngest observed benthic stages of most gastropods were first noted either during or just prior to the spring diatom bloom, which occurred in May and June. The positive relationship between juvenile recruitment and the diatom blooms was demonstrated in the case of M. costalis by the lack of correlation when juveniles were excluded from the analysis (Table X).

Whether the gastropod recruitment is actually triggered by the diatom bloom is uncertain. Synchrony between phytoplankton blooms and the spawning of several marine invertebrates with pelagic larvae has been observed by Thorson (1946, 1950) and Himmelman (1975). On the basis of these results, and the experimental induction of gamete release by Strongylocentrotus drobachiensis, Tonicella lineata, and Tonicella insignis, Himmelman proposed that phytoplankton blooms serve as spawning stimuli through the production and liberation of ectocrinal

substances. Since other factors, such as temperature change (Korringa 1956, Loosanoff 1968, Galtsoff 1940) and the presence of sperm (Galtsoff 1938, 1940, Young 1945) may cause spawning, Himmelman suggested that the phytoplankton are indicators of optimal environmental conditions for juvenile survival, and that other indicators of these conditions might exist as well. The selective advantages that would be conferred by such an adaptation are obvious, considering that the younger stages of many invertebrates are often less tolerant to extremes in temperature than the adults of the same species (Kinne 1964, Thorson 1950). It is equally likely that the co-occurrence of diatom blooms and invertebrate recruitment are caused by coincidental adaptation to the same physical factors. One could further suggest that the presence of a large amount of food is a major determinant of gastropod larval and juvenile survival, since during these phases, individuals grow more rapidly (Spight et al. 1974, North 1954) and have feeding requirements that are 5-10 times higher than adults (Thorson 1950). Benthically developing members of the assemblage, including the highly abundant M. costalis, L. marmorata, and L. carinata, cannot utilize suspended phytoplankton and should be particularly dependent upon blooms of benthic diatoms for juvenile survival. In terms of nutrition, therefore, there may be some selective advantage to the synchronization of spawning and diatom blooms. Contrary to Himmelmans's proposal, perhaps it is the physical factors which indicate whether conditions are optimal for survival.

It is reasonable to assume that the juveniles of some non-herbivorous species take advantage of the large food resource available in the form of benthic diatoms in the spring. Certainly all feeding planktotrophic veligers consume plankton (Yonge and Thompson 1976) and some probably continue to eat small organisms as young adults, even though there may be different diets when mature (Fretter and Graham 1962). At least one gastropod, the African pulmonate Achatina fulica, is known to switch from herbivory to omnivory as it grows older (Smith and van Weel 1950). The dietary shift of A. fulica corresponds to a decrease in the ratio of amalytic to proteolytic activity in the digestive gland diverticula (Prosser and van Weel 1958). This change of enzymatic complement could not be induced by an alteration of diet and so is probably a developmental response (van Weel 1959).

The feeding experiment conducted at Saturnina Island had the surprising result that M. costalis repeatedly situated themselves in an area of high diatom density, i.e. the plastic mesh cage covers, in preference to a naturally occurring substrate, Plocamium cartilagineum, which normally sustains large numbers of snails. Low densities of M. costalis on P. cartilagineum at the end of each 24 hour experimental trial could have been due to a depletion of food organisms on the seaweed surface caused either by rough handling or by grazing early in the trial. The results suggest that Margarites costalis will move toward locally high concentrations of

diatoms cells. There is , though, the posibility that factors such as the degree of water movement or the availability of oxygen in the cages acted as stimuli for snail movements.

The field experiment also demonstrated that heat and hydrogen-peroxide treatments tended to decrease the desirability of seaweed to M. costalis. Whether this lack of attraction is due to the decreased presence of diatoms or microorganisms, or to some other condition of the seaweed surface cells is not known.

Lacuna carinata and a trochid, Lirularia lirulata, were diatom grazers whose dispersions correlated to diatom abundance. Correlations to diatom density were not found for some species whose guts contained diatoms (Tables VIII and X). During periods when diatoms were present at relatively low densities, an adequate supply might still have been available for these species, and, therefore, food would not have been an abundance-limiting factor. Consumption of other foods, as in the case of M. gouldii, which was found to eat egg capsules containing opisthobranch veligers, would free a population from strict dependence on diatom abundance. Adult Margarites costalis, M. olivaceus, and G. margaritula might possibly utilize other foods as well. Factors such as predation, competition, parasitism, habitat selection, and physical conditions of the environment which also may be important in determining dispersion patterns, will be considered in further detail in the following sections.

PREDATION

Several species which can be considered potential gastropod predators were found at Saturnina Island, and mortalities due to predation may be responsible for some of the observed variations in gastropod abundance. Although no direct studies of predation were attempted, what little evidence is available is worthy of review.

Bottom-dwelling fish capable of taking snails (Fitch and Lavenberg 1975) were common at Saturnina. The most abundant fish Rhacochilus vacca (the pile-perch) ranged in schools to all depths at the site. Most of the other fish at the site were more solitary and territorial than the perch, and seemed more intimately associated with the bottom. Copper rockfish, Sebastes caurinus, blennies, Epigeichthys atropurpurescens, kelp greenling, Hexagrammus decagrammus, and sculpins, Oligocottus maculosus and Leptocottus armatus, were all commonly found.

Pisaster ochraceus and Leptasterias hexactis are two predatory asteriods found high in the subtidal zone at the Saturnina site. Menge (1972) reported that when these two species co-occurred, Leptasterias consumed small-sized food such as Margarites spp. and Lacuna spp. Pisaster was found to be an efficient predator of large gastropods such as N. scutum and C. pelta when more highly preferred foods were unavailable. Two highly favored foods of Pisaster, mussels and barnacles, were rare at Saturnina.

Diving ducks (Melanitta nigra americа, Melanitta fusca deglendi, Clangula hyemnali, Aythya marila, Bucephala albeola) overwinter nearshore in the Strait of Georgia (Godfrey 1966, Vermeer and Levings 1977) and great numbers of several carnivorous species can be found in the Flat Top Islands from mid-September through March. The gut contents of ducks at Boundary Bay, B.C., have been found to include Margarites, Lacuna, Alvania, Odostomia, Mitrella, Bittium, Nassarius, and Turbonilla (Vermeer and Levings 1977, Hilda L. Ching, personal communication). Stott and Olson (1973) observed that Lacuna vincta was the dominant prey of Clangula in New England. Vermeer and Levings (1977) reported that more snails were consumed in the winter than in the summer.

The wintertime decrease in gastropod abundance at station 1 relative to station 2 (Figure 5) could be explained by a decrease in bird predation with depth. Although such a phenomenon was not directly observed, it is logical to assume that diving birds would expend less energy in obtaining food if they fed close to shore where it is a shorter swim to the bottom. According to Vermeer and Levings (1977), ducks preying upon molluscs were seldom found in areas where the depth exceeded 3 m, further supporting this hypothesis.

Depth-related trends in predation might also account for the relatively low station 1 recruitment by species with benthic egg masses such as M. costalis and L. marmorata. That is, if large numbers of the adults of a species are removed from any given location, fewer egg masses would be deposited.

Adult M. costalis were, however, most numerous at station 1 during the breeding period in early spring, and in the case of this species, at least, the effects of bird predation upon reproduction may be discounted.

Recruitment may have been hindered partly by the consumption of eggs, veligers, and juveniles, although there was no direct evidence of this occurring at Saturnina Island. This form of predation could be practiced by any members of the gastropod assemblage with the ability to ingest food as large as gastropod eggs or egg masses, however only one species was found which consumed the eggs of other gastropods. The consumption of gastropod eggs by other gastropods is expected to be most intense at station 1 where, during the breeding season, the greatest numbers of young snails were found.

There were no observations of direct predation on adult snails by carnivorous gastropods such as Ocenebra, Odostomia, Balcis, and Turbonilla. The Pyramidellid Odostomia, however, was highly abundant and co-occurred with several other species of both high and low abundance (Figure 12). Published accounts of other Odostomia species reveal the ability to utilize prosobranch hosts (Clark 1971, Fretter and Graham 1949, Thompson 1976).

Robilliard (1971) observed that the nudibranch Dirona albolineata consumed, among other animals, Margarites pupillus, Margarites helcinus, and Lacuna carinata at various subtidal sites in the San Juan Islands. Solitary individuals of D. albolineata were occasionally observed during the monthly

visits to Saturnina Island, and were not restricted to any particular depth. Predation by Dirona upon the dominant snails of this study is, therefore, likely but unquantified.

There is some evidence that Robilliard misidentified both species of Margarites. Specimens labelled M. helcinus in the Friday Harbor invertebrate collection are identical to the Margarites olivaceus marginatus of this study (personal observation). There is some degree of confusion among workers at Friday Harbor concerning Margarites pupillus, which apparently is used as a catch-all taxon for all Margarites species with ridged shells (E. Kozloff, personal communication). It is possible that the M. pupillus of Robilliard is the M. costalis of this study, however another likely taxon is M. salmoneus (Ian McTaggart Cowan, personal communication.)

PARASITISM

During the course of this study larval trematode infestations were found among several gastropod populations. Some of the infestations were so heavy that parasitism must be considered as an important influence upon gastropod dispersion patterns. All of the identifications and counts of trematode larvae were performed by Hilda L. Ching, whose data are cited in Table XII.

M. costalis and M. olivaceus were the most heavily parasitized species, in terms of the number of individuals

Table XII. Summary of trematode parasites found to infect gastropods at Saturnina Island. Data from H. L. Ching, personal communication.

GASTROPOD HOST	PARASITE	DATE	STATION	%INFECTED[1]
M. costalis	*Parvatrema* sp.	Nov.&Aug./76	1	76
		"	2	33
		"	3	3
		"	4	0
		Jan.&Apr./77	1	77
L. marmorata	*Podocotyle enophrysi*	Apr./77	1	8
		Apr./78	1	10
A. compacta	HEMIURID	Nov./77	1	3
	ACANTHOCOLPID	Nov./77	1	1
		Nov./78	1	1
	Microphallus pirrim	Nov./77	1	14
		Nov./78	1	2
M. gouldii	LEPOCREADID	Oct./77	1	4

[1] Refers to the percentage of snails dissected that contained parasites. Sample sizes ranged from 58 to 357 snails.

infected. Multiple infections were common, and as many as 60 larval Parvatrema sp were found per individual Margarites. The Parvatrema assume an unusual and unique position within the extra-pallial cavity of adult snails (Ching 1979a). The digestive glands of individuals sustaining large numbers of trematodes were in extremely poor condition, suggesting that the larval Parvatrema feed in a manner similar to that of adult flukes.

