QUALITATIVE AND QUANTITATIVE STUDIES OF BENTHIC INFAUNAL COMMUNITIES IN BRITISH COLUMBIA COASTAL WATERS.

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We accept this thesis as conforming to the required standard

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ABSTRACT

In this study, I examine and compare benthic infaunal and environmental factors from the British Columbia coastline on a broader geographic and temporal scale than has been attempted in this area. The hypothesis that large and small macrofauna are distributed differently under different environmental conditions was examined by comparing results based on numerical abundance and biomass-weighted abundance data. Both data methods have drawbacks, but their combined use nullified the primary bias of each. I concluded that the combined results from numerical and biomass-weighted data provided a clearer picture of faunal and environmental interactions than either result alone.

The faunal data were analysed using cluster analysis in conjunction with an inferential bootstrap method called Sigtree, which places significance values on the cluster groupings. The multivariate results from both faunal data formats were compared to each other using a second non-parametric bootstrap method, Comtre2. Finally the two faunal dendrograms were inferentially compared with a dendrogram derived from environmental data, using the method Comtre1. The above analyses were conducted independently on the two faunal datasets from each survey area, then for data from all survey areas combined. I have included a discussion of the potential effects of sampling parameters on the results of inferential analyses, power and overall significance of the tests, and suggested an optimum approach for future studies.

The Sigtree analyses of significant cluster groups was the most valuable of the three inferential methods used, and was least affected by the multiple comparisons problem. The major drawback of this and

other bootstrap methods is their dependence on the raw data being manipulated. Despite the limitations of the method, the results of Sigtree analyses were believable and readily interpretable. The Sigtree analyses of the combined data for all survey areas indicated that most stations within a given survey area remained grouped together. Exceptions illustrated the consistency in faunal composition (including impoverishment) which may be expected for areas with similar environmental conditions, regardless of the geographic distance between stations. Results often revealed very different patterns in the distribution of small versus large fauna, particularly in disturbed areas such as Alice Arm and Vancouver Harbour, and in cases where only the small fauna or only the large fauna were impoverished. However, the Comtre2 comparison of results for the two data management approaches lacked sufficient discrimination to distinguish between the distribution patterns of large and small fauna for any survey area except Alice Arm. As well, the multiple comparisons problem was serious for Comtre2 for sets of data with many stations.

The Comtre1 results suggested that the distribution patterns of large fauna were more closely predicted than the distribution of small fauna, by the environmental factors measured. I concluded that Comtre1 was of limited use for the environmental data available (sediment particle size, depth and location) for all survey areas, but was of considerable value for interpreting relationships between complex sediment chemistry factors and the distribution of large fauna. The Comtre1 results were considered unreliable for analyses with many stations, because of the multiple comparisons problem.

Using the methods outlined in this study, comparisons of macrofauna

structure from different habitat types and geographic locations were feasible and informative even though sampling conditions were variable. The data management approach used to examine patterns in different size components of the assemblage could be expanded to focus in greater detail on size-related structural complexities within benthic communities.

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PROLOGUE

A. ORGANIZATION OF THE THESIS

This thesis is based on a comparative study of the benthic community structure of infauna from different habitats of British Columbia coastal waters. The work is presented in ten chapters. Chapter 1 includes the purpose and general approach to the study, as well as an introduction to the theory and application of methods used in benthic community studies (from Burd *et al.* 1990). Chapter 2 includes a description of sampling, data processing and management, analytical methods and a discussion of the assumptions and power of the analytical methods. Chapters 3 to 8 include the individual studies of different survey areas. The introduction, results and discussion for each area have been presented in arbitrary order as follows; four surveys in Alice Arm and Hastings Arm (Chapter 3); three surveys in Hecate Strait (Chapter 4); two surveys on the West coast of Vancouver Island (Shelf - Chapter 5); two surveys in Vancouver Harbour and Port Moody Arm (Chapter 6); one survey in Boundary Bay near the Canadian US mainland border (Chapter 7) and a survey of several mainland fjords (Chapter 8). In Chapter 9 an overall comparison is made of relationships between the faunal compositions of the survey areas and habitat variables, and among stations within survey areas. Chapter 10 includes the conclusions based on the purposes of the study (Chapter 1 section A).

B. HISTORY OF THE DATA

In 1981, Dobrocky Seatech Ltd. proposed (Unsolicited Proposals Program) the first set of two benthic infaunal surveys on the continental shelf. Dr. Brinkhurst, Ocean Ecology, Institute of Ocean Sciences (IOS), Department of Fisheries and Oceans (DFO), Sidney, British Columbia (B.C.), was the scientific authority. The sampling program, data processing, partial faunal identifications and some data analyses from the shelf surveys resulted in several contractor reports (O'Connell et al. 1983a,b). Later, additional animals collected during

the two cruises were identified and added to the dataset. Revisions to the taxonomic identifications continued over the next few years. Finally, the data were summarized in Brinkhurst (1987). Other surveys were initiated and samples collected under the supervision of Dr. Brinkhurst. Samples were processed in the laboratory and animals were sorted by a variety of people, including Mr. Douglas Moore of Ocean Ecology, IOS, personnel from Dobrocky Seatech Ltd., EVS Consultants Ltd. and Ms. Moira Galbraith of SyTech Research Ltd., Victoria, B.C.

In 1982 and 1983, personnel of Ocean Ecology (DFO) collected samples of the benthos in Alice Arm, B.C. Sample processing, preliminary data analyses and technical reports of these two surveys were prepared under contract between E.V.S. consultants and DFO (Kathman *et al.* 1983, 1984). D. Goyette and J. Boyd (Environmental Protection Service) assisted in sampling and providing background information. D. Moore assisted with all aspects of the cruises and performed the sorting and sediment analyses for several years.

All faunal identifications for data collected by IOS after the Shelf surveys were carried out by specialists. Most of the identifications and/or verifications were done by; H. Jones (Polychaeta), Marine Taxonomic Services, Corvallis, Oregon; G. Wilson (Isopoda), Friday Harbour Marine Laboratory, University of Washington, Friday Harbour, Wash.; R. Reid (Mollusca), University of Victoria, Victoria, B.C.; and W. Austin (Varia), Khoyatan Marine Laboratory, Cowichan Bay, B.C. Other authorities involved in identifications (particularly for the shelf study) are listed in the technical reports.

From late 1986 onwards, I have been responsible for the updating, correcting, database management, statistical analyses and production of all technical and data reports outlining the preliminary results from all surveys except the second Vancouver Harbour survey. I participated in the collection of samples for the second Vancouver Harbour survey, and the data report was prepared by Aquametrix Research Ltd., Victoria, B.C. (Cross and Brinkhurst 1991). All data used herein except the fjord sample set are therefore already published. The fjord dataset is currently being prepared for a report (DFO, Ocean Ecology).

In September of 1988 I began a Ph.D. program with Dr. R.O.

Brinkhurst. The data collected from the various surveys was generously contributed by IFO, Ocean Ecology, with the understanding that it would be used to examine large-scale patterns in benthic infaunal distributions in British Columbia. Dr. Brinkhurst agreed to partially support the Ph.D. program by providing some contract work to process recently acquired data from Vancouver Harbour cruise 1, several fjord surveys and Alice Arm 1989, which then provided data for the Ph.D. thesis. He also partially funded under contract the production of a literature review which was intended to provide an introduction to the PhD thesis and also provided the inspiration for the approach taken in the management and analysis of data (Burd *et al.* 1990). The literature review was completed during a directed studies course for the PhD program. Some assistance in critically reviewing the statistical literature and multivariate methodology was provided by Dr. A. Nemec. The statistical methods used in this study were developed by Dr. A. Nemec, under contract with Dr. Brinkhurst (Nemec and Brinkhurst 1988a,b).

I thank Dr. Brinkhurst for the opportunity to collect, process and use data from the benthic surveys, and for partial support of the PhD program. I also thank the taxonomic authorities listed herein, the personnel involved in rough-sorting and those at the Institute of Ocean Sciences, Sidney, B.C. who helped in numerous ways. Dr. Phil Symons, a friend and colleague, generously contributed his professional editing skills in the processing of the manuscript. I particularly thank Dr. Louis Hobson of the Biology Department, University of Victoria, for stepping in as supervisor and providing vital constructive criticism, administrative support and encouragement towards the end of the program.

CHAPTER 1. INTRODUCTION

A. PURPOSE AND GENERAL APPROACH

The purpose of the study was to compare and describe characteristics of communities of marine infauna from different B.C. coastal areas The approach was designed to specifically test the hypothesis that the small and large infauna were distributed differently under certain habitat conditions. Because the data were collected by others, without prior experience or consultation, and using a variety of sampling methods, the study was also an exercise in the aposteriori extraction of the maximum information from a less than ideal set of data. This situation can occur all too frequently in environmental studies which must include historical data.

The approach to the study was inspired by an examination of methods and data management strategies used by other researchers, as well as theoretical considerations of data transformations, abundance and biomass characteristics of communities and assumptions and statistical power of analytical methods. This theoretical background is considered in detail in section C of this chapter. It was obvious from the review of literature that the biomass of benthic communities could not be ignored, but that some approach combining abundance and biomass measures was required. The existing methods were unsatisfactory, both because of the loss of information inherent in the use of univariate data models and the frequent arbitrary transformation of data using mathematical models which cannot be justified ecologically Various multivariate methods were examined and described in section C, and it was decided that the use of non-parametric methods would eliminate the need to conform to distribution and variance assumptions of the "General Linear Model". The reader is warned that the literature review in section C is detailed in the discussion of methodology and certain sampling theories.

Species-abundance and mean biomass of each species from 13 surveys were collected and incorporated into two master databases. A third database containing environmental information (geographic location,

depth, sediment particle size) was developed to compare with the faunal databases. Patterns in taxa number, estimated total biomass and abundance of animals from different habitats and geographic locations were compared where sampling compatibility allowed.

The data management method consisted of transforming numerical abundance data by the mean biomass of each species, and comparing the analytical results from both the original untransformed and biomass-transformed sets of data.

Recently developed inferential classification methods were applied to the two sets of data to determine the significance of station groups, to compare faunal data with environmental data, and to compare station groupings resulting from the analysis of the two sets of data with each other. The analytical methods used in this study could have important applications in pollution monitoring studies, since the methods allow the combination of many variables for simultaneous comparison with faunal patterns. Chapter 6 illustrates the applicability of the aforementioned analytical methods in a polluted area.

1. Mean Biomass transformation of species abundance data

The first faunal set of data consisted of untransformed species-abundance data. The second faunal data matrix was constructed using the individual size of each species (mean wet weight) to transform abundance data to size-weighted abundance data. This is roughly equivalent to a species-biomass set of data, although in many surveys only an estimate of each species mean weight could be determined. Therefore I refer to the second set of data as "biomass-weighted" rather than simply biomass. An extensive review of methods used in benthic survey studies (Burd *et al.* 1990) suggested that most scientists consider the use of untransformed abundance data seriously flawed because of the uniform treatment of all species, which will cause the analysis to be dominated by the hundreds or thousands of specimens of the tiniest species, and will virtually ignore the large, relatively rare animals. This problem has usually been dealt with by applying some arbitrary geometric transformation to the data which de-emphasizes the quantitative

importance of species with many individuals and emphasizes the rare taxa regardless of form, size or function (Burd *et al.* 1990). Such transformations simply introduce a set of assumptions into the data analyses which have never satisfactorily been proven to have any sound ecological basis (Burd et al. 1990). Some similarity measures used in community analyses (classification or ordination) are more sensitive than others to the presence of rare species, however, the use of such measures produces similar assumptions and problems to those encountered using arbitrary geometric data transformations (Gordon 1987).

The transformation of abundance values by the relative size of each species was initially used to reduce the problems caused by inequity amongst numbers of small and large species within assemblages. The size-weighted set of data emphasizes the largest (often rare) species and deemphasizes the smallest (often abundant) species. Therefore the analysis of the original untransformed set of data and the size-weighted set of data highlight distribution patterns in the small and large fauna separately. A size-weighted transformation is specific to each species, as opposed to the uniform, arbitrary treatment of all species which occurs with geometric transformations such as log or square root. As well, the size-weighting method is ecologically rational because it conveys information about the size structure of the assemblages being examined. Finally, the use of biomass-weighted abundance should reduce the influence of different screen sizes used in the various studies since very small animals collected on small mesh screens, but which pass through large mesh screens, contribute very little to the size-weighted analysis. However, information about the shifts in the very small species which can occur in disturbed habitats would be lost by using only biomass-weighted analyses. As well, there are distinct limitations in the use of biomass as a faunal measure (see section C2a in this chapter) Therefore, I decided that use of both methods in concert would enhance my understanding of community patterns. Strong trends should appear in both patterns, and differing trends in small versus large fauna should show up as contrasting results from the analyses of the two sets of data.

2. Non-parametric multivariate methods

Another purpose of the study was to test the efficacy of a recently developed set of multivariate statistical methods for interpreting community structure on local, temporal and more global scales. The two faunal databases were subjected to multivariate classification analysis with concurrent significance testing of cluster groups (Sigtree), and compared statistically with each other (Comtre2) and with the environmental database (Comtre1). The significance testing methods (Nemec and Brinkhurst 1988a,b) offer an objective, non-parametric method for placing significance on the groupings of objects within an agglomerative, hierarchical cluster analysis. The "bootstrap" approach of Sigtree and Comtre2 have not been widely used, and there has been little discussion in the literature to date on the mathematical properties of these methods.

This approach was used on a local scale for each survey area (chapter 3-8), on a temporal scale for the time-series set of datas (chapters 3,4,5,6), and on a global scale for all studies combined. It was hoped that this scaled perspective would provide insight into the differences between local and coastal benthic faunal patterns, and how these relate to environmental factors.