Ching's data indicate that the Parvatrema infection decreased with depth. It is quite possible that the relatively low recruitment of M. costalis at station 1 is the result of parasitism since snails with diminished nutritional capabilities undoubtably have a reduced amount of energy available for gonad development.

Lacuna marmorata was also heavily parasitized (Ching 1979b). Although there was no attempt at assessing the relationship between Podocotyle enophrysi infections of Lacuna marmorata and depth, it was found that the infections were greater in April than in January. The gonads of infected individuals were virtually destroyed by larval Podocotyle and, thus, parasitism is a possible cause of decreased reproductive output for this species, as well.

SALINITY AND TEMPERATURE

Kinne (1964) noted that an organism's salinity tolerance is greatly modified by temperature. At low temperatures, animals seem to be able to tolerate salinities that would be lethal at high temperature. Kinne felt that this response is caused by an increased metabolic demand placed upon thermally conforming species involved in osmotic regulation, coupled with the low oxygen tensions in high temperature water. Kinne (1964) and Thorson (1950) emphasized that many marine and estuarine animals tolerate narrower ranges of salinity variation as eggs and larvae than as adults.

During the spring and early summer, the east-facing shores of the Gulf Islands are periodically exposed to the run-off plume of the Fraser River, for periods of up to two weeks in duration. When it first reaches Saturnina Island, this water mass is essentially a 2 to 5 m thick tongue of warm, low salinity water (Figure 14). Thus, the Fraser River plume may have caused a condition that was sufficiently adverse to limit the survival of *M. costalis* at station 1, during the spring and early summer. This provides an alternative to the notion that larval trematodes cause a decrease in recruitment.

Figure 14. Surface view of the Saturnina Island site viewed from the East. Note the Fraser River plume extending across the photograph from the left. Photograph courtesey of Dr. R.E. Foreman.

THE ROLE OF SUBSTRATE REQUIREMENTS IN HABITAT SELECTION

The distributions of certain gastropods may be largely controlled by specific substrate requirements. This form of habitat selection may be exercised either by the adults during egg laying or through the settlement patterns of juveniles.

In many cases, juveniles are known to settle in one area and later migrate to distant spawning positions. It appears that juveniles of the common intertidal limpet of Collisella pelta metamorphose from veligers subtidally and then migrate upwards, since only young specimens of this species were collected subtidally, and these were restricted to only a few months in the early summer, during which time their distribution became progressively shallower. Frank (1965) found a similar situation for Acmaea digitalis, and concluded that juveniles were less able to withstand desiccation in the intertidal zone, while the adults were probably escaping from subtidal predators. The utilization of intertidal habitats by C. pelta may be a useful adaptation for reducing predation in situations where subtidal predators are abundant, but this hardly seems the case at Saturnina Island, where bird predators are extremely prevalent and there is relatively little protective cover or shade afforded by the intertidal algae. The vertical migration behavior exhibited, however, may be partly reinforced by its role in the reduction of competition for food and space, at least at Saturnina Island. A similar situation probably exists for adults of another common intertidal species

of limpet Notoacmea scutum, which were also found subtidally. Notoacmea scutum, though, had slightly greater densities subtidally, and is usually found lower intertidally than C. pelta (Test 1945), perhaps reflecting a lower tolerance to desiccation, or a greater ability to compete for food when other gastropods are present.

Juveniles of other species may inhabit the same locations as the adults, in cases where the young indivduals have physiological requirements that are similar to the adults. In these cases there is a selective advantage to having benthic, rather than planktotrophic, development. The larvae of Margarites, Lacuna, and Lirularia develop benthically, but little is known of the physiology of these organisms when young. It is known, however, that adult trochids are virtually limited to the areas with hard substrates because their primitive, easily fouled gills, allow only limited exposure to silt laden water (Yonge and Thompson 1976). The trochids also display low tolerance to desiccation, and when found intertidally, are generally restricted to shaded or moist positions.

Grahame (1978) reported that Lacuna pallidula exclusively inhabits and deposits egg masses upon Fucus serratus, but no reason was offered for this relationship. There was the possibility that the relationship was due only to chance or that the Fucus was coincidentally located within an area that was optimal for the survival of the Lacuna. Another gastropod of this study, Velutina, is definitely known to be associated

with ascidians which it feeds upon, and excavates to form brood chambers for egg masses (Diehl 1956, Fretter and Graham 1965). It is likely that there is some chemical basis for specific relationships of this kind, but few studies have focused upon marine gastropods in this regard. Kreigstein (1974) discovered, however, that the swimming veligers of Aplysia californica would only metamorphose after settlement upon fronds of Laurencia californicum. The algae may have provided either tactile stimuli or a chemical cue.

In this study, no attempt was made to explore the relationships between the dispersions of gastropod species and the presence of specific macrophytic algae. The feeding experiment, however, suggested that the dominant snail Margarites costalis utilizes seaweed mainly as a surface which contains food organisms. If this is true, then there should be a definite correspondence between the numbers of snails and the amount of seaweed surface present at Saturnina Island. This hypothesis was not tested.

CONCLUSIONS

The distributions of the individuals of most of the gastropod species at Saturnina Island displayed definite similarities through both depth and time, suggesting that environmental conditions may have affected most of the species in a uniform manner. There still remains, however, the possibility of obtaining the same result from a group of organisms which respond independently to different environmental factors, as has been argued by Berstein et al. (1978).

There was some support for the initial hypothesis that the availability of diatoms was a major factor affecting snail dispersions. At stations 3 and 4 during the winter, and at all depths in the spring and summer, the total abundance and species richness of the gastropod assemblage corresponded closely to the number of diatom cells present. During the spring and summer, differences between diatom production between deep and shallow stations are more severe than in the winter, perhaps as a result of increased shading by phytoplankton and particulate matter of terrestrial origin. Thus the shallow-dwelling snails would have more food available and greater chances of survival. Greater food abundance, if important to a species, could also cause an increased growth rate. For M. costalis, the only species for which growth data are available, there is little indication that the station 1 individuals grew any faster than those at station 2. There may have been some balance between the rate of food production and

the number of utilizers present resulting in no net difference in the diatom availability between station 1, which had more diatoms and consumers, and station 2, with fewer of each. At station 3, where there were fewer competitors and diatom cells, M. costalis were significantly smaller.

The distribution of juvenile Margarites costalis cannot be explained entirely in terms of the availability of diatoms. There is a chance that very young adult M. costalis consume foods which are smaller than most diatoms cells, such as nannoflagellates, yeasts and bacteria. Among any of the diatom consuming gastropods, there could have been preferences for certain sizes or species of foods (Nicotri 1977), but no comparisons between the dispersion patterns of individual gastropod and diatom species can be made because the diatom assemblage was not examined in sufficient detail.

There were a great many factors, beside diatom abundance, which could have caused variations in gastropod abundances through depth and time. From a subjective point of view, some of the factors which seemed particularly important were: predation, parasitism, habitat selection, and the combined affects of of salinity and temperature.

Predation by birds provides an explanation for the wintertime depresssion in the number of snail species and individuals at station 1, relative to station 2. Although there is really no data with which to judge this contention, snails at deeper stations might have greater chances of survival due to increased protection from predation by birds. This advantage

is probably not important in the summer when there are comparatively few birds present at Saturnina Island.

The field experiment demonstrated that M. costalis can travel at least over short distances to areas of greater diatom density. Perhaps, then, M. costalis and L. marmorata migrate upwards in the spring, obtaining more food and replenishing numbers diminished by bird predation. This would account for the relatively high numbers of adults of these species that were found at the shallowest station. There is no direct evidence that this phenomenon actually occurred, but examples of both upward (Gendron 1977, Lambert and Farley 1969, Thorson 1950) and downward (Kain and Svendson 1969, Frank 1965) migrations of juvenile gastropods have been found, and used to explain depth zonation.

The use of heterogeneity indices in this study, as a means of determining the evenness of species representations, is perfectly justified, but it is important to note that heterogeneity is a concept of human origin which does not actually correspond to the ecological properties of an assemblage. Various models have been proposed to link richness and evenness to the nature of resource partitioning in communities (Mac Arthur 1960, Motomura 1932, Preston 1948). In practice, few assemblages have been found for which species abundance relationships fit either of the resource utilization/competition models (Whittaker 1975, King 1964). One of the models states that relative species abundance may be independent of resource availability, in which case individuals

are randomly apportioned among the species (Preston 1948). Most of the models, however, suggest, a priori, that the abundance of a species is largely determined by the availability of resources which is, in turn, a direct function of the number of other utilizers. This view is over-simplistic since the degree of competition and resource sharing between co-occurring species may be affected by factors other than the number of species and individuals present (Eagle and Hardiman 1977, King 1964). The relationship between the relative abundance of species and competition for resources is further complicated in non-equilibrium conditions where there is a turnover of species, or in environments consisting of patches of resources. Under these circumstances, the rates of such processes as colonization, local extinction, and migration to new resource patches are all important in determining the level of co-existence among several competing species (Horn and Mac Arthur 1972).

There is, therefore, little reason to assume a fixed relationship between the richness and evenness of the gastropod assemblage since little is known of the interspecific relationships, or whether equilibrium conditions exist. In the opinion of Foreman (1976), the shallow red algal communities can be subject to successional changes, particularly following periodic intensive grazing by sea urchins. Little attempt was made in the course of this study to assess the effect of either spatial or temporal changes in the macrophyte community but it is likely that variations in the algal community structure

could affect the resident invertebrates in profound ways, such as altering the habitat complexity by changing the amount of available surface area.

Even if the algal community at Saturnina Island was relatively stable through time, assemblages of resident invertebrates could be expected to show modifications as overly abundant species encountered increased competition from immigrants. If the share of resources available to a species then became reduced, through competition, to a level below that amount required for survival, the species would most likely become excluded from the assemblage. The two most abundant gastropods at Saturnina Island are apparently dependent upon large annual recruitments in order to maintain numerical dominance, and could be supplanted by other species if their high reproductive output were somehow decreased.

Although competition for resources by gastropods was not directly observed in this study, features of the dispersion patterns do suggest that competition is being decreased through habitat partitioning through depth and time. Apparently the two dominant snails, M. costalis and L. marmorata, share habitats and do not partition their feeding niches at Saturnina Island, which is not the case for their congeners, M. olivaceus and L. carinata. Lacuna carinata reproduces earlier in the year than L. marmorata and, in the summer, is distributed more shallowly. Temporal separation of recruitment was not so marked for the Margarites species, but M. olivaceus was clearly restricted to a depth zone were M. costalis was relatively low

in abundance.

Before any real assessment of competition can be made for the Saturnina Island gastropod assemblage, experimental investigations concerning growth rates, reproductive strategies, predators, and energetic requirments must be performed.

This study has elucidated many of the features of the subtidal gastropod assemblage at Saturnina Island. It is not possible to determine, at this stage of investigation, which factors are most important in controlling gastropod dispersion patterns, but it is likely that the importance of any one factor, in relation to all others, varies with both depth and season. There is little published information available to assist in understanding the observed features of the subtidal gastropod assemblage at Saturnina Island. The results of this study, however, provide a basis for further, more detailed inquiries into the structure of subtidal communities.

REFERENCES CITED

Andrews, H. 1925. Animals living on kelp. Publ. Puget Sound Biol. Sta. 5: 25-27.

Abbott, R.T. 1974. American Seashells. 2nd ed. Van Nostrand Reinhold Co., New York. 663 pp.

Aleem, A.A. 1949. Distribution and ecology of marine littoral diatoms. Botaniska Nortiser. 4: 414-440.

Allan, J.D. 1975. Components of diversity. Oecologia 18: 359-367.

Ankel, D. 1936 prosobranchia. In Gimpe, G., and E. Wagler, eds. Die tierwelt der Nord- und Ostsee, IXb, (in German). Akademische Verlagsgesellschaft, Liepzing.

Bernstein, B.B., R.R. Hessler, R. Smith and P. Jumars. 1978. Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific. Limnol. Oceanogr. 23: 401-416.

Bertness, M.D., and D.E. Schneider. 1976. Temperature relations of Puget Sound thaids in reference to their intertidal distribution. Veliger 19: 47-58.

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

Calow, P. 1975. The feeding strategies of two freshwater gastropods, Ancylus fluviatilis Mull. and Planorbis contortus Linn. (Pulmonata), with a comparison of field and laboratory estimates of food food absorbtion rates. Oecologia 20: 33-49.

Carefoot, T.H. 1967. Growth and nutrition of Aplysia punctata feeding on a variety of marine algae. J. Mar. Biol. Ass. U.K. 47: 335-350.

Carlton, J.T., and B. Roth. 1975. Phyllum Mollusca: shelled gastropods. Pages 467-514 in R.I. Smith and J.T. Carlton, eds. Light's Manual: intertidal Invertebrates of the Central California Coast. 3rd ed. University of California Press, Berkeley. 716 pp.

Carlisle, J.G., C.H. Turner, and E.E. Ebert. 1964. Artificial habitation in a marine environment. Calif. Fish and Game Dept., Fish. Bull. 124. 93 pp.

Castenholz, R.W. 1961. The effects of grazing on marine littoral diatom populations. Ecology 42: 783-794.

Castenholz, R.W. 1963. An experimental study of the vertical distribution of littoral marine diatoms. Limnol. Oceanogr. 8: 450-462.

Chandler, D.C. 1944. Limnological studies of western Lake Erie. 4. Trans. Amer. Microsc. Soc. 63: 203-236.

Ching, H.I. 1979a. Description of a trematode (Digenea: gymnophallidae), ectoparasite of the marine snail, Margarites costalis (Gould) in British Columbia, Canada. Can. J. Zool. Manuscript in press.

Ching, H.I. 1979b. The life cycle of Podocotlye enophrysi Park, 1937 (Trematoda: Opercoelidae). Can. J. Zool. Manuscript in press.

Clark, K. 1971. Host texture preference of an ectoparasitic opisthobranch, Odostomia columbiana Dall and Bartsch, 1909.

Colwell, R.K., and D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Curl, H., and G.C. McLeod. 1961. The physiological ecology of a marine diatom, Skeletonema costatum (Greve.) Cleve. J. Mar. Res. 19: 70-88.

Dall, W.H. 1921. Summary of marine shell bearing molluscs of the northwest coast of North America. Bull. U.S. Nat. Mus. 112, 217 pp.

Darwin, C.H. 1860. The voyage of the Beagle. Republ., 1962. Doubleday and Co., New York. 524 pp.

De Felice, D.R., and G.W. Lynts. 1978. Benthic marine diatom associations: upper Florida Bay (Florida) and associated sounds. J. Phycol. 14: 25-33.

De Jong, T.M. 1975. A comparison of diversity indices based on their components of richness and evenness. Oikos 26: 222-227.

Diehl, M. 1956. Die raubschnecke Velutina velutina das feind und bruteinmieter der ascidie Styela coriacea (in German). Kieler Meersforsch 12: 180-185.

Duffas, J.H. 1969. Associations of marine mollusca and benthic algae in the Canary Island of Lanzarote. Proc. Malac. Soc. Lond. 38: 343-349.

Eagle, R.A., and P.A. Hardiman. 1977. Some observations on the relative abundance of species in a benthic community. Pages 197-208 in B.F. Keegan, P.O. Ceidigh, and P.J.S. Boaden, eds. Biology of benthic organisms. 11th European Symposium on Marine Biology. Pergammon Press, Oxford. 630 pp.

Elton, C. 1927. Animal ecology. Sidgwick and Jackson Ltd., London. 207 pp.

Farger, E.W. 1972. Diversity: a sampling study. Amer. Natur. 106: 293-310.

Fenchel, T. 1975a. Factors determining the distributional patterns of mud snails (Hydrobiidae). Oecologia 20: 1-17.

Fenchel, T. 1975b. Character displacement and coexistence in mud snails (Hydrobiidae). Oecologia 20: 19-32.

Fitch, J.E., and R.J. Lavenberg. 1975. Tidepool and nearshore fishes of California. University of California Press, Berkeley. 156 pp.

Foreman, R.E. 1975. Nearshore benthic biota study in Rupert and Holberg Inlets. Report to Island Copper Mine as requested by the independent agency of the Environmental Control Program. University of British Columbia, Vancouver. 63 pp.

Foreman, R.E. 1977. Benthic community modification and recovery following intensive grazing by Strongylocentrotus droebachiensis. Helgolander wiss. Meeresunters. 30: 468-484.

Forster, G.R. 1959. The ecology of Echinus esculentis L. Quantitative distribution and rate of feeding. J. Mar. Biol. Ass. U.K. 38: 361-367.

Fralick, R.A., K.W. Turgeon, and A.C. Mathieson. 1974. Destruction of the kelp, Laminaria, by Lacuna vincta (Montagu). Nautilus 88: 112-114.

Frank, P.W. 1965. The biodemography of an intertidal snail population. Ecology 46: 831-844.

Franz, D. 1976. Benthic molluscan assemblages in relation to sediment gradients in northeastern Long Island Sound, Connecticut. Malacologia 15: 377-399.

Fretter, V, and A. Graham. 1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. J. Mar. Biol. Ass. U.K. 28: 493-532.

Fretter, V. And A. Graham. 1962. British prosobranch molluscs. Ray Society, London. 755 pp.

Galli, D.R., and A.C. Giese. 1959. Carbohydrate digestion in a herbivorous snail, Tegula funebralis. J. Exp. Zool. 140: 415-440.

Galtsoff, P.S. 1938. Physiology of reproduction of Ostrea virginica. II. Stimulation of spawining in the female oyster. Biol. Bull. Mar. Biol. Lab. Woods Hole 75: 286-307.

Galtsoff, P.S. 1940. Physiology of reproduction of Ostrea virginica. III. Stimulation of spawning in the male oyster. Biol. Bull. Mar. Biol. Lab. Woods Hole 78: 117-135.

Gendron, R.P. 1977. Habitat selection and migratory behavior of the intertidal gastropod Littorina littorea (L.). J. Anim. Ecol. 46: 79-92.

Ghelardi, R.J. 1971. Species structure of the holdfast community. Pages 381-420 in W.J. North, ed. The biology of giant kelp beds (Macrocystis) in California. Nova Hedwigia 32. J. Cramer, Lehre. 600 pp.

Gini, C. 1912. Variabilita e mutabilita, studi-economico-giuridici (in Italian). Fac. Giurisprudenza Univ. Cagliari.

Gislen, T. 1930. Epibiosis of the Gullmar Fjord. Kristinebergs Zoologiska Station 1877-1927, nos. 3-4. 503 pp.

Godfrey, E.W. 1966. The birds of canada. Natl. Mus. Canada Bull. 203. Ottowa. 258 pp.

Grahame, J. 1977. Reproductive effort and r- and k- selection in two species of Lacuna (Gastropoda: Prosobranchia). Mar. Biol. 40: 2 218-224.

Green, R.H., and G.L. Vascotto. 1978. A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. Water Res. 12: 583-590.

Guillard, R.R.L. And J.H. Ryther. 1962. Studies of marine planktonic diatoms. I. Cyclotella nana Hustedt, and Detonula confervacea (Cleve) Gran. Can. J. Microbiol. 8: 229-239.

Gruendling, G.k. 1971. Ecology of te epipelic algal communities in Marion Lake, British Columbia. J. Phycol. 3: 239-249.

Himmelman, J.H. 1975. Phytoplankton as a stimulus for spawning in three marine invertebrates. J. Expt. Mar. Biol. Ecol. 20: 199-214.