B. BENTHIC SURVEYS IN THE PACIFIC NORTHWEST

There is little quantitative information on benthic invertebrate communities in British Columbia. The extant information is restricted mainly to the southern coast, and particularly the Strait of Georgia and surrounding inlets. Benthic studies in Puget Sound, the American portions of the Strait of Georgia and the continental shelf are more extensive. A few surveys in B.C. coastal waters will also be mentioned, however work by agencies such as the Environmental Protection Service is available only in internal reports. Thse unpublished reports will not be discussed, as they tend to be qualitative.

Quantitative surveys of major taxonomic infaunal and epifaunal

groups in Georgia Strait and adjacent inlets were carried out by Ellis (1968a,b,c, 1969, 1971). Bernard (1978) listed major megafaunal species in Georgia Strait and provided a reference list for other faunistic lists and surveys, most of which are located in government technical and manuscript reports. A checklist for Otter-Trawl and dredge collections off the Oregon coast was given by McCauley (1972). Carey (1965) examined the relationship between fauna and sediment types off the coast of Oregon.

Levings (1980a,b) described the ecology of the megafauna of Howe Sound on the mainland coast just north of Vancouver (Levings (1980a,b), and in Port Alberni Inlet off the west coast of Vancouver Island (Levings *et al.* 1985). He examined effects of wood-fibre beds and ocean dumpsites respectively, on the benthic fauna. Smith (1981) studied organisms in intertidal sandbeds of Boundary Bay. These surveys all focused on local communities and conditions. Levings *et al.* (1983) reviewed the sparse literature on benthic hard and soft substrate fauna in southern B.C.

By far the most extensive and detailed infaunal surveys in the Pacific Northwest have been done in Puget Sound and the coast of Washington (Lie 1968,1969, 1974, Lie and Evans 1983, Lie and Kelley 1970). Jumars and Banse (1989) reviewed benthos studies on the continental shelf in the Pacific Northwest, focusing on macrofaunal biota and sediment interactions. Extensive benthic faunal work has been carried out in coastal waters of southern Alaska (Feder *et al.* 1973, 1976, 1979, 1980, 1981a,b, 1983).

The surveys on which the current research is based represent the most extensive collection in Canadian waters, to the best of my knowledge. Thorson's (1957, 1966) work on "parallel" benthic communities in temperate climates, although not quantitative, was the most recent attempt to compare benthic infaunal community composition on a global scale.

C. THE DEVELOPMENT AND APPLICATION OF ANALYTICAL METHODS IN BENTHIC MARINE INFAUNAL STUDIES

This review was included to provide a rationale for the data management and analytical approach used in this thesis. The reasons for the methodology selected in this study are not obvious without a fairly thorough examination of alternative methods and their assumptions and limitations. The review is an updated extract of Burd *et al.* (1990). Dr. A. Nemec, a statistician and second author on the paper, provided interpretation of relevent statistical papers, as well as editorial criticism throughout. Dr. Brinkhurst, the third author, provided partial funding for the review and Dr. Nemec's time and expertise, as well as editorial criticism.

The review covers what Hurlbert (1984) described as mensurative or survey research, which is non-experimental. The material covered is limited mainly to the literature dealing with shipboard sampling of marine macrobenthic infauna which inhabit soft substrates. Examples of studies and theories derived from meiofaunal, intertidal, freshwater and some land-based study areas are included where they have contributed to theories for surveying marine benthos.

There are three issues which have been prominent in benthic ecological research in one form or other over the years, and which were of particular concern in this thesis:

1. What is the most efficient and accurate means of extrapolation from a sample to the faunal structure of a community? How does this depend on the concept of a "community" in benthic ecology?

2. How can the faunal structure of samples be distinguished from each other over time and space?

3. How do natural and anthropogenic habitat variables affect the faunal structure of samples, and can these two types of effects be distinguished?

From time to time, attempts have been made to synthesize or standardize approaches to benthic sampling and analysis (for recent examples see Boesch 1977, Verner *et al.* 1985, Chapman *et al.* 1987 and Becker and Armstrong 1988) by discussing statistical problems, sampling

practices and new methods (c.f. Green and Vaccotto 1978, Tetra Tech Inc. 1986, GEEP workshop - *Mar. Ecol. Prog. Ser.* 46 - 1988). Recently, Lopez (1988) discussed comparative aspects of studies of limnological and marine benthic macrofauna, a rare effort indeed.

Section 1 of this review defines sampling terms and basic considerations. The important sampling parameters (size and number of samples) can only be confidently decided upon after preliminary reconnaissance sampling and analysis of organisms from a study site. Therefore methods for sampling design are reviewed in the appropriate section of analytical methods in section 2.

Section 2 discusses the organization (2a) and analysis (2b-2e) of data in benthic studies, starting with the simple methods developed early in benthic ecological study, and progressing to the computer-intensive methods for multivariate models. The development of each stage in analysis has continued in parallel to some extent. Therefore the discussion does not attempt to present a chronology of methodological development. The types of analyses in order of discussion include:

(2b) The subjective approach - Community concepts: An understanding of the term "community" and such related concepts as "continuum" is perhaps the primary requirement for the analysis and interpretation of benthic survey data. Petersen's pioneering work in the early 1900's marks the first serious attempt to study these issues. Although Petersen used subjective methods to describe and compare benthic communities, he recognized the need for an objective and systematic approach. However, it was only with the development of computer technology that the necessary methods were to become readily available. Consequently, more or less subjective methods were employed until recently, and many continue to be used today.

(2c) Descriptive univariate community analyses: Since Petersen's time, ecologists have sought to describe communities using graphical and mathematical models which reduce all the data from a given sampling station to a single number, index or function. Univariate models do not recognize the multidimensional effects of species interacting with each other. Nevertheless, their simplicity makes these models popular, particularly in pollution contexts. This phase in the evolution of an

objective methodology is dominated by the diversity index in applied aquatic studies in North America, and by the pseudoquantitative Saprobian system once popular in Europe (c.f. Leppakoski 1977), particularly in freshwater studies.

(2d) Most of the recent advances in hypothesis testing have focused on computer-intensive analyses which are descriptive, and are based on data which are often too complex to interpret subjectively.

(2e) Multivariate community analysis: though some of these methods are quite old, they have gained wider acceptance in recent years than the methods discussed in section 2c. These methods incorporate the multi-dimensionality of species relationships within benthic assemblages.

(2f) Most time-series studies use multivariate methods because of the increased dimensional complexity added by temporal considerations. Time series studies are still relatively rare, but are becoming more prevalent in the literature as computer-intensive multivariate methods develop.

1. Collection of Data

In this section the choice of a suitable sampling device, the sieve size of screens, and the number, spatial distribution and temporal distribution of the samples are discussed briefly. The aforementioned sampling parameters are reviewed extensively elsewhere.

The data collected from one unit of sample effort, whether by grab, core, quadrat, photograph, trawl or other, is referred to in this review as "the sample unit" or "replicate". The term "sample" has been used in benthic studies in a variety of different ways, but is used in this review to refer to all the data from the replicates for a given location (station). In a data matrix in which the stations are listed across the top and the species are listed in a column, the sample therefore refers to all the replicate data within the columns corresponding to that station. In statistical analyses, an inverse analysis is often performed in which the "sample" refers to the total complement of a given taxon across all sample units, or the data of a single row in the

data matrix corresponding to that taxon.

a. Sampling Devices

Grabs and cores have traditionally been used for quantitative sampling of infaunal animals since the early 1900's, whereas sleds, dredges and trawls have been used for qualitative sampling of larger and more dispersed epifauna.

In 1957, Thorson drew attention to problems caused by the shock wave created in front of many sampling devices as they approach the bottom. Since that time there have been a number of good descriptive reviews of sampling devices (Eleftheriou and Holmes 1984, Hopkins 1964, Holme 1964 and McIntyre 1970, Hartley and D[illegible] 1987). Statistical tests have been published discussing the efficacy of different samplers. Grab or core-type samplers can profoundly affect the numbers of animals collected from coarse sediments and at shallow depths (Wigley 1967, Christie 1975, Tyler and Shackley 1978, Hartley 1982). Gerlach *et al.* (1985) pointed out that the loss of meiofaunal animals using remote grabs or cores was very high compared to direct sampling with SCUBA.

Rutledge and Fleeger (1988) describe a laboratory experiment designed to test the effects of core penetration rates on the efficiency of sampling meiobenthos. Hartley (1982) cites an example of an inter-calibration experiment between laboratories from which he concluded that differences in results were related partially to the differences in design of two different Van Veen grabs. Dybern *et al.* (1976) reviewed and recommended standard procedures for sampling in the Baltic Sea, in order to avoid sampling discrepancies among studies. Many authors have their own justifications and reasons for using specific sampling devices, or make it clear that convenience or cost is of primary importance.

b. Sieving of Samples

An important consideration in quantitative sampling of the benthos is choice of screen size. Historically, benthic fauna have been

delimited into three groups based on the size of organisms trapped by different sized screens (see Reish 1959, Thorson 1966, Schwinghamer 1981, Warwick 1984, Gerlach *et al.* 1985, Platt 1985). In general, researchers have recognized up to four size groups usually referred to as: microbes (bacteria, etc.); meiofauna (including foraminifera and the smallest invertebrate fauna); macrofauna (most of the biomass of benthic animals); and megafauna (often lumped with macrofauna; low in abundance but with high individual biomass). Over the years, there has been disagreement as to the optimum screen sizes for benthic studies, although most researchers have focused on the middle group (macrofauna).

Reish (1959) indicated that a screen as small as 0.27mm is required to sample 95% of the animals, whereas a 1mm mesh will sample 95% of the biomass, and therefore all of the megafauna and most of the macrofauna. The 1mm mesh screen has been applied most often in studies of the effects of pollution on macrofauna, and in those studies in which the primary concern is to sample most of the biomass of animals present (c.f. Pearson 1975, Poore and Kudenov 1978a,b). Studies of meiofauna commonly employ 0.063 to 0.1mm mesh screens. Holme and McIntyre (1984) have recommended the lower size limit of 0.5mm for macrofaunal sampling, based on their belief that the smaller macrofauna are an important component of benthic assemblages even if they do not make up a significant portion of the biomass. Rees (1984) also notes that many polychaete species fragment into pieces smaller than 1mm during shipboard processing, and recommends the use of 0.5mm screens. Becker and Armstrong (1988) recommend an initial sieving with a 1mm screen, then a secondary sieve with a 0.5mm screen (the material from the latter may or may not be processed, but is available if required). The choice of screen size obviously depends on the objectives of the study. For example, in areas of gross pollution there may be no macrofauna. Therefore the only sensible sampling program is designed to capture meiofauna, since some meiofaunal species tend to be more tolerant to pollutants than the macrofauna. Studies of energy flow or respiration may require a more comprehensive sample. The smaller the screen, the greater the cost and time required to process samples, particularly if taxonomic expertise for the smaller groups is not readily available.

c. Sampling Effort

The balance between volume (or area) of sample unit, number of replicates and number of sample stations is necessarily dependent on the overall objectives of the study. The importance of designing the sampling program to suit the statistical methods employed cannot be overstressed. For example, some inferential methods require a minimum number of sample replicates for reliability (see Nemec and Brinkhurst 1988a).

Since benthic infauna are relatively immobile, much of the theory that has been developed for sampling plant communities is applicable to benthic communities (Greig-Smith 1964, Kershaw 1973). Green (1979), Holme and McIntyre (1984), Hurlbert (1984) and Baker and Wolff (1987) review most of the important issues in sampling. Cochran (1963) provides the standard reference on sampling techniques from a statistician's perspective. Ripley (1981) discusses various spatial sampling schemes, including;

1) uniform random sampling where a sample area is defined and sites within that area picked at random in sufficient quantity to produce an approximately uniform spacing of samples;

2) stratified random sampling, which is appropriate if some information about the sample area is available, and involves selecting sites from non-overlapping areas (strata) that are usually delineated by environmental factors (e.g. depth, substrate type). Within each stratum the sampling conditions should be as homogeneous as possible so that the different strata themselves can be compared. Within each area the sampling follows a uniform random pattern as in (1);

3) systematic random sampling which involves sampling at regular intervals, usually along a gradient (e.g. pollution). At each point along the gradient a sample area or quadrat is selected, in which replicates are selected at random (as in 1). These sampling schemes are three of many which may be acceptable. Random samples may be most amenable to statisical community analysis but non-random or systematic samples are often used to examine the spatial distribution of a

community (c.f. Cliff and Ord 1981). The sampling pattern should be designed to cover the area about which inferences are to be made, so that sampling bias is reduced to an acceptable level. Hurlbert (1984) emphasizes the importance of suitable sample replication for testing hypotheses, and warns of the problem of pseudoreplication in ecological studies. Green (1979) recommends the use of stratified random sampling when there is a large-scale environmental pattern (e.g. a salinity gradient along an estuary), and discusses the use of nested random sampling (i.e. random sampling on several spatial scales within a sample area) when sources of variation are hierarchically related or when the environment is known to be spatially patchy but not on a sufficiently large scale to define strata. For example, hypotheses concerning the spatial aggregation of species or assemblages may require a nested random design, with the use of a series of sampling devices of different sizes, in order to examine the dispersion of animals on different spatial scales. Saila *et al.*(1976) suggested an optimal allocation of survey resources based on stratified sampling in the New York Bight. Cuff and Coleman (1979) discussed the benefits of a random stratified design for determining the mean number of individuals per taxon, and concluded that a simple uniform random sampling pattern was just as good. Interestingly, they claimed that if the number of stations was increased at the expense of decreasing the number of grabs per station to one, the efficiency of the estimate of mean abundance per taxonomic group increased. This is not necessarily true for inferences about other aspects of faunal structure, or for statistical hypothesis testing.