Holland, A.F., and T.T. Polgar. 1976. Seasonal changes in the structure of an intertidal community. Mar. Biol. 37: 341-348.

Horn, H.S., and R.H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53: 749-752.

Hutchinson, G.E. 1967. A treatise on limnology, Vol II. John Wiley and Sons, New York. 1115 pp.

Hylleberg, J. 1975. The effect of salinity and temperature on egestion in mud snails (Gastropoda:Hydrobiidae). Oecologia 21: 279-289.

Jones, D.J. 1971. Ecological studies on macroinvertebrate populations associated with polluted kelp forest in the North Sea. Heloglander wiss. Meeresunters. 22: 417-441.

Jones, L.G. 1971. Small herbivorous invertebrates of the canopy and holdfast. Pages 343-367 in W.J. North, ed. The biology of giant kelp beds (Macrocystis) in California. Nova Hedwigia 32. J. Cramer, Lehre. 600 pp.

Kain, J.M., and G.E. Fogg. 1958. Studies on the growth of a marine phytoplankton. 1. Asterionella japonica Gran. J. Mar. Biol. Ass. U.K. 37: 397-413.

Kain, J.M., and P. Svendson. 1969. A note on the behavior of Patina pellucida in Britain and Norway. Sarsia 38: 25-30.

King, C.E. 1974. Relative abundance of species and MacArthur's model. Ecology 45: 716-727.

Kingston, R.S. 1968. Anatomical and oxygen electrode studies of respiratory surfaces and respiration in Acmaea. Veliger 11, Supplement: 73-78.

Kohn, A.J. 1959. The ecology of Conus in Hawaii. Ecol. Monogr. 28: 47-90. Maldive and Chagas Islands. Ecology 49: 104-1062.

Kohn, A.J. 1968. Microhabitats, abundance and foods of Conus on atoll reefs in the Maldive and Chagas Islands. Ecology 49: 1046-1062.

Kohn, A.J. 1971. Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. Limnol. Oceanogr. 16: 332-249.

Kohn, A.J. And P.J. Leviten. 1976. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. Oecologia 25: 199-210.

Kinne, O. 1964. The effects of temperature and salinity on marine and brakish water animals. II. Salinity and temperature combinations. Oceanogr. Mar. Biol. Ann. Rev 2: 281-339.

Korringa, P. 1957. Water temperature and breeding throughout the geographical range of Ostrea edulis. Ann. Biol. 33: 1-17.

Kreigstein, A.R., V. Castellucci, and E.R. Kandel. 1974. Metamophosis of Aplysia californica in laboratory culture. Proc. Nat. Acad. Sci. U.S.A. 71: 3654-3658.

Lambert, T.C., and J. Farley. 1968. The effect of parasitism by the trematode Cryptocotyle lingua (Creplin) on zonation and winter migration of the common periwinkle, Littorina littorea (L.). Canad. J. Zool. 46: 1139-1147.

Lee, J.J., M.E. McEnery, E.M. Kennedy, and H. Rubin. 1975. A nutritional analyis of a sublittoral diatom assemblage epiphytic on Enteromorpha from a Long Island salt marsh. J. Phycol. 11: 14-49.

Leighton, D.L. 1971. Grazing activities of benthic invertebrates in southern California. Pages 421-423 in W.J. North, ed. The biology of giant kelp beds (Macrocystis) in California. Nova Hedwigia 32. J. Cramer, Lehre. 660 pp.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton. 120 pp.

Leviten, P.J. 1978. Resource partitioning by predatory gastropods of the genus Conus on subtidal Indo-Pacific coral reefs: the significance of prey size. Ecology 59: 614-631.

Lindstrom, S.C., and R.E. Foreman. 1979. Seaweed associations of the Flat Top Islands, British Columbia: a comparison of community methods. Syesis. Manuscript in press.

Loosanoff, V.L. 1968. Maturation of gonads of oysters, Crassostrea virginica, of three different geographical areas subjected to relatively low temperatures. Veliger 11: 153-163.

Lund, J.W.G. 1949. Studies on Asterionella. 1. J. Ecol. 37: 389-419.

MacArthur, R,H. 1960. On the relative abundance of species. Amer. Natur. 94: 25-36.

McIntire, C.D., and W.S. Overton. 1971. Distributional patterns in assemblages of attached diatoms from Yaquina Estuary, Oregon. Ecology 52: 758-777.

Main, S.P., and C.D. McIntire. 1974. The distribution of epipyhtic diatoms in Yaquina Estuary, Oregon (U.S.A.). Bot. Mar. 17: 88-99.

Markel, von K. 1966. Uber funktionelle radulatypen be: gastropoden unter besonder berucksichtigung der Rhipidioglossa (in German with summary in English). Vie et Milieu Ser. A, Biol. Mar. 17: 1121-1138.

Menge, B.A. 1972. Competition for food between two intertidal starfish species and its effect on body size and feeding. Ecology 53: 635-644.

Montgomery, R.T., W.I. Miller, and A.W. Collier. 1977. A preliminary investigation of the structure of diatom communities associated with Florida Keys coral reefs. Proc. 3rd Intl. Coral Reef Symp. (biol.): 357-363.

Morton, J.E., and C.M. Yonge. 1964. Classification and structure of the Mollusca. Pages 1-58 in K.M. Wilbur and C.M. Yonge, eds. Physiology of Mollusca. Vol. I. Academic Press Inc., New York. 473 pp.

Motomura, I. 1932. A statistical treatment of associations (in Japenese). Japan. J. Zool. 44: 379-383.

Motyka, J., B. Dobrazankski, and S. Zawadski. 1950. Wstempne badania nad lakami poludniowo-wsxhodneij Lubszczyny (in Polish with summary English). Ann. Univ. Mariae Curie-sklodowska, Sect. 3, Biol. 5: 367-447.

Muller, J.E. 1971. Geological reconnaissance map of Vancouver Island and Gulf Islands. Revised. Geological Survey of Canada open file map.

Nassichuck, M.D. 1974. Structural and interactive relationships between intertidal Fucus populations associated with faunal assemblages. MsC. Thesis, University of British Columbia. 139 pp.

Nicotri, M.,E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. Ecology 58: 1020-1032.

North, W.J. 1954. Size distribution, erosive activities and metabolic efficiency of the marine intertidal snails, Littorina planaxis and L. Scutulata. Biol. Bull. Mar. Biol. Lab. Woods Hole 106: 185-198.

North, W.J. 1971. Introduction and background. Pages 1-97 in W.J. North, ed. The biology of giant kelp beds (Macrocystis) in California. Nova Hedwigia 32. J. Cramer, Lehre. 660 pp.

North, W.J., M. Neushul, and K.A. Clendenning. 1964. Successive biological changes observed in a marine cove exposed to a large spillage of mineral oil. Symp. Pollut. par. Microorgan. Prod. Petrol. Monaco: 335-354.

Nybakken, J. 1978. Abundance, diversity and temporal variability in a California interitidal nudibranch assemblage. Mar. Biol. 45: 129-146.

Odum, E.P. 1971. Fundamentals of ecology. 3rd ed. W.B. Saunders and Co., Philadelphia. 574 pp.

Olroyd, I.A. 1924. Marine shells of Puget Sound. Publ. Puget Sound Biol. Sta. 4: 1-272.

Olroyd, I.A. 1927. The marine shells of the West coast of North America. II., Part I. Stanford University Pres. 247 pp.

Owen, G. 1966a. Feeding. Pages 1-51 in K.M. Wilbur and C.M. Yonge, eds. Physiology of Mollusca. II. Academic Press Inc., New York. 645 pp.

Owen, G. 1966b. Digestion. Pages 53-96 in K.M. Wilbur and C.M. Yonge, eds. Physiology of Mollusca. II. Academic Press Inc., New York. 645 pp.

Paine, R.T. 1965. Natural history, limiting factors, and energetics of the opisthobranch Navanax inermis. Ecology 46: 603-619.

Paine, R.T., and R.L. Vadas. 1969. The effects of grazing by sea urchins, Strongylocentrotus spp. on benthic marine algal populations. Limnol. Oceanogr. 14:710-719.

Parson, T, M. Takahashi, and B. Hargrave. 1977. Biological oceanorgraphic proesses. Pergammon Press, London. 332 pp.

Patrick, R.E. 1969. Some effects of temperature on freshwater algae. Pages 161-185 in P.A. Krenkel and F.C. Parker, eds. Biological aspects of thermal pollution. Vanderbilt University Press, Nashville. 407 pp.

Patten, B.C. 1962. Species diversity in the net plankton of Rariton Bay. J. Mar. Res. 20: 57-75.

Peet, R.K. 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. 4: 285-307.

Pielou, E.C. 1967. The use of information theory in the study of the diversity of biological populations. Proc. Berkeley Symp. Math. Stat. Prob., 5th 4: 163-177.

Pielou, E.C. 1972. Niche width and niche overlap: a method for measuring them. Ecology 53: 687-692.

Pielou, E.C. 1977. Mathematical ecology. J. Wiley and Sons. New York. 385 pp.

Powell, J.H. 1964. The life-history of the red alga, Constaniea. PhD. Thesis, University of Washington. 154 pp.

Preston, F.W. 1948. The commoness, and rarity of species. Ecology 29: 1254-1283.

Prosser, C.L., and P.B. van Weel. 1958. Effect of diet on digestive enzymes in the mid-gut gland of the African giant snail Acatina fulica. Fer. Physiol. Zool. 31: 171-178.

Quast, J.C. 1971. Observations on the food of kelp bed fishes. Pages 541-579 in W.J. North, ed. The biology of giant kelp beds (Macrocystis) in California. Nova Hedwigia 32. J. Cramer, Lehre. 660 pp.

Rabinwitch, E., and Govindjee. 1969. Photosynthesis. J. Wiley and Sons, New York. 272 pp.

Rex, M.A. 1977. Zonation in deep sea gastropods: the importance of biological interactions to rates of zonation. Pages 521-530 in B.F. Keegan, P.O. Ceidigh, and P.J.S. Boaden, eds. Biology of benthic organisms. 11th European Symposium on Marine Biology. Pergammon Press, Oxford. 630 pp.

Robilliard, G. 1971. Predation by the nudiranch Dirona albolineata on three species of prosobranchs. Pac. Sci. 25: 424-435.

Round, F.E. 1968. Light and temperature. Pages 73-100 in D.F. Johnson, ed. Algae, man, and the environment. Syracuse University Press. 554 pp.

Round, F.E. 1971. Benthic marine diatoms. Oceanogr. Mar. Biol. Ann. Rev. 9: 83- 139.

Saito, I., and M. Nakamura. 1961. Biology of the sea hare, Aplysia juliana as a predator of the brown seaweed, Undaria pinnatifida. I. The feedomg habit. Bull. Jap. Soc. Sci. Fish. 27: 395-400.

Sepkoski, J.J. 1974. Quantified coefficients of association and measurement of similarity. Math. Geol. 6: 135-152.

Shannon, C.E., and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana. 117 pp.

Simpson, E.H. 1949. Measurement of species diversity. Nature 163: 688.

Shelford, V.E., and E.D. Towler. 1925. Animal communities of the San Juan Channel and adjacent areas. Publ. Puget Sound Biol. Sta. 5: 33-73.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York. 312 pp.

Simmons, A. 1957. An ecological survey of the upper Laguna Madre of Texas. Publ. Inst. Mar. Sci. Univ. Texas 4: 156-200.

Smith, D.A.S. 1973. The population biology of Lacuna pallidula (da Costa) and Lacuna vincta (Montagu) in northeast England. J. Mar. Biol. Ass. U.K. 53: 493-520.

Smith, A.C., and P.B. van Weel. 1960. On protease and amylase production in the midgut of young and mature African snails. Experentia 16: 60.

Sneath, P.H., and R.R. Sokal. 1976. Numerical taxonomy. W.H. Freeman and Co., San Francisco. 573 pp.

Sokal, R.R., and C.D. Michener. 1958. A statistical method for evaluating systematic relationships. Univ. Kansas Sci. Bull. 38: 1409-1438.

Southwood, A.J. 1958. The zonation of plants and animals on rocky sea shores. Biol. Rev. Camb. Phil. Soc. 33: 137-177.

Spight, T.M. 1974. Sizes of populations of a marine snail. Ecology 55: 712-729.

Spight, T.M. 1977. Ecology of hatching size for marine snails. Oecologia 24: 283-294.

Spight, T.M., C. Birkeland, and A. Lyons. 1974. Life histories of large and small murexes (Prosobranchia: Muricidae). Mar. Biol. 24: 229-242.

Stott, R.S., and D.P. Olson. 1973. Food habit relationships of seaducks on the New Hampshire coastline. Ecology 54:996-1007.

Test, A.R. 1945. Ecology of California Acmaea. Ecology 26: 395-405.

Thompson, T.E. 1976. Biology of opisthobranch molluscs. I. Ray Society, London. 207 pp.

Thorson, G. 1933. Investigations on shallow water animal communities in the Franz Joseph Fjord (East Greenland) and adjacent waters. Meddr. Gronland 100: 1-69.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. Meddr. Kommn. Danm. Fisk.-og havunders., Ser. Plankton 4: 1-523.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25: 1-45.

van Weel, P.B. 1959. The effect of special diets on the digestion processes (enzyme production and reabsorbtion) in the African giant snail, Achatina fulica Bowidich. Physiol. Comparata et Oekol. 2: 1-19.

Vermeer, K., and C.D. Levings. 1977. Populations, biomass and food habits of ducks on the Fraser River delta intertidal area, British Columbia. Wildfowl 28: 49-60.

Wallace, N. 1955. The effect of temperature on the growth of some freshwater diatoms. Nat. Acad. Natur. Sci., Philadelphia 280: 1-11.

Warmke, G.L., and L.R. Almodovar. 1963. Some associations of marine mollusks and algae in Puerto Rico. Malacologia 1: 163-177.

Whittaker, R.H. 1972. Evolution and the measurement of species diversity. Taxon 21: 213-251.

Wing, B.L., and K.A. Clendenning. Kelp surfaces associated with invertebrates. Pages 319-341 in W.J. North ed. The biology of giant kelp beds (Macrocystis) in California. Nova Hedwigia 32. J. Cramer, Lehre. 660 pp.

Young, R.T. 1945. Stimulation of spawning in the mussel (Mytilus californicanus). Ecology 26: 58-69.

Yonge, C.M., and T.E. Thompson. 1976. Living marine molluscs. W. Collins Sons and Co., London. 288 pp.

Appendix A. Dominant and common algae found at the Saturnina Island site.

DOMINANT ALGAE
Microcladia coulteri Harv.
Odonthalia floccosa (Esp.)Falk.
Plocamium cartilagineum (L.)Dixon
Laurencia spectabilis Post. and Rupr.
Constantinea subulifera Setchell
Prionitis lanceolata Harv.
Cryptopleura ruprechtiana (J. Ag.)Kylin

COMMON ALGAE
Pterosiphonia dendroidea (Mont.)Falk.
Ulva fenestrata Post. and Rupr.
Iridaea cordatum (Turn.)Bory
Callophyllis edentata Kylin
Callophyllis flabellulata Harv.
Gelidium purpurescens Gard.
Gelidium crinale (Turn.)Lamouroux
Lithothrix aspergillum J.E. Gray
Corallina officinalis var. *chilensis* (Harv.)Kuetzing
Ralfsia fungiformis (Gunn.)Setch. and Gard.
Ceramium spp.
Polysiphonia spp.
Laminaria groenlandica Rosenvinge
Gigartina sp.

Appendix B. The names, acronyms, and families of twenty-five gastropod species found at Saturnina Island.

NAME	ACRONYM
ACMAEIDAE	
Acmaea mitra Rathke, 1833	ACMAMIT
Collisella pelta (Rathke, 1833)	COLLPEL
Notoacmea scutum (Rathke, 1833)	NOTOSCU
TROCHIDAE	
Lirularia lirulata (Carpenter, 1864)	LIRULIR
Margarites costalis (Gould, 1841)	MARGCOS
Margarites olivaceus marginatus (Gould, 1841)	MARGOLI
LACUNIDAE	
Lacuna carinata Gould, 1848	LACUCAR
Lacuna marmorata Dall, 1919	LACUMAR
RISSOIDAE	
Alvania carpenteri (Weinkauf, 1885)	ALVACAR
Alvania compacta Carpenter, 1864	ALVACOM
CERITHIIDAE	
Bittium eschrichtii (Middendorf, 1849)	BITTESC
Cerithiopsis stejnergeri Dall, 1884	CERISTE
Cerithiopsis sp.	CERISPP
MELANELLIDAE	
Balcis micans (Carpenter, 1864)	BALSMIC
CREPIDULIDAE	
Crepipatella lingulata (Gould, 1846)	CREPLIN
VELUTINIDAE	
Velutina laevigata (Linnaeus, 1767)	VELULAE
MURICIDAE	
Ocenebra interfossa Carpenter, 1864	OCENINT
COLUMBELLIDAE	
Amphissa columbiana Dall, 1916	AMPHCOL
Mitrella gouldii (Carpenter, 1857)	MITRGOU
Nassaridae	
Nassarius mendicus (Gould, 1849)	NASSMEC

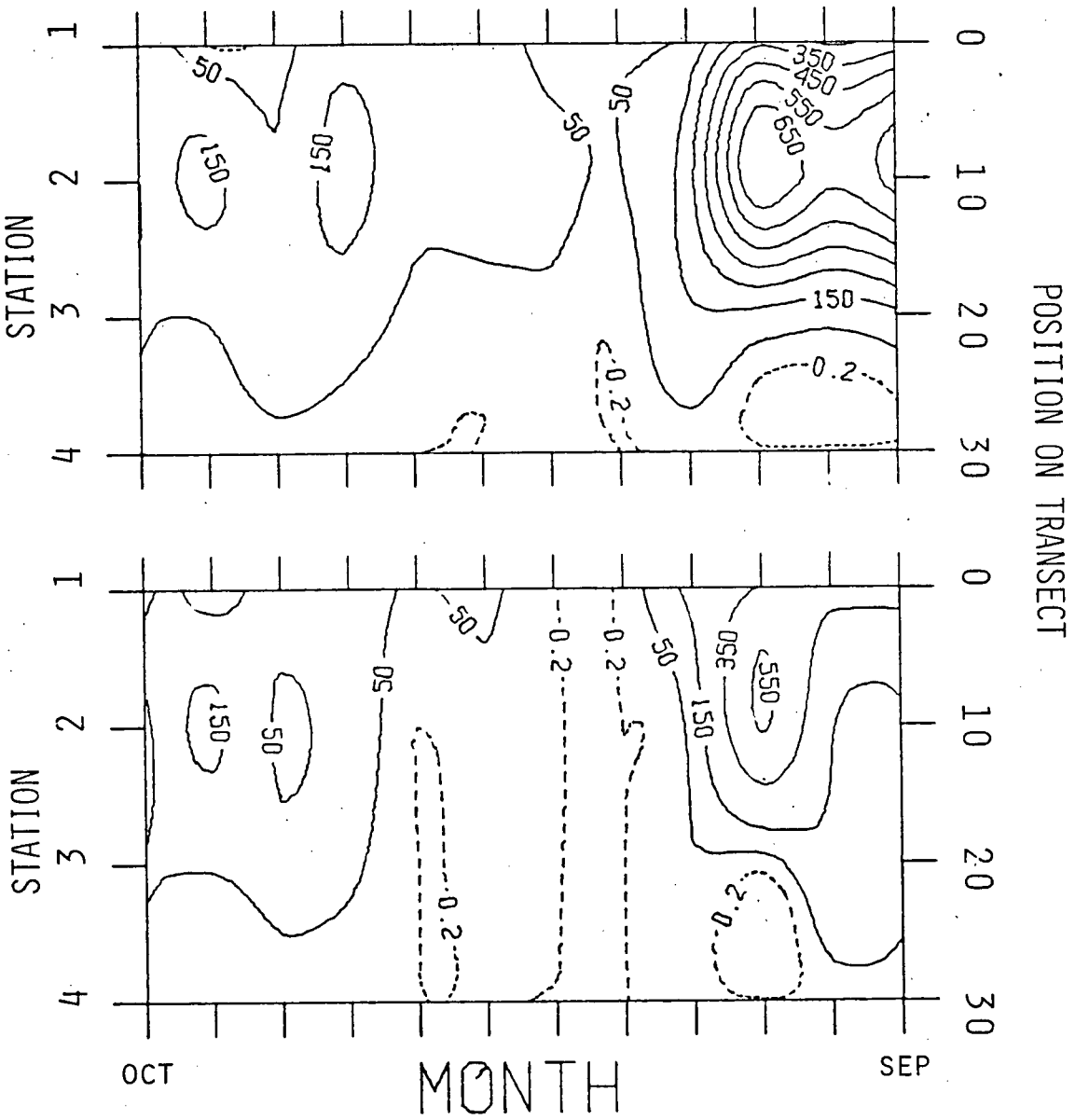
Appendix B. Continued.