The choice of sediment volume and number of replicates is based on obtaining representative coverage of the number of species and individuals (and biomass if applicable), and accuracy (or power - see section 2d) of the statistical analysis. Various methods have been developed to examine optimum sampling effort and these will be discussed in those sections of the review that pertain to the application of the analytical models. Choice among these depends upon knowledge obtained from a previous set of samples. Otherwise, the number of sample units or replicates to be obtained at each station must be determined subjectively. Traditionally, researchers have used between 2

and 5 replicates per station. Hartley (1982) and Holme and McIntyre (1984) recommend 5 replicates of 0.1m2 area (sampler size) for macrofaunal sampling, but point out that faunal density has an overwhelming influence on accuracy (see section 2c).

d. Temporal Sampling Design

Sampling design must take into consideration that fact that most benthic assemblages exhibit some degree of seasonal variation, and may vary on shorter time scales (tidal, daily). Govaere *et al.* (1980) described the Nyquist criterion for time series analysis which states that "sampling frequency must be at least twice the highest frequency of the phenomenon studied". For "patch" studies (related to diversity mechanisms - section 2c) the implications can be staggering since life cycles may be very short in some species. Therefore, design considerations such as aliasing that are discussed in books on the analysis of time series data are often not applicable to benthic surveys, since data are not collected with sufficient regularity or frequency to test for periodicity or other temporal effects.

Barnard *et al.* (1986) discuss the trade-off, with respect to estimates of the mean abundances of species between detailed surveys at a single time point and less detailed, long- term surveys (see also Smith 1978). An extreme example is given by Legendre *et al.* (1985) in which one station was examined many times to study community successional stages. Long-term sampling on specific sites is particulary difficult in deep sea for reasons of logistics and cost, particularly since the low abundance of fauna requires large-scale, often semi-quantitative samples to ensure a reasonable coverage for rare species (see Gage *et al.* 1980). In many cases, annual surveys of an area are conducted at a time of year when neither major recruitment nor mortality is occurring in the assemblage.

2. Analysing the Data Matrix

Although there has been little change in the basic sampling

procedures for benthic infaunal surveys, both the analytical method and theory of sampling strategy have changed dramatically. Benthic ecologists have borrowed heavily from theory developed in earlier ecological studies of terrestrial habitats, since the similarities between sessile terrestrial and marine communities are obvious. The logical starting point in a review of methodology is the description of the data set.

a. Organization of the Data

In most studies the faunal data matrix includes abundance data (counts per sampling unit). The data may be abundances standardized to some surface area sampled, or it may be a presence/absence indicator. There is a great deal of variation in the degree of taxonomic effort applied to the compilation of benthic faunal data. Long and Lewis (1987) and Warwick (1988a) found that for macrobenthic samples, identifications to family only was good enough for broad community identifications based on abundance. However, Popham and Ellis (1971) indicated that phyletic or class identifications alone did not delimit associations based on abundance, unless a selected number of dominant species was included (an uncomfortably subjective method). Herman and Heip (1988) suggested that meiobenthos may be diagnostic of community structure at the genus or even higher taxonomic levels, though Warwick (1988a) was less enthusiastic about grouping of meiofauna at higher taxonomic levels. It is generally accepted that the more detailed the taxonomic identification of samples, the more reliable the interpretation of results (despite the fact that this valuable information is largely ignored during the application of univariate measures such as diversity indices).

In most benthic survey studies, there has always been a presumption that the underlying taxonomy was sound. Ellis (1985) reviewed the potential scale and ramifications of this problem.

The faunal data matrix may also consist of weight measurements. Much controversy exists in the literature as to which type of weight measurement should be used. Possibilities include wet weight (usually

blotted or slightly air dryed), dry weight (oven or freeze-dried) and organic weight (ash-free dry weight or labile organic carbon). Wet weight is often the most feasible of these alternatives, and several authors have published approximate conversion values to organic weight for different taxonomic groups (c.f.Thorson 1957, see also Crisp 1984). Brey *et al.* (1988) discuss conversion of dry and ash-free dry weights of macrobenthic invertebrates to energy units.

The use of wet or dry weights is not entirely reliable in benthic invertebrate studies because of the difficulty in separating out large masses of inorganic material such as the shells of pelecypods and gastropods. A few such shelled specimens may be weighed separately and a rough correction factor applied for a set of samples. A potential error involved in this method is that shells can contain a substantial amount of organic matter (Kuenzler 1961). Even the careful measurement of organic weights is not entirely satisfactory unless a large area can be sampled quantitatively because the presence of the odd large, rare specimen can greatly increase the weight in one sample unit, making replicates extremely variable. On the other hand, removal of large specimens can produce an unrealistic result in the biomass analysis since the space requirements of the benthic fauna may be an important factor in community structure. A further complication of using weight data is that in most cases, the specimens are wet-preserved (alcohol or formalin, etc.), which can cause shrinkage and leeching of organic material. Proper preservation methods for marine macrobenthos are reviewed by Holme and McIntyre (1984), Crisp (1984), Ellis (1987).

Recently, Warwick (1986) suggested a pollution monitoring method which uses a comparison of biomass and abundance data. Combination methods will undoubtedly become more popular as scientists continue the struggle to accurately describe communities, and to predict changes in them.

Faunal analyses proceed by describing relationships and general trends that exist either a) between the columns or stations of the population or environmental matrix (Q-mode or normal analysis); or b) between the rows or taxa of the faunal matrix (R-mode or inverse analysis). Most researchers concentrate on comparison of sites (normal

or Q-mode analysis). Methods are also available which attempt to relate Q and R mode analyses, or the environmental and faunal data matrices (see section 2e).

Data reductions:

Data matrices obtained from benthic survey studies commonly include hundreds of species (rows) and several replicates each for a large number of stations (columns). The sheer size of the array may be unmanageable. A review of different strategies for data reduction is given by Stephenson and Cook (1980). Data can be reduced in several ways. One way is to reduce the number of samples in the data matrix by averaging or pooling across replicates. This is often done so that existing computer programs can manage the entire data set. Unfortunately, the loss of information about variance around the mean (abundances, biomasses or other) severely limits the use of inferential statistics and the reliability of interpretations based on comparing mean abundances between stations. Therefore, replicates should only be averaged or pooled once it is determined that there is little variability for a given station (see Hurlbert 1984).

A second method of data reduction affects the number of species (rows). Many of the species sampled may be extremely rare. Researchers frequently reduce the data set either by eliminating species that are deemed "rare" according to some set of criteria, or by grouping species into taxonomically higher groups such as genera or families. This is done to make the analysis of data less unwieldy and time-consuming, and to reduce the complexity of multivariate studies caused by the inclusion of "unimportant" species. Another rationale for data reduction is to produce a set of symmetrical data matrices (all the same dimensions) to accomodate the type of multivariate analysis being used, particularly when several matrices are being compared.

Statistical procedures have been used to test the significance of the relationship between each individual species and an environmental matrix or variable. Species showing a non-significant relationship are subsequently eliminated. Such a set of tests suffers from the multiple comparisons problem (progressive increase in family-wise error rate with

increasing number of comparisons) familiar to users of univariate tests such as Analysis of Variance (ANOVA).

Multivariate methods often have biases with respect to the relative weighting of species in the analysis. The Bray-Curtis similarity coefficient (see section 2e) for instance, places the most emphasis on the abundant taxa, with minor consideration of rare species. Euclidean distance, unlike many other metric similarity measures, is unbounded, and can become infinitely large if there are many zero entries in the data matrix. The resulting distortion of results in a multivariate analysis can be alleviated if an appropriate data reduction or grouping is performed. The reduction deemphasizes the abundance of common species and increases the emphasis on rare species in the analysis. Of the two, roll-up is probably preferable, to avoid loss of rare species data which may actually be vital in delimiting or defining a community (c.f. Brinkhurst 1987, Burd and Brinkhurst 1987). Numerically rare but large specimens can be important in community structure and should therefore not be eliminated. For example, Gray and Pearson (1982) pointed out that Stephensen *et al.* (1972) in this way eliminated one of the original community - defining species in their reanalysis of Petersen's (1911-1915) data. This points out that what constitutes an "abundant" or "non-abundant" species is species dependent and should be viewed with caution. To overcome this type of problem Smith *et al.* (1988) recommend the use of "species standardized abundances" in the data matrix (see next section).

Data transformations:

Prior to descriptive or inferential analysis, raw data (usually abundances) are often transformed. This section will discuss such *apriori* or "primary" transformations, and it should be clarified from the beginning that secondary transformations of manipulated data (e.g. rotations used in classification and ordination analyses for optimal interpretation of results) are not included in the discussion. Primary transformations are performed for several reasons, which are rarely stated clearly in applied studies. It is unfortunate that transformations are often used arbitrarily without any examination of

their effect on the data or their utility. Furthermore, the analytical results of data subjected to different transformations are not readily comparable, unless trends are strong enough to be evident regardless of the treatment or method of analysis (in which case the transfomation was probably pointless). Transformations are often used in conjunction with similarity measures for multivariate statistical analyses, which in some cases have biases related to abundant versus rare species (for discussion see Clarke and Green 1988).

Data transformations are sometimes used to correct biases such as those described in the preceeding section. Transformations prior to data analyses usually reduce the disparity in emphasis on different species evident in the original abundances. For example, many researchers apply geometric transformations, so that instead of a small species (represented by 100 animals) being ten times more important than a large one (represented by only 10 animals), it is only two times more important (log base 10 transformation), or about three times more important (square root transformation). This may or may not be intended by the researcher, who must then interpret the results for the transformed data in terms of the original distribution.

Transformations are not necessary for descriptive analyses such as classification and ordination, but Clarke and Green (1988) suggest that data reductions combined with transformations are usually needed to correct problems caused by a large number of zero entries in the data matrix. More importantly, many statistical analyses assume that the data describe a normal distribution. This assumption is unlikely to be true in aggregated or clumped assemblages where most species are over - dispersed (see section 2c). Hughes and Thomas (1971a,b) point out that in ordination, the proportion of the total variance accounted for by the first few factor axes is generally increased if the data approximate a multivariate normal distribution, thus the incentive for data transformations. Multi - species density data are rarely multivariate normal. Many parametric tests are robust enough to handle skewed data, especially if the other assumptions are met, and the populations being compared have similar distributions.

Another assumption for parametric statistical analyses is that the

variance of the variable of interest is independent of its mean. This can be tested by plotting logarithmic values of the mean (x) versus the variance (S^2) for all species at a station (or group of stations combined in some rational manner) and performing a regression analysis (see Downing 1979) to obtain the equation $S^2 = ax^{-b}$ (refer to Taylor's power law discussion - section 2c). If the variance is related to the mean in this manner, a variance stabilizing (power) transformation (in which the exponent is equal to 1-b/2) can be applied to remove the effect (Downing 1979). Square root and log transformations tend to be at extreme ends of the transformation scale, and therefore should be used only if there is a relationship between the variance and the mean (Downing op. cit.). By extrapolation, samples of multi-species communities taken at different times would not necessarily require the same transformation, if the community structure has changed. L.R. Taylor (1980) also points out the fact that greater error in aggregation estimates (b) is introduced by lumping of species into higher taxa. For further comments on this topic see Chang and Winnel (1981), and Downing (1980, 1981, 1986).

A third assumption of parametric analyses is that the variance is additive. In aggregated assemblages the variance is commonly multiplicative. Stabilizing the variance may increase the probability of additivity by alleviating skewness in the distribution of the sample means. One problem with data transformations is that if the best transformation is to be chosen, it will probably be different for every station. Yet it does not seem feasible to use a series of different data transformations when performing analyses using the combined data from all stations. A common transformation must be selected, by estimating the degree of clumping in the entire data set. Therefore the usefulness of transformations for stabilizing variance is questionable in analyses of large and diverse data sets. The most commonly used data transformations in benthic studies are the square root, root-root (or fourth root - see Field *et al.* 1982), cube root and log transformations (log or ln (x+1) for data sets with zero entries). Reviews of this topic are common, and include Hoyle (1973), Tukey (1977) and Hoaglin *et al.* (1983). To eliminate the problem of zero entries in the data matrix,

researchers often add a small value to each entry (usually 0.1 to 1) before transformation (depending on the biases of the analytical method to be used - see Clifford and Stephenson 1975) This is necessary for log transformations since log 0 is undefined. Such an augmented transformation can produce further interpretation problems. Downing (1979) examined many benthic freshwater studies and concluded that the fourth root (root-root) transformation (b=1.5, 1-b/2 = 0.25) was of general utility for stabilizing variance in benthic studies. Vezina (1988) suggests that b = 1.22 is more appropriate for stabilizing variance in marine invertebrate assemblages. Josefson (1981) applied Analysis of Variance (ANOVA) to log-transformed and untransformed abundance and biomass data and found no difference in results, suggesting some resilience with respect to normality and homogeneity of variance requirements for this type of test. Field *et al.* (1982) suggest that coding abundances (e.g. using a scale of relative abundance from 0-5 for absent to dominant) often has the effect of normalizing data. An extreme example of data transformation is the conversion of abundance data to binary (presence/ absence) data, which is appropriate when only the occurrence of a given species is in question. If there is low confidence that the variance and the underlying distribution of the measurement of interest meet the assumptions of normality, the researcher should either decide upon a useful data transformation or should consider the use of non-parametric inferential statistics which do not require prior knowledge of the underlying frequency distribution (though they may still require a symmetric distribution of data). Whatever the rationale for use, the selection of a transformation should have some ecological basis, though most researchers ignore this aspect entirely. For example, Clarke and Green (1988) argue that log transformations have a sensible basis because they transform the variance (of density measures, etc.) to percent variance of the measure, and population density tends to vary spatially and temporally on a percent basis. No corroborating evidence or discussion is given on this point, or on the behaviour of multi-species assemblages. Field *et al.* (1982) suggest that data "standardization" (Bray and Curtis 1957, Clifford and Stephenson 1975, Smith *et al.* 1988) or "relativization"

should be done when quantitative R-mode (inverse) analyses are carried out (see also Boesch 1973, Hailstone 1976). In other words, fractions of the maximum abundance sampled over all stations for a species, can be used to replace actual abundances for that species. The authors suggest that species which are functionally interdependent (e.g. host and parasite) may otherwise be separated into different groups because their relative abundances are different. Other alterations which Clifford and Stephenson (1975) include in this category include standardizing the data by dividing by the standard deviation (Z scores).

b. The Subjective Approach: Community Concepts

What is a benthic community and how can we characterize it? From 1911 to 1918, Petersen (c.f. 1913,1914,1915a,b) and later Thorson (1957) described benthic population structure in a subjective manner and introduced the concepts which would become the foundation for benthic studies. In particular, the definition and practical usage of the term "community" has been a cornerstone of benthic analytical development. It is appropriate, therefore, to preface the discussion of analytical methods (sections 2d-2f) with a review of some important community concepts.