NAME	ACRONYM
CANCELLARIDAE	
Admete circumcincta	ADMECIR
MARGINELLIDAE	
Granulina margaritula	GRANMAR
PYRAMIDELLIDAE	
Odostomia sp.	ODOSTOM
Turbonilla vancouverensis	TURBVAN
DIAPHANIDAE	
Diaphana californica	DIAPCAL

APPENDIX C

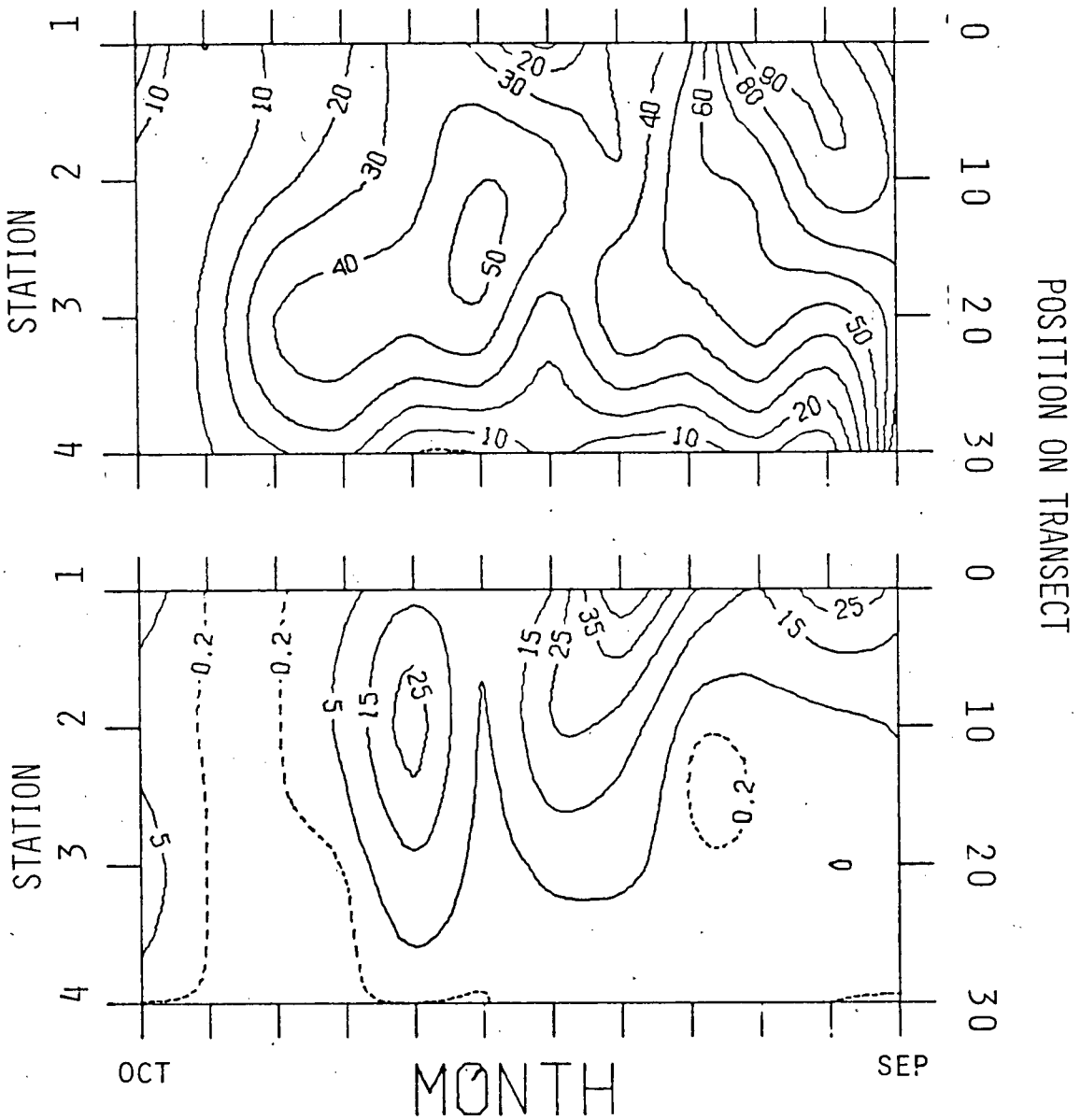
Mean density for sixteen gastropod species contoured against station and month of collection.

Margarites costalis



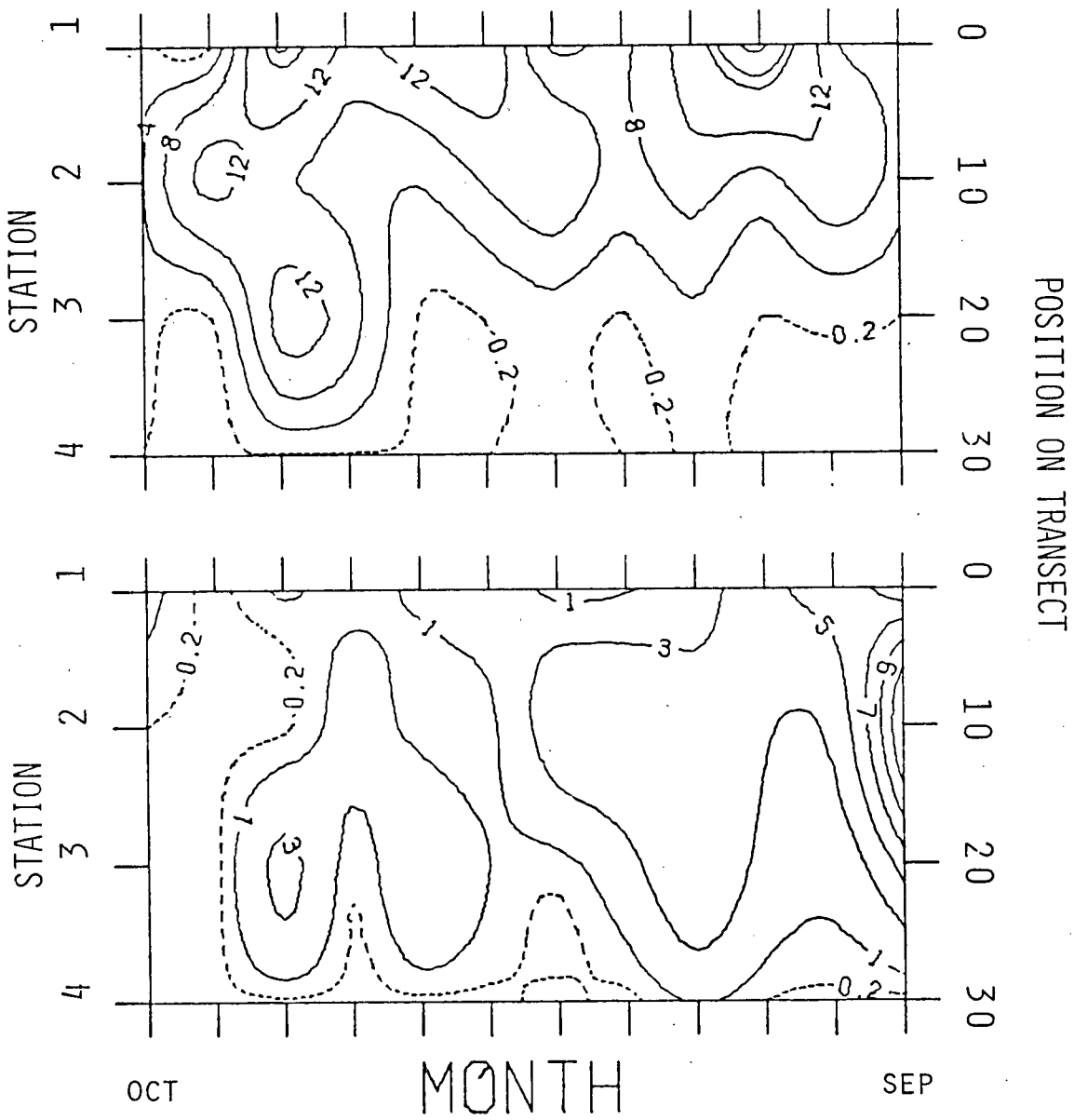
Lacuna marmorata

Alvania compacta



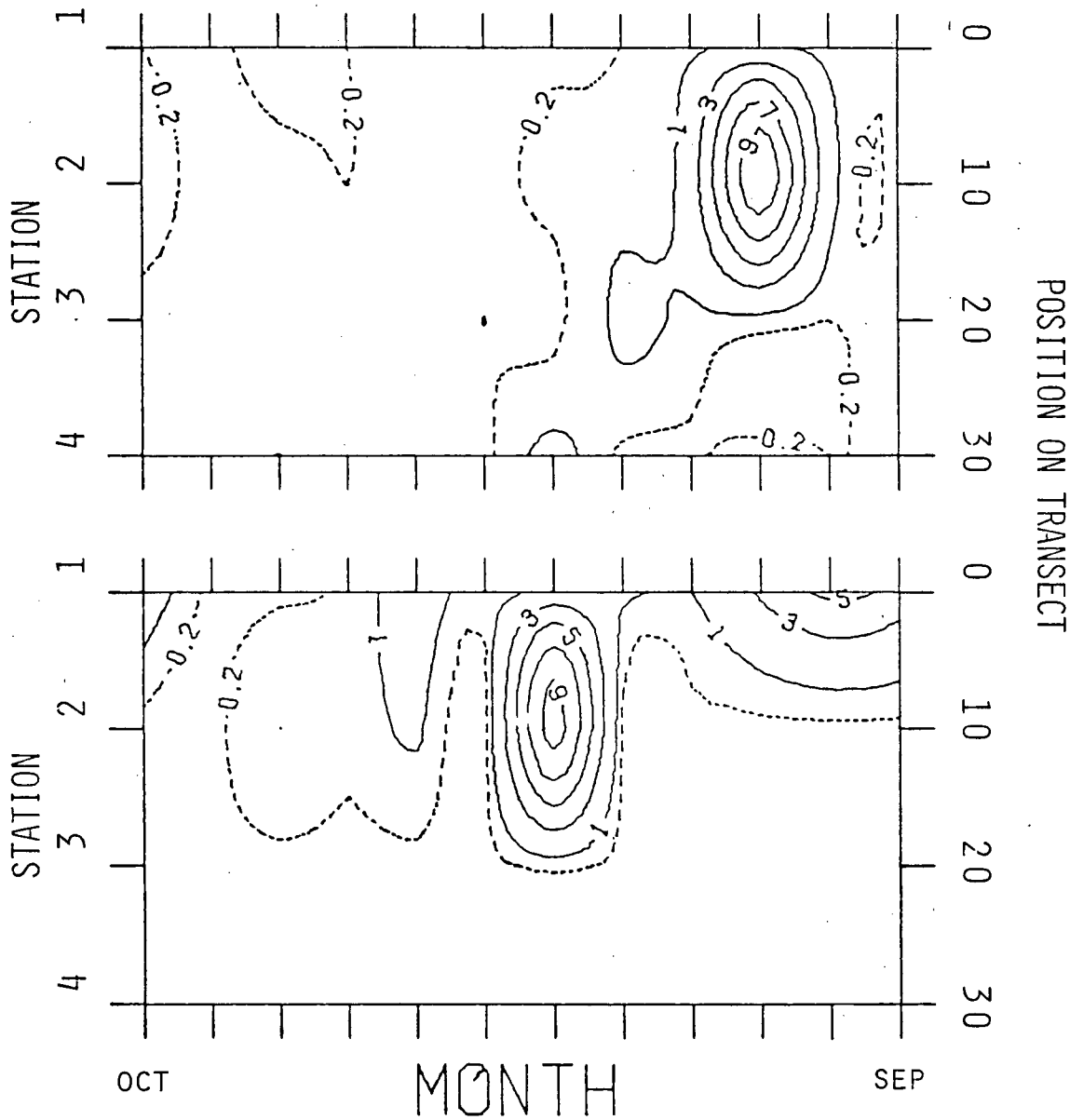
Lacuna carinata

Granulina margaritula



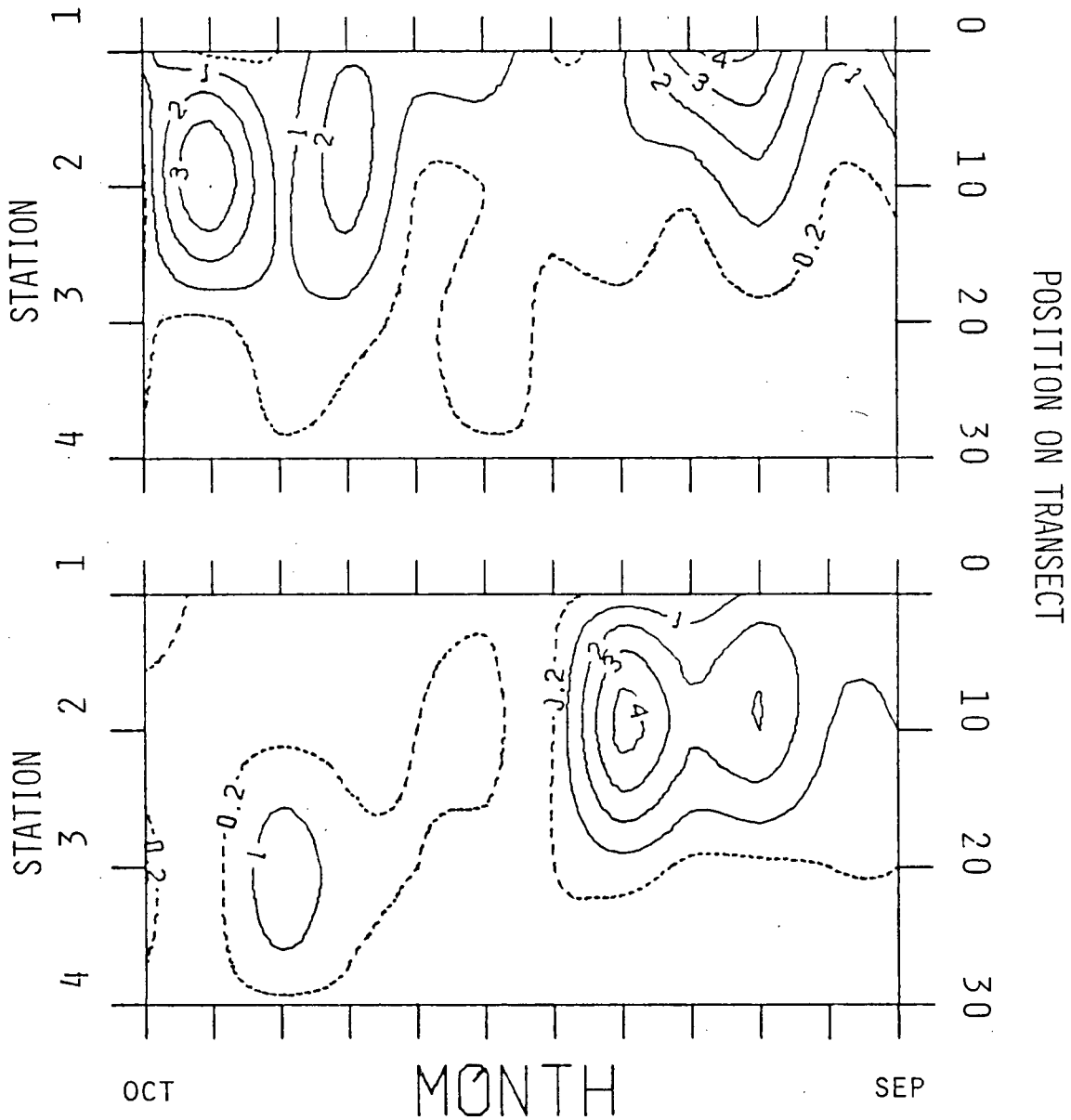
Odostomia sp.

Lirularia lirulata



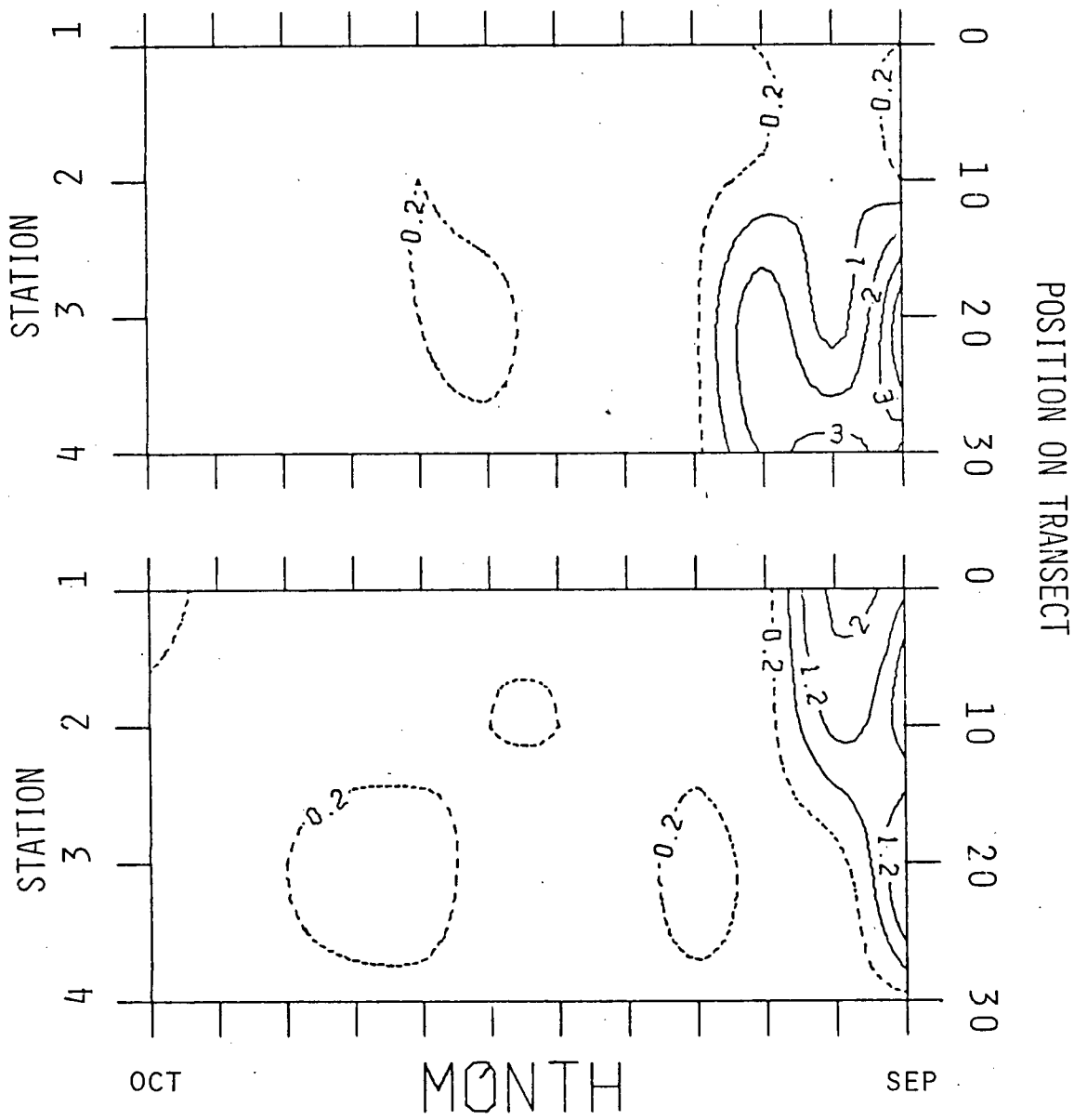
Cerithiopsis sp.