Community Versus Continuum:

The first quantitative ecological studies on marine benthos were carried out in Northern Europe by Petersen (1913,1915a,b). Using subjective judgement and his expertise as an ecologist, Petersen described a series of benthic communities which he considered to be relatively stable and cosmopolitan. Petersen was fairly conservative in his conclusions about these communities, describing them as "statistical units only", although no statistical analysis of data was done. The units were dominated by recurrent indicator species which gave the community its name, and were related to typical coastal and sediment types. The search for indicator species is a persistent theme in benthic ecology, particularly in pollution studies (see next section). Petersen (1914 - cited in Thorson 1957) stated that: "the animals, which

are not seasonal and which comprise an important part of the whole mass of the community, owing to number or weight will presumably be best suited for characterization of the community." In 1957, Thorson refined Petersen's work and developed the "parallel communities" hypothesis, based on studies in Northern Europe. Thorson suggested that Petersen's communities were not cosmopolitan at the species level, but rather at the genus (or family) level. Therefore, researchers studying benthos in areas outside Petersen's locales (irrespective of latitude) could expect to find persistent communities with dominants of the same genus or family as the classic Petersen communities, but not necessarily the same species. These could be considered "parallel" communities or "community-units" by terrestrial botanists (Whittaker 1970). Illies and Botosaneanu (1963) used a similar approach in designating stream communities (see also Harrison and Hynes 1988). Like Petersen, Thorson was concerned that the subjective skill used by experienced ecologists to characterize communities be substantiated by quantitative sampling and data analysis, although few statistical methods were in use in benthic ecology in the 1950's.

Thorson (1966) reiterated his theories of parallel communities by describing the bottom types associated with specific communities (regardless of latitude). He also revised his earlier theories (1957) by admitting that communities without dominant species (i.e., with many low-abundance species) cannot fit into the parallel community structure. This is evident in tropical and many deep-sea benthic communities. The parallel theory also does not take into account abundant meiobenthic species, where these animals dominate the fauna.

Researchers are still citing examples of Thorson's parallel macrobenthos communities in various parts of the world (e.g. Shelford 1935, Buchanan 1963, Horikoshi 1970, Ellis 1971, Masse 1972, Warwick and Davies 1977, Govaere *et al.* 1980, Shackley and Collins 1984). Horikoshi described a Thorson Maldane/Ophiura community as far away as the Sea of Japan. Buchanan and Moore (1986) described long-term stability in one of Petersen's *Amphiura filiformis* communities and cited evidence that biotic and abiotic factors affected this stability. The recurrent and persistent nature of such assemblages of animals suggest that the

concept of ecologically significant, interactive groupings of animals cannot be dismissed completely as "coincidence", as suggested by Gleason (1926). Most researchers subscribe to the belief that the range of cited examples lends credence to the Thorson parallel community theory, but that its simplicity and subjectivity makes it useful only as an overview or reference point for more detailed ecological study.

Petersen and Thorson, though concerned with the quantitative description of communities, did not satisfactorily define the term "community" from either the statistical or ecological point of view, except to indicate that a community was a discrete and repetitive unit characterized by certain dominant species and specific habitat types. The concept of discrete communities as depicted by Petersen and Thorson has been challenged over the years (Gleason 1926, Jones 1950, Burbanck *et al*. 1956, Lie 1968, Mills 1969, Gray 1974).

Many botanists are inclined towards the "continuum" viewpoint (for reviews of the early development of the community concept in terrestrial systems, see Whittaker 1967, 1970), which suggests that species composition changes along gradients of habitat properties rather than forming discrete communities. For example, if samples are taken from two distinct but homogeneous substrate types, two distinct species groups may be collected and these might be called "communities". If a third sample, taken between the first two substrates, contained a mixed group of species, this assemblage might be called a "transitional" community by some researchers. Alternatively, the entire set of three samples could be considered a "continuum" of species. Spatial distribution of species groups depends on particular environmental and biological gradients. However, the spatial distribution of a group of species tentatively labelled a "community" may be simply a sampling artifact or a convenient descriptive unit (Gray 1974).

Mills (1969) provided an excellent review of the community/ continuum debate, discussing the classical definitions of the terms "community", "formation", and "association" as they apply to terrestrial ecology, and the use of such terms as "community" and "biocoenoesis" in benthic ecology. He redefined a benthic "community" in accordance with the concept of a climax community in botany. A "major" benthic community

is one which is self-sustaining without other communities, and is defined as:

> "a group of organisms occurring in a particular environment presumably interacting with each other and with the environment, and separated by means of ecological survey from other groups" (Mills 1969).

Identifying such a "major" community is no small matter, and since Petersen and Thorson's descriptions of recurring communities, no real attempts have been made in benthic ecology to identify major communities. Determining the functional boundaries of a "community" requires some consideration of the stability and equilibrium conditions in the succession of the fauna. DeAngelis and Waterhouse (1987) reviewed the concept of successional equilibrium and stability, and suggested that it could be identified or predicted only on such a large scale as to be virtually unmeasurable or untestable.

Most authors avoid the argument of "continuum" vs "community", but tend to lean in favour of one or the other, or use a compromise approach incorporating both viewpoints. In practice, the distribution of the animals collected will determine the method of analysis, as will the philosophical view of the researcher. Lie (1968) discussed the controversy between the theories of bounded communities and continua based on the overlapping and varied niche requirements of all the species in the sample set. Lie (op.cit.) concluded that discrete communities are absent in Puget Sound, where there are strong environmental gradients. This absence of discrete communities is also evident in many polluted areas (Anger 1975, Pearson and Rosenberg 1978).

Allee *et al.* (1949) and Burbanck *et al.* (1956) described the "Ecotone", which is a transitional zone or gradient between two different communities. The breadth of the ecotone varies with the rate of environmental gradient change in physically controlled benthic habitats characterized by biotic and physical instability. Therefore estuaries represent ecotones between the surrounding freshwater and marine communities. This concept has been supported by the findings of Ristich *et al.* (1977), Kay and Knights (1975) ,Burns (1978), and Maurer *et al.* (1978), though the term "Ecotone" seems not to have become common

in usage except in descriptions of the transitional fauna along pollution gradients (e.g. Pearson and Rosenberg 1978, Knox and Fenwick 1981). The validity of both the "community" and "continuum" concepts has led in present day practice to a compromise concept of "intergrading communities".

Maurer *et al.* (1978) describe estuarine faunas as a "mosaic of assemblages" some of which are distinct, others amorphous, and which are associated with salinity and sediment type. This description highlights the important observation that an assemblage (or community) may be separated into small patches, with other assemblages intermixed spatially or temporally. Chapman and Brinkhurst (1981) described estuaries in which benthic communities migrated along a changing salinity gradient. These communities seem to respond to the strong annual rhythmicity in undammed rivers with high altitude sources, such as the Fraser River on the west coast of Canada. Certain identifiable species groups are located further downstream during freshwater intrusions (high runoff periods) than during periods of strong marine incursions and low runoff. Similar cycles of spatial shift in communities have been detected in data from other rivers, such as the St. John River estuary, (Gillis 1978), River Tees estuary (Gray 1976) and estuaries of the Georgia coast (Howard and Frey 1975).

Indicators of Anthropogenic Impacts on Communities:

Methods similar to those described by Petersen (1913-1915) and Thorson (1957) are still commonly used to select species or assemblages indicative of pollution. There is some validity to this approach since Pearson and Rosenberg (1978) suggest that certain species (or genus) groups occur in organically enriched habitats everywhere. Leppakoski (1979) concurs with this viewpoint, but cautions that it is based almost entirely on work with boreal bottom communities.

Traditionally, species used as indicators of organic pollution have included a number of opportunists which are primary colonizers in naturally anoxic basins (Rosenberg 1980). Perhaps the most common of these is the *Capitella capitata* complex (c.f. Rosenberg 1973, Pearson and Rosenberg 1978, Gray and Christie 1983, Levings *et al.* 1983), which

is in reality not one, but a series of sibling species (Grassle and Grassle 1976). Generally the presence of such species coincides with an increase in the number of deposit feeders which move into areas of organic enrichment (Pearson and Rosenberg 1978). The use of such species as pollution indicators is becoming less and less popular, because they tend to be ubiquitous, and are often found in even higher abundances in non-polluted areas than in polluted areas (see Botton 1979, Gray and Pearson 1982). Washington (1984) reviews the historical development of biotic indices (i.e. methods or indices which use indicator organisms for pollution monitoring), advocating the use of intolerant species which disappear under various conditions of pollution, rather than the use of tolerant species which can be ubiquitous.

Meiofaunal species have also been used as indicator species. Nematodes and a few oligochaete species can be very abundant in extremely polluted sites, which cannot be inhabited by the macrobenthic opportunists (Nichols 1977, Lepakoski 1977, 1979, Elmgren 1978). These taxa decline in abundance with increasing distance from the pollution source and are of limited value as pollution indicators at sites with less extreme conditions. Meiofaunal ratios (such as nematodes/copepods, known as the N/C ratio) have occasionally been used as gross indicators of pollution (Raffaelli and Mason 1981). The N/C ratio is simple to use, but is reliable only on sandy intertidal beaches, where nematode populations increase and copepod populations decrease with increasing pollution. The ratio is affected by changes in sediment type (for review and discussion of the relative behaviour of these meiofaunal groups in different environmental conditions, see Raffaelli 1987). Soule and Keppel (1988) discuss much of the current philosphy on the use of indicator organisms in marine systems.

The concept of indicator species has been replaced with models of indicator communities. In marine environments objective analytical methods for identifying indicator species or groups of species are being attempted (see sections 2c and 2e). Some researchers use higher order taxonomic groups as indicators of pollution, to economize on sampling and processing costs and to reduce taxonomic discrepancies (c.f. Pontasch and Brusven 1988, Warwick 1988a). However, the potential

reliability of results at different taxonomic levels is not adequately proven. It is not safe to assume that species or genera which share an evolutionary relationship (and are thus taxonomically linked) also share ecological requirements, and can therefore be lumped together for comparison of community structure.

The use of indicator species to describe communities has not been as prevalent in recent years as it once was. In the following sections, it will become obvious that the focus of most benthic studies has been to integrate and describe the entire faunal composition of a community.

c. Descriptive Univariate Community Indices

Many researchers have sought to describe the underlying structure of communities in an objective manner. This has resulted in the development of various univariate community indices, which will be described below. The methods described have been criticized as being too simplistic, since they attempt to reduce complex multivariate associations to a single number. Despite this, many of these indices have become entrenched in regulations governing waste disposal. Because of their greater descriptive specificity, multivariate methods (described in section 2e) are rapidly replacing univariate indices. Since many univariate methods are still in common usage in benthic studies, and are often useful for an initial characterization of a community or sampling strategy, a selection of these indices will be described. The coverage is far from exhaustive, and the reader is referred to the other reviews cited throughout the section.

In most survey studies, abundance and the number of species are measured. In some cases, biomass has been used to describe communities, although the difficulties involved with using such a variable character have made biomass analyses unpopular (Day 1983). Only recently have new approaches to modelling the dynamic interactions of biomass and trophic flow in benthic communities begun to emerge in the literature (see section 2c).

Inferential methods for testing hypotheses with univariate data models are commonly found in introductory statistics textbooks and will

not be discussed in this review. These include normal - theory methods such as t-tests, ANOVA, regression and correlation. Many non-parametric methods are used as well, including rank order techniques for monotonic data and bootstrap and randomization methods (see Diaconis and Efron 1983, Felsenstein 1985). The latter two types are increasing in popularity (see Clarke and Green 1988) but are still rarely found in introductory statistics textbooks. Both bootstrap and randomization methods are non-parametric because they do not require specific assumptions about the distribution and variance of the data.

Spatial Distributions and Sampling Design:

Ecologists continue to theorize about the relationships between species abundances and the spatial distribution of assemblages. Brown (1984) discussed niche size relative to the dispersion and abundance of species on different spatial scales. Many methods have been used to describe the spatial distribution of communities. One way of doing this is through "frequency distributions" which relate sample counts (such as number of individuals in a sample) to frequency of counts (such as number of samples - c.f. Elliott 1977, Devore 1987, Tukey 1977) in a histogram or curvilinear graph. Each point on the graph typically represents a single sample unit.

If the abundance data can be fitted to one of the standard frequency distribution models, the model can then be used to make decisions on the sampling effort required to collect a given percentage of the animals in the assemblage. Elliott (1977) described several commonly used frequency distribution models including the positive and negative binomial and Poisson distributions, and discussed methods for testing the fit of data to these models. Elliott pointed out that for benthic invertebrate assemblages, the efficacy of the positive binomial is rare, unless the assemblage is regularly or uniformly dispersed, in which case, the variance is expected to be less than the assemblage mean. Holme (1950) cited an example of uniform spacing in a population of intertidal bivalves, which was possibly related to the foraging behaviour of the species. Wilson *et al.* (1977) described a uniformly spaced brittle star assemblage. Territoriality may result in a regular distribution of

members of a species, but it is almost impossible to conceive of this occurring in multi - species assemblages.

The Poisson distribution is a limiting case of the positive binomial, which occurs when the variance is approximately equal to the mean. This implies a random (rather than regular) distribution of individuals within a given area. Taylor *et al.* (1978) suggested that Poisson distributions are unlikely in benthic assemblages, except at very low assemblage densities (c.f. Clarke and Milne 1955).

The negative binomial distribution is one of many possible models which can be used when the assemblage is clumped or contagious (aggregated) and the variance is greater than the mean. This distribution was described in some detail by Elliott (1977), who also mentions several other possible "clumped" assemblage models. Most assemblages will show some degree of clumping, since most abiotic factors affecting that assemblage are rarely uniformly or randomly distributed.