Mitrella gouldii



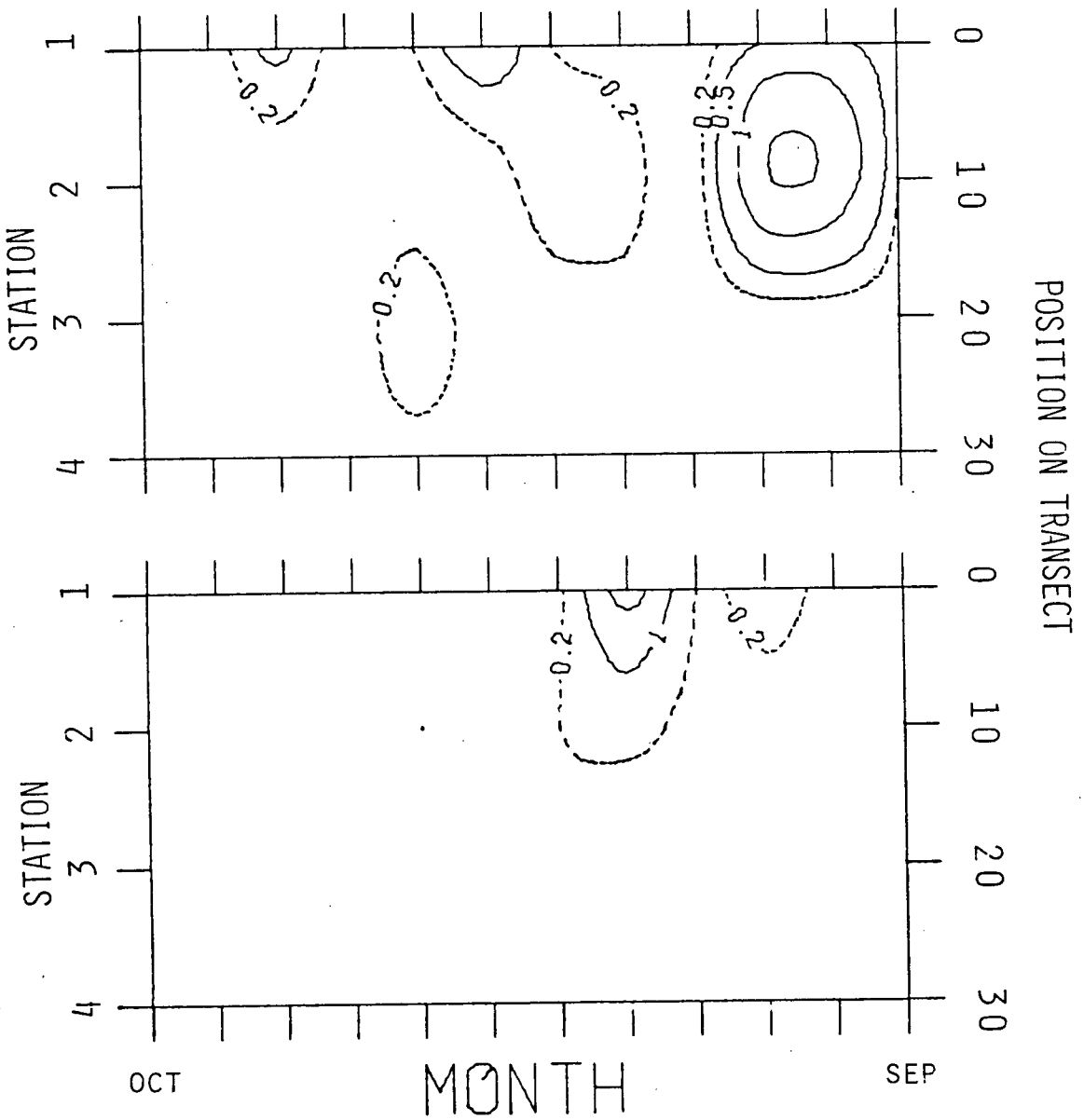
Admete circumcincta

Margarites olivaceus



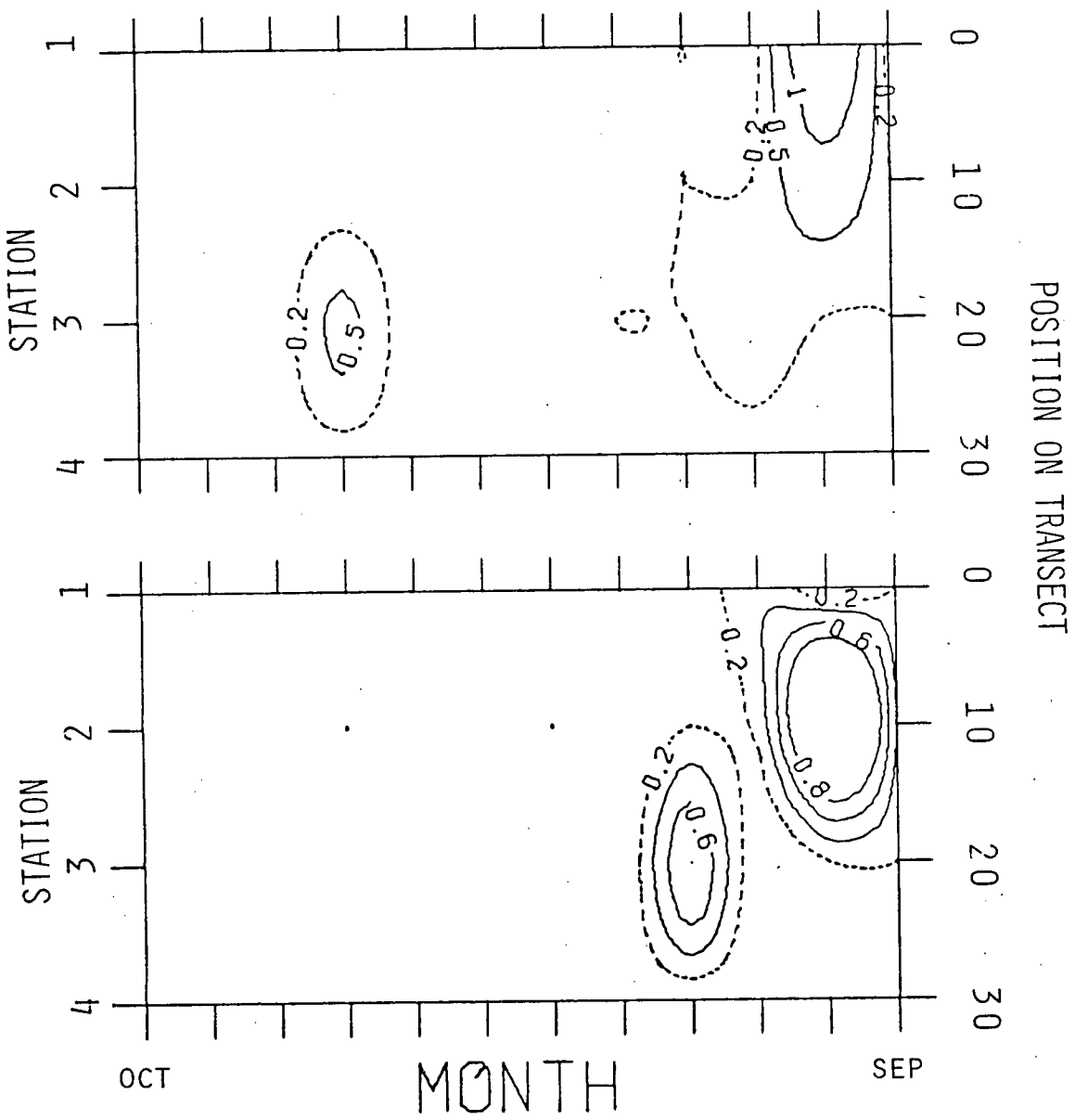
Notoacmea scutum

Diaphana californica



Alvania carpenteri

Amphissa columbiana



Balcis micans

Appendix D. The mean number of individuals per quadrat, or mean density, for ten gastropod species of low abundance.

SPECIES	MONTH	STATION	MEAN DENSITY
Collisella pelta	May	2	0.2
	Jul.	1	1.0
	Jul.	2	1.0
Bittium eschrichtii	Jan.	1	0.2
	Mar.	1	1.4
	Apr.	2	1.4
	May	1	0.2
Cerithiopsis stejnegeri	Dec.	2	0.2
	Dec.	3	0.2
	Jan.	1	0.2
	Feb.	3	0.2
	Jun.	1	0.2
	Jun.	2	0.2
	Jun.	3	0.2
	Jun.	4	0.2
	Sep.	3	0.2
Ocenebra interfossa	Dec.	3	0.2
	Jun.	2	0.8
	Jul.	4	0.2
	Aug.	1	0.4
Nassarius mendicus	Jan.	1	0.6
	Feb.	1	0.2
	Jun.	3	0.2
	Aug.	3	0.2
Velutina laevigata	May	2	3.0
	Jul.	1	0.2
	Jul.	3	0.2
	Sep.	3	0.2

Appendix D. Continued.

SPECIES	MONTH	STATION	MEAN DENSITY
Crepipatella lingulata	Mar.	1	0.2
	Jul.	1	0.2
	Jul.	2	0.4
	Aug.	1	0.2
Acmaea mitra	May.	3	0.2
	Jun.	1	0.2
	Sep.	3	0.2
unidentified rissoid	Jun.	2	0.2
	Jul.	2	0.2
Turbonilla vancouverensis	Aug.	3	0.2