Apart from describing community structure, frequency distributions are useful for selecting a data tranformation to produce a normal data distribution, which is a prerequisite for many parametric statistical analysis. Various methods described in most introductory statistics textbooks (e.g. Chi-squared goodness of fit, Kolmogorov- Smirnov test for distributions with mean and variance unknown - see Lilliefors 1967, probability plots) can be used to assess how well a theoretical distribution (normal, Poisson, etc.) fits the faunal data.

It is not always feasible to fit a statistical distribution to clumped assemblage data. Consequently, indices that measure the degree of clumping or aggregation have been used to describe the spatial distribution of these aggregations of species (for review see Elliot 1977, Morisita 1959, Taylor 1961, Taylor et al. 1978). One currently popular index ("b") is given by the exponent in the power law decribed by W.D. Taylor (1961, 1980, Taylor et al. 1978), which is discussed below.

Taylor's power law relates the sample variance (S^2) to the mean faunal density (x) as described in section D3 ($S^2=ax^{-b}$), where a is constant and b has been used as a dispersion index. As b increases,

aggregation or clumping increases (although Taylor suggests that a is also an important indicator of dispersion). The value of this type of function is that it does not presuppose a specific frequency distribution. This is important since, as L.R. Taylor (1980) pointed out that "There is, in practice, no good biological reason to expect the same statistical frequency distribution to fit data for the same species at different (population) densities."

Downing (1986) examined the arguments for explaining the dependence of the value of b on the species or group being examined. He argues that b is not species specific, but is environmentally related. Gage and Geekie (1973a,b) used an index similar to Taylor's b to examine the deviation from random (Poisson) of the spatial dispersion of fauna in a series of benthic samples in Scottish sea-lochs. They found that faunas from shallow, current- swept areas of muddy sands were more aggregated than deeper, faunas found in the soft mud of quiet waters.

Taylor's b and other currently used indices of dispersion (see Elliott 1977) are all sensitive to the size of the sample quadrat. Such indices are also sensitive to the number of replicates and sample coverage, and therefore should be used with caution when comparing faunas sampled using different methods (Elliott 1977, Downing 1986). This problem is related to the fact that the dispersion pattern may change as a larger and larger sample of the substrate is examined. For example, in a small sample quadrat the assemblage may seem to be randomly dispersed, whereas a larger sample would reveal a pattern of high density separated by gaps of low density.

Based on empirical data, Downing (1979) suggested a "universal" power law for all freshwater benthic taxa. The suggested value for Taylor's b was 1.5. More recently, Vezina (1988) applied the power law to marine benthic assemblages and concluded that b was consistently close to 1.2 for all size groups and sediment types examined. Thus he concluded that marine benthos are generally less aggregated than freshwater benthos. Interestingly, the variance versus density relationship in marine benthos showed little variation among studies, suggesting that preliminary sampling may be unneccesary in many cases. The attraction of using Taylor's power law to obtain some generalized

"b" value is that the value can be useful for deriving "variance stabilizing transformations" (Downing 1979, and see section III.A.2).

Dispersion measures can be used to examine how representative the sampling pattern is with respect to the number of species and number of individuals in the assemblage. Measures of aggregation give a good indication of the evenness of the assemblage. This information can be used to predict the size of the sample unit required to collect a representative number of individuals, and the total number of sample units required to obtain acceptable within-site variance (Downing 1979, Elliott 1977, Holme and McIntyre 1984). Downing (1979) utilized the relationship between variance and mean given by Taylor's Power Law (Taylor 1961) to devise an equation for estimating the sampling precision (= standard error) for the mean density of animals. The equation is based on the total area sampled, and the mean density of animals to be encountered at any given station, and can be used to determine the number of replicates required for the desired degree of precision. Downing (1979) and Downing and Anderson (1985) discuss the assumptions of the method. In general, to gain acceptable precision, many replicates must be taken when small samplers are used and when the densities of the animals are low. Holme and McIntyre (1984) discuss a similar method of estimating sampling efficiency (from Elliott 1977), based on the sample mean, the degree of clumping, and the precision required. At an expected density of about 100 animals per replicate (regardless of sampler size), and $b = 1.5$ (according to Taylor's Power Law), a precision of 20% (i.e. 20% uncertainty) would require a total of 12 replicates. At 1000 animals, the same conditions would call for only 5 replicates.

Using Downing's method, a sampling program which includes high and low density assemblages will have to include enough replicates to sample adequately the latter. Unfortunately, this may mean oversampling high density stations if an equal number of replicates is taken at all stations, which has implications for the acceptance or rejection of statistical hypotheses describing the assemblages (see Toft and Shea 1983). Alternatively, for economic reasons, it might be advisable to consider the use of a different number of replicates or a different

quadrat size at each station, so that standard error of the estimated mean density would be similar for all stations. It is conceivable that researchers might be uncomfortable with this method although it has an appealing logic.

Community Structure:

In the preceding section the spatial distribution of an assemblage was considered. This section is concerned with the species composition of the assemblage and the univariate approaches to examining community structure. This section will discuss the concept of diversity and related issues which have resulted in a host of information indices, distributions and graphical displays. Many simple indices have been proposed and used, particulary for pollution studies (e.g. Satsmadjis 1985). These are often misleading, or may be no more effective than the visual subjective conclusions of experts.

Diversity theories:

There are numerous definitions of diversity (see Washington 1984 for review) but a good general definition commonly used by ecologists is "a measure of the species composition of an ecosystem, in terms of the number and relative abundance of the species" (Legendre and Legendre 1983). Specific definitions and related algorithms are numerous (see Washington 1984). Hurlbert (1971) suggests that diversity is an abused "non-concept" in current ecological use. Certainly there is considerable controversy about the validity of the use of diversity measures.

The term "species richness" has commonly been used interchangeably with "diversity", although most authors use species richness to describe only the total number of species in an assemblage. Dominance refers to the degree to which an assemblage is "dominated by" individual species. Therefore an assemblage with many species of relatively equal abundance has a low degree of dominance. The inverse of dominance is "evenness", so that an assemblage with low dominance will have high evenness. Diversity therefore combines the concepts of dominance, evenness and species richness, and is a measure of the relationship between species richness (number of species in the community) and the distribution of individuals among the species.

Traditional ecological theory from terrestrial biology states that there are fewer numerically dominant species in species-rich communities than in species-poor ones. This seems to apply generally to tropical marine habitats and the deep-sea (for review see Birch 1981), although there are numerous exceptions. Many general theories attempt to relate diversity to latitudinal and temporal gradients. Pianka (1966) described six such theories which are strongly interrelated. No attempt will be made here to discuss separate theories, but some of the factors believed to be fundamental to the maintenance of diversity will be briefly described in the following sections. For a more recent review of diversity theories see Washington (1984).

Perhaps the most simplistic mechanism thought to control diversity is time. There is a persistent traditional belief amongst ecologists that over time, assemblages become more complex, and therefore more diverse. This theory is somewhat difficult to test, and unlikely considering the wide range of other factors that are known to affect species richness and evenness, and which vary over time. Time is therefore not seriously discussed in relation to diversity maintenance in benthic communities.

In resource limited assemblages, intraspecific competition has traditionally been considered the most important mechanism in the evolution and maintenance of species diversity. Ecological theory from Hutchinson's time states that competing individuals of a given species would be selected according to those traits that reduced intraspecific competition, thus resulting in diversification and eventually speciation or geographic separation (competitive exclusion) of two closely related species (e.g., island biogeography - Simberloff 1978). Similar niche separation between species may occur due to competition, although Levinton (1982) points out that there is surprisingly little evidence of niche separation even in intensely competitive species from marine benthic assemblages. Interspecific cooperation can also play an important role in assemblage structure (e.g. in food exploitation by tubificid oligochaetes - Brinkhurst 1980).

There have been opposing schools of thought on the importance of competition and cooperation as factors in community structure.

Competition theory is in itself a complex issue beyond the scope of this review. Some ecologists state that competition per se is non-existent in certain communities and that factors such as predation and mutualism are most important for sustaining community diversity and structure (for review see Levinton 1982, Strong 1983). Commito and Ambrose (1985) reviewed the roles of predatory infauna in the control of trophic assemblage structure of infaunal communities. The authors make the interesting observation that botanists and invertebrate biologists seem rather unimpressed by considerations of interspecific competition, while vertebrate zoologists are more inclined to seek such relationships. Perhaps this is because behavioural interactions can be more readily observed in vertebrate communities than in benthic infaunal assemblages.

Several theories are briefly mentioned here because of their application to, and influence on, benthic ecological theory. In aquatic ecosystems the most important aspect of diversity has traditionally been its relationship to stability. Unfortunately, it is not clear from the on-going arguments amongst ecologists that there is any relationship between diversity and stability, especially since few can agree to a clear-cut definition of stability. Coupled with this problem is the difficulty in measuring or proving the existence of assemblage equilibrium points around which species composition may fluctuate. Stability itself is defined in various ways, but perhaps the most commonly used definition originated with Margalef (1969 -see Smedes and Hurd 1981): stability is the resistance of the community to change from stress caused by external disturbance. Such resistance may be different for different components of the assemblage (e.g., meiofauna and macrofauna). DeAngelis and Waterhouse (1987) review the related concepts of community stability and equilibrium.

Despite the difficulties in definitions and measurements, theories have been put forward as to the factors which affect stability and diversity. Competition and cooperation have already been mentioned briefly as factors affecting diversity. Such biotic factors are notoriously difficult to measure. Theories describing abiotic (particularly disturbance and perturbation) effects on communities have had a particular influence on benthic infaunal ecology. A brief

description of a few of these follows.

The Stability-Time hypothesis was introduced by Sanders (1968) along with a univariate graphical method of depicting diversity known as rarefaction (see Simberloff 1977 for review of rarefaction methods in ecology). Rarefaction has since been used extensively to determine sampling efficiency in benthic studies. The theory states that an increase in benthic diversity within a community is established in two ways (paraphrased):

1. short-term, non-equilibrium or transient diversity is induced by a low level, unpredictable physical or biological perturbation or stress, resulting in biological undersaturation. In effect, small scale disturbances produce empty patches which can be filled temporarily by non-equilibrium species, thus increasing diversity.
2. long-term, equilibrium or evolutionary diversity is a result of past biological interactions in physically benign and predictable environments. This is seen most clearly in deep-sea habitats in which diversity usually increases with increasing depth (Rowe *et al.* 1982). Long and Lewis (1987) disputed the idea that diversity increases offshore in most cases.

Pearson (1975) suggested that serial succession in polluted habitats is best explained by the Stability-Time hypothesis. The simplicity of the theory has been disputed by several authors, however. Thistle (1983a,b) and Shin and Thompson (1982) provided contradictory examples from marine benthic ecology. Abele and Walters (1978, 1979) and Josefsen (1981) introduced a different hypothesis which states that a species - area relationship is sufficient to account for observed patterns of species richness (diversity). This "area effect" means that variations in habitat heterogeneity, either physically (Abele and Walters, op.cit., Kay and Knights 1975, Probert and Wilson 1984) or biologically induced (Josefsen, op.cit.) can account for variations in assemblage diversity. The larger the area sampled, the greater the effect.

One aspect of Sander's (1968) Stability - Time hypothesis has received some attention in recent benthic ecological studies. The concept of maintenance of high diversity in communities by a patchy

"mosaic" of disturbed sites with a predominance of short-term non-equilibrium species, has led to the postulation that species richness in stable communities is maintained by a temporal mosaic of former disasters. Therefore, a community is a collection of relics and recoveries (Johnson 1973, McCall 1977). This patchy nature evident in the benthic environment leads to questions about the efficiency of sampling design in benthic studies (Thistle 1983a,b). Thistle (1981) has reviewed this concept in light of recent benthic ecological studies. If disasters occur frequently enough that there is a reasonable expectation that one will occur within the range and lifetime of an individual opportunist, this is an important mechanism for maintaining diversity in a community in equilibrium. He pointed out that such patchy disturbances are caused by pollution sources (see Pearson and Rosenberg 1978) as well as natural causes (see Maurer *et al.* 1978). Other theories for modeling transient patches are discussed by DeAngelis and Waterhouse (1987). They point out that if the scale of a stochastic disturbance is smaller than the the range of the biological assemblage in question, the disturbance will help to maintain diversity, since the ability to recolonize patches from surrounding areas will offset local extinctions, particularly for species which are less competitively effective in successionally advanced locales.

The quantification of this temporal mosaic phenomenon in benthic studies was discussed by Abugov (1982). He pointed out that the maintenance of competitively inferior ("fugitive") species, by colonization of disturbed patches in a community, was dependent upon the frequency and spacing of patches. To measure this, he described a model of patch occurrence and developed a "phasing parameter" which represents the spatial and temporal environmental phasing rate of patches (see also Levin 1984). He concluded that diversity was maximized at "intermediate" levels of disturbance. Rhoads and Germano (1986) have introduced a method for mapping successional mosaics on the sea-floor. The researcher uses a sediment-profile camera to monitor long-term changes in benthic community structure, or the effect and duration of patches. A more practical approach might be to study specific communities in which detailed information can be obtained from living and dead assemblages.

Foraminifera would provide such a diagnostic tool since their taxonomy is totally dependent on the shell or test (see Smedes and Hurd 1981).

The temporal mosaic theory has raised numerous questions about succession and recolonization in disturbed and normal communities. This has led to a series of laboratory and in-situ patch experiments (c.f. McCall 1977, 1978, Leppakoski 1975, Winiecki 1986) to examine the time sequence involved in returning a bare patch to the same composition as the surrounding community. There are numerous discussions of these succession patterns and some interesting observations have emerged. For example, McCall (1977) pointed out that although the colonization sequence always proceeds with the same "types" of species groupings, the actual colonizer species will vary in any given area. Results of recolonization experiments in intermittently low-oxygen areas indicate that communities may never reach stability in an abiotically controlled environment (Leppakoski 1975).

The aformentioned theories about development and maintenance of diversity in benthic communities are only briefly touched upon here. The original sources should be consulted for detail. Many graphical methods and mathematical models have been developed for depicting diversity and related concepts. Once again, a small selection of these is included because they have strongly influenced the way benthic ecologists interpret community structure. For a historical review of these methods and theories see Washington (1984). The following selection assumes implicitly that diversity can be expressed by any monotonous function having a minimum when all elements belong to the same class and a maximum when all belong to a different class.

Rarefaction methods:

Sanders (1968) introduced the use of rarefaction methods for describing the relationship between species richness and dominance, based on his Stability-Time hypothesis. Rarefaction involves the classification of entities of one hierarchical level into entities of a higher level. For example, one might relate number of species from a series of sample units to the number of genera. In the most common form, often called a species abundance curve, the number of species is plotted

against the number of individuals. Each point in the plot corresponds to a sample unit. Typically, a power function is fitted to the data. This produces a characteristic curve describing the distribution of individuals over species in the set of samples. In relation to the Stability - Time hypothesis, Sanders (1969) suggested that the flatter the species abundance curve the more the distribution approximates the idealized physically controlled community, whereas steep curves reflect biotically accommodated communities with large numbers of species per unit number of individuals.

Engen (1979) points out the confusion relating to the names of species abundance curves. Often they are called species area curves, although Holme and McIntyre (1984) distinguish species area curves as the cumulative number of species versus number of sampling units (or sampling area). This is still a form of rarefaction.

Species abundance and species area curves have been used in the design of sampling programs (see Jumars 1975 and section 2e). It is particularly important to know the expected number of species in a sample drawn from low diversity habitats or from areas where the density of animals is low (e.g., deep sea). In a species area rarefaction plot of a given assemblage (this can be one station or many depending on the assumptions made about the assemblage), sampling bias can be reduced by calculating the number of species for one sampling unit using the mean value of all the units sampled, then for two sampling units using the mean of the sum of all the pairs, and so on (see Holme and McIntyre 1984). This should give some indication of the relative increase in species coverage expected if the number of replicates is increased. Simberloff (1978) points out that a "best fit" power curve derived from rarefaction plots assumes a random spatial distribution of individuals, which is rarely true. The result is that the more clumped the assemblage in a community, the more rarefaction overestimates the number of species expected in a sample. By extrapolation, the larger the individual sample size, the less likely that clumping will affect the sampling results.

Birch (1981) and Simberloff (1978) discuss the applicability and limitations of rarefaction methods in marine ecology. Simberloff (op.cit.) points out that the calculation of a series of diversity

indices (such as mentioned in the next subsection) for each sample unit (or station) is often not specific enough for community descriptions, and is therefore less valuable than plotting the data from a set of sample units as a simple rarefaction curve.

Diversity Indices:

Other representations of diversity based on species richness and relative abundance of species have been suggested. Diversity indices can be calculated for each station or replicate, or may be calculated using pooled data from a number of stations grouped for some rational reason. Computation of a diversity index reduces each column of the data matrix (or group of columns) to a single number. Therefore sites can be compared and sorted according to diversity, as long as the researcher takes into consideration the fundamental limitations in specificity of such measures.

Birch (1981) discussed the use of diversity indices in benthic studies and cautioned that they assume dominance decreases with increasing species richness. There are many marine situations where dominance increases with increasing species richness (see also Hurlbert 1971, 1984), particularly in tropical areas. This controversy about the positive or negative relationship between species richness and dominance was further discussed by Rejmanek *et al.* (1985) who concluded that the two are not linearly related except over small intervals of J'(evenness, the inverse of dominance), but are related by a quadratic function. At low values of J' the relation is positive, and at high values of J' the relation is negative (Rejmanek *et al.* 1985). Unfortunately, the fit of this function to the data given by Rejmanek is not too convincing. Other problems with diversity indices are illustrated by limnological studies. For example, the reduction in diversity and increase in dominance of certain tolerant "indicator" species below sewage effluents produces obvious shifts in diversity. Similar shifts might be produced by sampling in near-shore, surf-affected sandy bottoms instead of mud habitats just below the surfzone. Diversity indices might therefore fail to distinguish between communities with totally different taxonomic and environmental structures. Environmental deterioration that causes a

drastic loss of diversity is readily detectable by diversity indices, as well as any number of other simple methods. More subtle but often seriously damaging factors can cause the substitution of one "suite" of species for another, or shift dominance from one taxonomic group to another with profound ramifications up the food chain. Diversity measures may overlook such changes entirely.

Pielou (1969) discussed the relative merits of different diversity indices, including the most commonly used in benthic ecology, the Shannon-Wiener H' (described by Shannon and Weaver 1963) and Margalef's "d" (Margalef 1958). The Spearman rank correlation coefficient is often used to compare dominance (1-J' where J' is evenness - Pielou 1966; 1-J'=0 where there are no dominants; =1 where there is only 1 species) with species richness (S). There are other diversity indices which are not commonly used in benthic literature. Washington (1984) provides a discussion of terminology and historical perspective on the development of the many different indices.

An alternative way to depict diversity developed from empirical plots of the distribution of individuals amongst species (grouped in a geometric series of abundance classes) versus number of species. The entire plot will normally represent one station (or the combined data from a group of stations assumed to have a common diversity). Such distributions are sometimes called species abundance curves, but should not be confused with rarefaction curves, since they do not involve classification of one hierarchical level into another, and usually represent only one sample unit or station.

A theoretical distribution (such as normal or Gaussian), is often fitted to the aforementioned distribution (which is often referred to as a "diversity distribution"). The fitted functions can then be compared for different stations, times, etc. Fisher *et al.* (1943) suggested the general applicability of the log series distribution for describing such abundance distributions. Later Preston (1948, 1962) discussed the utility of the canonical log normal distribution for this purpose. The latter has gained more empirical support in benthic studies than the log series distribution (see Engen 1978, 1979). Gauch and Chase (1974) compare methods for fitting a Gaussian curve to abundance data. Among

these is the method of least squares estimation, which is described in many statistical packages and textbooks. Iterative maximum likelihood methods may become commonly used for this purpose in future.

The log normal distribution is based on the observation that the distribution of the number of species versus individuals per species (in geometric classes) often gives a truncated normal distribution, with more of the normal curve evident as sample size increases (Preston 1962, 1980). The portion of the curve evident in a given sample is bounded by the veil line (Preston 1962). Plotted on a scale of percent of total species or cumulative species, the log normal distribution produces a straight line. The slope of this line indicates the comparative degree of dominance versus species richness for the sample. In their search for biological justification of the log normal distribution, Ugland and Gray (1982) concluded that most communities are not actually based on a single log normal distribution. Instead, rare species, moderately common species and abundant species produce a mixture of three or more log normal distributions. In many plots of individuals per species versus number of species, these separate distributions are evident (see Gray and Pearson 1982). This points out the importance of ensuring that comparisons of log normal distributions are based on the same total abundances in all cases (Hurlbert 1971), otherwise the percentage of rare species obtained will be different and the position of the veil line will not be comparable.

Like other diversity indices, the log normal method has been criticized because it assumes that dominance declines as species richness increases. In some tropical ecosystems there can be many species with high abundances (see Birch 1981), producing severe departure from the log normal curve. As well, the more aggregated an assemblage, the poorer the log normal approximation to the data (as with rarefaction).

Assuming that log normal distributions provide an adequate model for data from some benthic assemblages, changes in a given distribution over time or space may be used to study the effects of organic pollution on benthic community structure. Ugland and Gray (1982) suggested that benthic assemblages are really made up of a mixture of three or more

abundance distributions which can be approximated by symmetrical (discrete) binomial functions. These distributions represent rare, moderately abundant and common species groups respectively. The binomial functions are usually closely overlapped in undisturbed or equilibrium communities, so that the resulting overall distribution closely fits a single log normal function (see Figure 1 in Ugland and Gray 1982). However, these separate binomial functions tend to spread apart in organically enriched communities, thereby causing a deviation from the log normal distribution (see Figure 7 - taken from Gray and Pearson 1982). Gray and Pearson (1982) point out that this traditional method of assessing the fit of a log normal curve to benthic assemblage data (see Figure 1 in Ugland and Gray 1982) is insensitive for separation of the component binomial distributions inherent in benthic assemblages, particularly in polluted areas. Gray and Pearson (op. cit.) prefer to use simple plots of number of species versus abundance per species to clearly delineate the multiple peaks in abundance of benthic assemblage data. They use this latter plotting method to try to objectively select pollution indicator species which are "moderately common" in polluted areas (specimens found in abundance classes IV to VI). Their rationale for using these species as indicators seems to be mainly that they are not ubiquitous, and are therefore disciminatory (see also Pearson et. al. 1983).

Rygg (1986) indicated that the log normal distribution is not a valid model for areas of heavy metal pollution, since the abundance of all species tends to decline as pollution increases, and no dominants emerge. Rygg (1985a) examined the effects of various heavy metals on diversity of communities and suggested the use of the diversity indices E(Sn) (= expected number of species per 100 individuals) and H' (Shannon and Weaver 1963) to identify groups of negative indicator species, or those species groups most likely to disappear along a variable gradient of pollution (1985b). The system apparently works in industrial pollution conditions as well as organic, although the levels of diversity indicative of different levels of pollution must still be arbitrarily selected.

Some authors have contended that the log normal distribution does

not fit the diversity patterns of many soft-bottom assemblages, impacted or otherwise (c.f. Platt 1985, Hughes 1984). Nelson (1987) examined an extensive number of marine studies and found frequent examples of considerable variation from the log normal and log series distributions. Preston (1980) suggests some potential data problems which may cause deviations from the canonical log normal distribution.

Hughes (1984) has suggested that assemblage growth in benthic communities is often arithmetic instead of geometric (as assumed by the log normal method) because of limiting factors such as predation and environmental influences. Therefore many diversity distributions become increasingly more concave rather than linear (as in log series) or truncated (as in log normal), as the number of rare species increases (especially in the tropics).

Schmidt and Garbutt (1985) suggested that the Gamma distribution may be useful for fitting concave diversity distributions without a mode (as described by Hughes 1984). They found that 128, out of 136 marine fouling communities tested, conformed to the Gamma distribution. Other distribution models have been suggested for describing communities, including the Poisson - Inverse Gaussian distribution (Ord and Whitmore 1986). None of these distributions addresses the basic limitations inherent in a univariate abundance model.

Biomass distributions:

Benthic assemblage structure can be described in terms of weight instead of abundance data, though there are problems related to the use of biomass as a quantitative measure. This section describes a few such methods. Biomass is used as a general term in benthic studies, but can refer to a wide range of measures of weight (see section 2a). Unfortunately, biomass data are usually more variable than abundance data, both within and between samples. Long term studies of the relationship between biomass and benthic community structure are rare. One such study was done over a 6 year period by Moller *et al.* (1985) at 15 different shallow soft-bottom locations on the Swedish west coast.

Of increasing interest to benthic ecologists is the use of combined abundance and biomass descriptions of community structure. A classic

biomass/ frequency model can be represented by an Eltonian Pyramid of animal abundance vs animal weight, or an inverted pyramid using biomass versus animal weight (described by Sanders 1960). The use of such a model was first discussed for pelagic ecosystems by Sheldon *et al.* 1972 (see also Sheldon *et al.* 1977), who hypothesized that roughly equivalent concentrations of material occur at all particle sizes from 1u to 10^6u (bacteria to whales). Kerr (1974) also noted that particle density is a linear function of log particle size over all trophic levels in the pelagic community, and that the relationship is mediated by some environmental factors, particularly depth. Sheldon *et al.* (1972, 1977) provided a number of empirical plots of particle concentration versus log particle diameter. Some of the generalizations in the Sheldon model were later modified by other researchers, in particular the contention that biomass concentrations are equivalent over all size classes. Even Sheldon's data do not consistently follow this pattern and the generalization was obviously too broad.

Platt and Denman (1975) reviewed the use of power spectral analysis in community ecology, particularly for periodic multicyclical phenomena. In 1977, they introduced a biomass spectral analysis model for pelagic phytoplankton communities, which incorporated mass scaled respiration and growth factors. The advantages of the model were that it was steady-state, and did not rely on the delineation or consideration of specific trophic levels. The constants used for metabolism (respiration) and growth were derived from empirical generalizations in the literature. Unlike Sheldon's model, the model of Platt and Denman (1978) suggested that biomass in a given size class decreases in a regular manner with increasing size. Like Sheldon's, this model assumes a regularity in the difference and direction of predator/ prey size relationships. As well, it assumes that very little (about 5%) of food particles in the pelagic open ocean are lost directly to the benthos. In essence this model attempts to track biomass (or energy) as it flows through the spectral bands from small to larger organisms, as distinguished from following the increase in size of given organisms.

In 1978, Silvert and Platt addressed some questions about the steady-state assumptions of this model, and introduced modifications to

the equations to track "spikes" in biomass spectra through time and over different spectral bands. Denman *et al.* (1990) extended this spectral analysis to describe the propagation of disturbances through biomass spectra in pelagic ecoystems, and to estimate time scales required for energy transfer through trophic groups.

Platt (1985) reviewed the ecological concept of "Trophic Level Formalism" (see also Schwinghammer 1981) and its problems as a model for describing the relationship between organism size and its position in the trophic structure. He also summarized the pelagic and benthic research contributions to biomass size modelling. Assuming that large quantities of organic matter are not tied up in the sediment, and that all available organic material is in use, the total primary productivity of a given community should be equal to the sum of the biomass of all the different trophic groups within that system. Borgmann (1987) more recently reviewed the variation in results and assumptions of the different biomass spectrum models. He found that the basic formulation of the model was consistent and conservative throughout the literature, particularly if some simple assumptions are made about somatic growth and mortality of organisms. He does, however, point out the dangers of deriving biomass spectra based on only two trophic levels of organisms.

Schwinghamer (1981) adapted the power spectrum biomass model for use in benthic ecosystems, although he pointed out that stable surface dwellers compete for food and space in a fundamentally more complex way than pelagic organisms. In particular, predator/ prey relationships are not unidirectional or consistently size scaled. Instead of particle volume, Schwinghamer measured biomass, converting this to volume to use the same model as the Sheldon papers. In plots of biomass concentration as a function of logarithmic intervals of organism size (rather than biomass, and with no species identifications), three biomass/size peaks are evident (Schwinghamer 1981, 1983). It turns out that the minima between peaks effectively separate the grain surface dwellers (bacteria) from the interstitial organisms (meiofauna), and the meiofauna from the burrowing or surface- dwelling macrofauna. These peaks in size distribution are surprisingly conservative spatially and temporally, and vary only in relative magnitude under different environmental conditions

(particularly sediment type - Schwinghamer 1983). Schwinghamer noted potential scaling factors for this model. For example, sediment disturbance reduces macrofaunal biomass to a much greater degree than it does interstitial meiofauna, and total microbial biomass is strongly dependent on organic content (and therefore texture) of the sediment. Schwinghamer (1983) expanded on Sheldon *et al.*'s model (1972, 1977) by attempting to integrate it with generalized size scaled respiration and Production/Biomass (P/B) ratios to approximate benthic community production and metabolism. Values were based on generalized mass scaled allometric functions of P/B ratios described by Banse and Mosher (1980), who hypothesized that mass on reaching maturity is a good estimator or scaling factor of annual P/B for invertebrates. The relationship holds reasonably well for animals living at temperatures between 5 and 20°C.

Schwinghamer (1983) suggested the use of causal analysis (multiple correlational pathways) to describe the effects of various environmental factors on the biomass/volume model in marine benthos. One serious limitation of the use of the Sheldon spectrum in benthic ecosystems is that there is not an even distribution of biomass over all size classes, since most (up to 90%) of biomass is held in the largest benthic classes (macrofauna). In attempts to examine the effects of a mesocosm and natural pollution gradient on the size structure of benthic communities, Schwinghamer (1988) concluded that there may be some relation between the size structure of benthic communities and their proximity to pollution sources. The size distributions proved to be less consistent than taxonomic ones, and may be useful only for baseline monitoring functions where taxonomic analysis is not feasible.

Warwick (1984) differentiated between meiofaunal and macrofaunal groups using plots of log normal frequency distributions of species body dry weight, and suggested that the differentiation between meio- and macrofauna is the result of evolutionary optimization, so that sizes in between these groups (around 45 ug) are inefficient. Banse (1982) described generalized mass scaled respiration and growth rates, concluding that small invertebrates (i.e. meiofauna) have much lower respiration and growth rates than would be expected from scaling down rates of larger invertebrates (macrofauna) or poikilotherms. These

respiration results tend to support Warwick's bimodal benthos model. Dickie *et al.* (1987) propose a similar model for fisheries production based on the concept of biomass/ size (rather than trophic level) spectra.

Warwick (1984) discussed the effects of environmental factors on the relative contributions of meiofaunal and macrofaunal groups. Sediment disturbance, grade or granulometry affected the proportions, salinity did not. The major difference between Warwick's and Schwinghamers' work is that Warwick assigned each species to a size class instead of ignoring species identifications, producing a species biomass distribution rather than an abundance biomass one. Yet surprisingly, the same conservative patterns described by Schwinghamer were evident.

Both Schinghamer (1981) and Warwick (1984) agree that there are no functional limitations on sizes of organisms that can move within a fluid mud sediment. The pattern also appeared to break down in the antarctic and in the deep sea. Shirayama and Horikoshi (1989) agree, since in the deep sea meiofaunal and macrofaunal size categories significantly increase in overlap in the 0.5 to 1mm range due to dwarfism in macrofauna. Gerlach *et al.* (1985) point out problems with lumping the foraminifera in with meiofauna, particularly in deep sea size distributions. Otherwise, Gerlach *et al.* confirmed Schwinghamer's (1981, 1983) results, converting biomass to organic carbon values, and postulating metabolic peaks for the meiofauna and macrofauna.

A different approach to abundance and biomass descriptions was introduced by Warwick (1986, Warwick *et al.* 1987) for analysing pollution gradients. The method, termed ABC, is based on the assumption that as pollution disturbance increases, the large dominants in the normally stable assemblage decline in biomass and abundance. Simultaneously, the smaller opportunists increase in biomass and abundance. In polluted stations, total biomass decreases with respect to total abundance. K dominance plots of the relative biomass and abundance distributions illustrate normal, moderate and grossly polluted stations. This method has several important drawbacks. Firstly, the method assumes that the assemblage was initially stable or in equilibrium, a condition

which implies no appreciable disturbance from natural sources. This is rarely true in environmentally controlled habitats (e.g. estuaries or tidal flats - see Beukema 1988). In fact, extensive theoretical discussion has revolved around the related concepts of diversity and stability as they are affected by the frequency of temporal and spatial "patches" of disturbance (see temporal mosaic theory Johnson 1973, McCall 1977). Secondly, the moderately polluted stations which are often of greatest interest, produce the most ambiguous results. This may be partially because disturbances other than pollution are affecting the community, or that the community is inherently unstable or in equilibrium on an oscillating scale to which the method is insensitive. This is a common problem with most current pollution indices, partly because of their univariate assumptions and "point in time" sampling nature. Warwick (1988) suggested that the use of taxonomic groupings higher than species may partially alleviate the first problem since the higher groups are less sensitive to natural habitat factors than individual species. This proposition is arguable, and would require convincing verification. Another problem with ABC is that the K-dominance curves require adequate sampling replication to capture rare, high biomass species. Otherwise results may be skewed. Warwick (1986) suggests that even 5 replicates of $0.1m^2$ benthic samples may be insufficient. Very few benthic field studies include greater than five replicate samples per station.

All of the methods mentioned in this section require greater scrutiny. Platt (1985) points out the limitations and obsolescent aspects of taxonomic descriptions of marine communities, although Warwick (1984) clearly suggests that combined taxonomic/biomass descriptions of communities may be stronger than either type alone. Schwinghamer (1983) also points out that size comparisons in benthic assemblages cannot supplant taxonomic descriptions for characterizing communities, but that the two approaches can be complementary. This combined approach is still relatively rare in benthic ecology. In fact, there is no adequate model to link theories of species distributions with size distributions in benthic communities.

In speculating on the usefulness of the aforementioned

biomass/frequency models for describing the impact of anthropogenic effects on the benthos, it is important to consider the limitations and assumptions inherent in the models described above. Schwinghammer (1988) and Warwick (1986, *et al.* 1987, 1988) have attempted to examine changes in biomass spectral distributions with pollution gradients (temporal or spatial) and have met with limited success. In the case of Schwinghamer's model a major weakness may be the lack of any taxonomic discrimination, allowing the composition but not biomass of the community to change drastically without any visible effect on the model. As well, the use of equivalent spherical diameters as size indicators is problematical with oddly shaped benthic invertebrate fauna. This formulation seems strange since the volumes were directly estimated from individual biomasses.

Warwick (1984) indicated that the separate meiofaunal and macrofaunal log-normal frequency/biomass distributions should be conservative in terms of the slopes of the lines when plotted as cumulative functions. However, the elevations would vary considerably. To date, the varying effects of pollution on such functions has not been described. However, seasonal effects exist which would disrupt this pattern. Settlement of larvae produces biomass peaks between the meiofaunal and macrofaunal functions. Warwick's ABC approach seems more promising, but is still univariate, ignoring the multidimensionality of benthic communities based on the distinct identifications of different species. It may be that Warwick's data accumulation methods are effective, but his modeling is inadequate.

It is obvious that sediment type, depth and disturbance affect combined biomass/frequency ratios, as well as species abundance patterns. Therefore, the sensible combination of both abundance and biomass measures should yield promising results in benthic assemblages. However, some of the simpler assumptions inherent in the planktonic volume/frequency models (steady state conditions, unidirectional trophic flow, consistent volume-scaled division or production rates, uniform size scaled predator/prey intervals) could not readily be made for benthic systems. Marshall (1973) reviews food sources of benthic organisms, suggesting that many macrofauna and fish utilize bottom

particulate matter directly, often bypassing intermediate trophic levels (such as meiofauna) so that varying amounts of organic material can become tied up and unavailable to animals higher in the food chain. As well, estimates of even the relative productivity of the two major groups of benthic organisms, and their contribution to primary productivity in coastal areas are highly variable (for review see Mann 1982, Chapter 7). The determination of production or productivity requires not only information about flow rates of organic biomass between species in the assemblage, but also about the trophic relationships between them. A review of considerations and methods for analysing energy flow or rates of change of biomass through benthic systems is given by Crisp (1984).

d. Statistical Inference

Historically, there has been little emphasis placed upon hypothesis testing in benthic studies. For the analytical methods described in section 2c, statistical hypotheses are not required. The only situation in which statistical inference might be applied is in the estimation of an assemblage or sample parameter (e.g. mean abundance of a given species). In that case bias, standard errors or confidence limits are important concepts. As well, the "goodness of fit" of the data to a certain model or distribution may be tested. In such a case the hypothesis being tested is straightforward, and the results readily interpretable. Methods of estimation are included in all introductory statistical textbooks and will therefore not be discussed further in this review.

Recently, several papers have been published (Roughgarden 1983, Simberloff 1983, Quinn and Dunham 1983), discussing the rigor and application of hypothesis testing in mensurative (survey) ecological studies. In practical terms, it is difficult to test independent and mutually exclusive hypotheses in a multi-factor system, in which each factor may have a proportional or partial effect on the hypothesis being tested. Therefore strict falsification by independent tests of hypotheses concerning any one factor is impossible. As well, definitive

statements about causality in a multivariate situation must assume that every alternative hypothesis has been identified and rejected. In many cases it is impossible even to identify every alternative hypothesis (concerning biotic and abiotic factors). Furthermore, one cannot control environmental fluctuations between replicates in survey studies, so that generalizations beyond the sample are exceptionally difficult.

In practice, therefore, most hypotheses in benthic studies involve making predictions about the degree of effect or the probability that factors are affecting a community or organism. The veracity of the test depends on a number of factors, including clarity and discreteness of the hypothesis, adequacy of sampling, conformity of data to the underlying probability distribution (i.e. normal, Chi squared, etc.) and other assumptions on which the test is based. Throughout section 2e commonly applied inferential tests will be discussed in connection with multivariate data analyses.

Statistical Power:

There are two types of error (I and II) associated with inferential hypothesis testing. The probability of making a type I error (a), is the probability of mistakenly rejecting a true null hypothesis. In practice, a is usually set at a value between 1 and 10%. However, the probability of making a type II error (b) is the probability of accepting a false null hypothesis. The complement of b ($1-b$) is equivalent to the power of the statistical test, which indicates the reliability of the statistical result. The probability of a type II error is not commonly calculated, nor are standard acceptable levels (20% is considered reasonable) in use. The power of a statistical test is valuable to know when the value of a is being used to measure the degree of an effect. If b is known to be very low, one can confidently use a as a measure of effect. As well, the unexpected failure to reject a null hypothesis may sometimes be explained by the value of b. An explanation of the use of power in ecological research is given by Toft and Shea (1983). Some contingency tables for b at different levels of a are given by Cohen (1977) for standard univariate statistical tests.

Several factors affect the size of b. These include the value of a,

the sample size, and the magnitude of the critical effect being measured by *a*. Obviously, the more stringent the requirement for *a* (i.e. 1% or less) the more likely the probability of making a type II error and therefore the lower the power of the statistical test. The larger the sample size, the lower the probability of making either type of error. Fortunately, most benthic studies have reasonably large sample sizes. The "effect size" or magnitude of the effect being measured is important since the stronger or more obvious the effect to be measured the greater the power of the test. This also means that with large sample sizes, even biologically trivial effects may be statistically significant. Obviously, what constitutes an important biological effect is somewhat arbitrary, and standard guidelines are not often available. Cohen (1977) has made an attempt to standardize effect sizes for different types of application.

The calculation of statistical power is complicated except in very simple inferential tests of univariate hypotheses (e.g. ANOVA, t-test), since the underlying probability distribution of the data must be taken into consideration. In multivariate hypotheses the calculation is extremely complex and unwieldy. Therefore such calculations are rarely practical for multivariate tests. There is, however, some hope that bootstrap methods can be used to estimate the power of multivariate tests (see Beran 1986). Such methods have not yet been applied in benthic community studies, but are appealing because they are distribution-free.

The evaluation of the power of a statistical method is the only statistically correct method for determining the proper number of replicates and samples required in order to use correctly statistical inferential methods. For example, an undersized sample can make it difficult to detect departures from the null hypothesis. On the other hand, very large samples tend to detect even small and inconsequential departures from the null hypothesis. In this way, a priori decisions about "effect size" or the magnitude of departure from the null hypothesis that is worth testing, can help determine sample size.

e. Multivariate Data Analyses

Each column or sample unit of the faunal data matrix (see section 3a) can be considered a multivariate dependent variable. The inherent limitations involved in univariate community descriptive indices as discussed in section 2c are: 1) the exclusion of information on actual taxonomic content of data, which makes it difficult to compare effectively two different communities, or to monitor temporal changes in non-polluted community structure; 2) the difficulty associated with fitting multivariate assemblages into preconceived univariate distributions; and 3) the difficulty in examimining the relationship among more than two variables (faunal or environmental variables) using multiple univariate comparisons (both because of escalating error and interdependence between comparisons).

Because of these limitations, benthic marine ecologists have borrowed and adapted multivariate descriptive methods which were introduced in terrestrial ecological study. Multivariate statistics are not described in introductory textbooks as they are considered advanced topics in statistical study.

Mills (1969) described the two basic groups of statistical analysis that have developed out of the "community" and "continuum" viewpoints, as "classification" (grouping of stations or species according to relative similarity) and "ordination" (distribution of stations or species along a small number of ordinate axes which reduce the dimensionality of the assemblage as much as possible). The distinction between classification and ordination is somewhat artificial as they are usually just different graphical manipulations of the same data analysis, and many researchers use a combination of methods to show trends in data. In fact, one is usually most confident in the robustness of results if several descriptive and inferential methods lead to similar conclusions.

Similarity Indices:

A similarity (or inversely distance) coefficient measures the similarity between the community structure of any two sample units. For

a faunal data matrix (see Table 1), this means that a similarity coefficient can be calculated for each pair of sample units or replicates (columns). The collection of pairwise similarities is typically summarized as a symmetric similarity matrix. This is the most common usage and will be described in section 2e. Alternatively, similarity indices can be used to compare each sample unit (or station) with some reference value (site) (see Pontasch and Brusven 1988).

There are many kinds of similarity measures in common use in benthic studies, including: the Bray-Curtis coefficient (Bray and Curtis 1957- alternatively called index of affinity, percent similarity or Czekanowski coefficient); the Canberra-Metric (Lance and Williams 1967); Jaccard's index (Jaccard 1908 - presence/absence data only); Steinhaus' coefficient (refer to Motyka *et al.* 1950); the Zurich-Montpellier index (Kuchler 1967 - presence/absence only); NESS (see above); Morisita's Index (refer to Lopez-Jamar 1981); Fager's index of Affinity (Fager 1957); and Euclidean distance measures (such as Orloci's index, Orloci 1975 or the Manhattan metric - refer to Legendre and Legendre 1983).

Reviews of similarity methods and their various advantages and shortcomings include Boesch 1977, Clifford and Stephenson (1975), Legendre and Legendre (1983), Washington (1984), Cormack (1971), Williams (1971), Goodall (1973) and Green and Vascotto (1978). In examining the mathematical formulation of different indices, assumptions and biases can be inferred. Since the benthic studies of interest include count or meristic data, the use of binary (presence/absence) measures will not be discussed.

Most currently used similarity and distance measures are derived from the basic formula for the Manhattan metric. This measure is unbounded so that distances can get enormous for diverse data sets. For this reason, constrained measures (similarity) were developed. Because they are bounded, similarity indices are relatively insensitive to really high or low resemblances between pairs. The middle range of resemblances are most accurately reflected. Smith *et al.* (1988) point out that dissimilarity indices can therefore be skewed along a strong environmental gradient as dissimilarity approaches 0 and 100%. In cases where the data set is diverse, Smith *et al.* (op. cit.) recommend several

modifications to correct this, including the use of a "step-across" procedure originally described by Williamson (1978), which results in a matrix which may include dissimilarities greater than 100%. This suggests that the scale of measurement has been changed, which is problematical since dissimilarities greater than 100% are only meaningful if one can assume that some strong environmental factor is affecting assemblage distribution in a simple, linear way. An alternative method for transforming the raw dissimilarity indices to avoid skewness utilizes a dissmilarity measure coined as Zero Adjusted Distance (ZAD - c.f. Mahon *et al.* 1984).

Of the similarity measures in use in ecology today, the Bray-Curtis is perhaps the most commonly applied. Because of its formulation, attributes (species in normal analysis) with high scores largely determine the measures, whereas low scores are less influential. In extreme cases, this may mean that 1 or 2 out of a hundred species may determine the measure. This is a difficult problem in scale, since benthic data sets inherently include small, abundant species at one end of the spectrum, and rare, large species at the other. Modifications to the Bray Curtis (percent similarity or Dominance Affinity) are equivalent except that scores are standardized by entity total (station totals in Q mode analysis). This reduces the scale of the problem, but is somewhat arbitrary in ecological terms. Percentage Similarity also fails to distinguish situations where the relative proportions of taxa remain the same but the overall abundances have changed. Ironically, Pinkham and Pearson (1976) developed an index which produces the reverse species scale problem. It overemphasizes changes in rare species and deemphasizes changes in dominant ones. Therefore the measure is sensitive to normal sampling error and is not used in ecology. This species scale problem is unfortunately compounded by Euclidean measures, which typically use the squares of distances between attributes. Orloci (1975) addressed this problem by replacing absolute euclidean distance with relative, standardized values. As well, euclidean measures assume that the attributes are orthogonal (independent), an unsafe assumption in multi-species assemblages. For this reason, euclidean measures are always preceded by data standardizations or transformations, which make

interpretation of results problematical.

To overcome this scale problem, the Canberra Metric has been suggested as a similarity measure by some authors. In this measure, the formulation produces attribute standardization (instead of entity standardization), placing each species on the same scale. Unfortunately, there is no way to know if this bias is ecologically valid. The Canberra Metric ignores 0-0 pairs and considerably deemphasizes large number - 0 pairs. This measure therefore requires data transformation and is rarely used.

Morisita's index has characteristics of information content measures and correlational measures. It has the desirable property of being bounded between 0 and ¶1¶, but leads to heavy weighting of attributes with high scores, since it uses the product of 2 scores in the resemblance measure, thus compounding the scale problem. However, in R-mode analyses, correlational measures are less influenced by scale differences between entities (species) than the previously discussed metric expressions, since they are shape rather than size measures. Even so, measures such as Morisita's and the Product-Moment correlation coefficeint are rarely used in benthic ecology. If there are too many zeros in the data matrix (a common condition in benthic faunal data), spurious patterns of resemblance can occur and perfect correlations are possible between non-identical entities.

Information content measures (such as the Shannon-Weiner diversity index - Shannon and Weaver 1963) are occasionally used in ecology for examining niche or habitat overlap between species, but are not commonly used in community analysis (i.e. Horn's Overlap coefficient - Horn 1966,. Their use has been confined to binary methods (presence/absence).

Unfortunately, it is difficult to identify an appropriate (justifiable) set of criteria by which comparisons of similarity indices can be made, or decide which biases most closely resemble true ecological situations. Thus researchers have resorted to comparisons based on the analysis of real data and what the results "should" look like. Pontasch and Brusven (1988) compared Morisita's, Canberra Metric, Bray-Curtis and Average chi2 and found only the last two successfully tracked the progress of pollution in a freshwater creek. Grassle and

Smith (1976) compared the Bray-Curtis, Canberra-Metric and NESS similarity methods and preferred the latter. Further studies have used simulated data. Bloom (1981) found that the Canberra-Metric, Morisita's and Horn's Information Theory all diverge greatly from the theoretical standard. Only the Bray-Curtis (=Czekanowski) coefficient accurately reflected predicted similarity. Some researchers have applied intuitive criteria such as dependence of the similarity measure on sample size (e.g. Kobayashi 1987). Field *et al.* (1982) recommend the Bray-Curtis coefficient as a good all-round similarity measure for abundance data, but suggest that the Canberra-Metric may be more useful for biomass data since it weights all species equally, thus avoiding gross skewing of data by a few large specimens. In species impoverished areas, the Manhatten metric may be appropriate, since it is a measure sensitive to the total number of species present. The variation in emphasis of different similarity measures points out the difficulty in comparing benthic studies which use different indices. Poore and Rainier (1979) compared the two most commonly used measures, the Canberra-Metric and Bray-Curtis coefficients. Grassle and Smith (1976) compared the Bray-Curtis, Canberra-Metric and NESS similarity methods and preferred the latter. Popham and Ellis (1971) compared the Jaccard and Zurich-Montpellier indices (presence/absence data only), and decided that the latter provided more information with which to distinguish species and atypical samples.

Similarity matrices have also been used to examine sampling efficiency. The species abundance (or species area) curves described in section 2c are of limited value for determining sampling coverage because of their univariate nature and the underlying assumption that the distribution is random. To overcome this problem, a method has been developed which uses similarity (presence/absence only) in a similarity/area curve to determine the sampling effort required to obtain an acceptable percentage of species (for discussion of similarity area curves, see Kronberg 1987). Weinberg (1978) compared a qualitative similarity index (presence/absence) with a quantitative one (abundance) to determine community minimal area for sampling.

Classification:

If the data set comprises sample units from discrete community structures (whether a sampling artefac· or not), a classification approach may be used to separate the sample sites into a moderate number of clusters. Cluster analysis is an objective method for grouping the objects (sites or species) according to similarity of community structure. The main advantage of this approach is its simplicity of interpretation (IF the clusters are sufficiently distinct).

Cluster analysis is an objective method for grouping the objects (sites or species) according to pair-wise similarities or distances (as discussed above). The grouping can be hierarchical (groups linked together progressively such that the end product is one big group), partitioned (groups or classes are mutually exclusive - this is sometimes called "Dissection" or "non- hierarchical"), and clumping (groups can overlap -also called "non- exclusive"). The third group (non-exclusive) has rarely been used in benthic ecology (except Yarranton *et al.* 1972). If groups are allowed to overlap, the analysis is not classifying communities, but identifying continua. Methods available for non-hierarchical clustering tend to be impractical. The only method occassionally used in benthic ecology is Fager's Recurrent Group analysis (Fager 1957), in which the association level for defining exclusive group membership has to be decided subjectively, and apriori. For ecological communities, there is rarely (if ever) any rational criteria for determining such levels. Although methods like Fager's are occassionally used for R-mode binary analysis, they have more or less become obsolete (Boesch 1977) in ecological study.

The classification methods used most commonly in ecology include those which hierarchically sort distance or dissimilarity matrices. Hierarchies form the basis of systematic taxonomy and therefore the basis of ecological research based on taxonomy. Hierarchical methods proceed with progressive fusions or fissions of the groups to produce a "tree" diagram. These fall into four categories: agglomerative, divisive, constructive and direct optimization (see Gordon 1987). Agglomerative linkage rules define a measure of the similarity between two arbitrary groups of sites, building hierarchically until all groups

are linked as one cluster. Divisive methods work in the opposite manner, splitting groups progressively. Since divisive methods start out with all the available data at the beginning of the process, Boesch (1977) suggests that they are theoretically more promising than agglomerative methods. However, most methods are monothetic (i.e. split groups based on only 1 of the many attributes), which may be effective for binary data only (Gordon 1987). Polythetic methods (which base similarities on all attributes) are theoretically ideal, but are computationally expensive for large databases because the optimal division has to be found by iteration at each step. Methods have not been adequately developed for use in quantitative (non-binary) ecological studies (Boesch 1977, Gordon 1987). Short-cuts are being developed for polythetic divisive linkages which will eventually be tested in ecology.

Constructive methods are specifically designed for the addition of new objects to an existing hierarchy of groups. They have been used with single and complete linkage dendrograms (see below), but there is rarely any requirement for placement of new objects into an existing analysis in ecological study designs.

Direct optimization methods are similar to divisive ones in that they attempt to transform a matrix of pairwise dissimilarities (or distances) into optimally separated groups by iteration. However, the clustering strategies contain assumptions about the underlying distribution of the data, which probably do not apply to complex, multispecies datasets.

Agglomerative linkage methods are therefore used almost exclusively in ecological study (see Gordon 1987, Sneath 1966 and Cormack 1971). These are all based on the generalized equation of Lance and Williams (1966, 1967), who also introduced the concept of space distortion in linkage methods. Some selected agglomerative linkage rules include:

1) Single linkage (or nearest-neighbor) is a space contracting method in that the distance between groups is based on the resemblance of the most similar entities from the two groups. This tends to "reduce" the distance between clusters following amalgamation, and produces chaining, which is undesirable because no coherent groups can be identified. As well, distortion results from

the fact that much of the dissimilarity information is lost in the clustering process.

2) Complete linkage produces the opposite effect of single linkage in that distances are calculated based on the resemblances of the least similar members of the two groups. Therefore the method is strongly space-dilating, producing intense but often artificial or misclassified clusters. As in single linkage, much information is lost during clustering.

3) Unweighted or weighted pair group mean average (GMA Sneath and Sokal 1973) join two groups at the collective average similarity level for each group, thereby using all the information in the procedure and producing little distortion of the actual resemblance relationships. GMA is therefore considered space conserving, monotonic and not prone to misclassification (Clifford and Stephenson 1975). In fact, it may be considered useful as a means to check for misclassification by more intensely clustering methods. The skewed nature of the extreme values in some similarity matrices (discussed by Smith *et al.* 1988) can be lessened using GMA cluster analysis, since it tends to average the similarity between stations.

4) In Centroid clustering, resemblance is defined as geometric points in Euclidean space (see Boesch 1977). This is only suitable for euclidean or variance/covariance distance measures, which Gordon (1987) points out are extremely space contracting, although Lance and Williams (1967) suggest that it is space conserving. Sneath and Sokal (1973) and Clifford and Stephenson (1975) point out that centroid clustering can produce ambiguities or "reversals", so the method has been disfavoured in ecological study. A modified version, known as Median linkage, is a weighted centroid method with all the same problems.

5) Flexible sorting (Boesch 1977, Lance and Williams 1967, Clifford and Stephenson 1975) is a method commonly used in ecology. The clustering intensity (space distortion) can be varied to produce results similar to single linkage, complete linkage or any level between. However, the decision regarding the intensity coefficient (beta) is arbitrary. In practice, a value of -.25 has become

standard. This is moderately space-dilating and intensly clustering, so that misclassifications or overclassification can occur. The method is best used for R-mode analyses when there are a large number of species of varying abundance.

Interpretation of a cluster analysis is usually done by optimally rotating the results of the hierarchical linkage and plotting a dendrogram. In the plotting of the linkages from a hierarchical classification, optimal rotation simply refers to the rearrangement of stations about the linkage nodes to avoid crossing branches in the resulting dendrogram (this is a geometric rotation which results in no mathematical transformation of data). There is some loss of information using dendrograms derived from a cluster analysis since the multivariate similarity between sites has been reduced to a single number by the linkage method (i.e. the similarity between any pair of sites cannot be determined from the dendrogram and similarity scale alone). Measures are available for assessing the loss of information in a cluster diagram, though this is rarely done in benthic application studies (e.g. "cophenetic correlation coefficient" used in numerical taxonomy - see Sneath and Sokal 1973 and Gordon 1987). The skewed nature of the extreme values in some similarity matrices (discussed by Smith et al. 1988) can be lessened using cluster analysis, since it tends to average the similarity between stations for hierarchical clustering, and because the intermediate levels of comparison are usually of more interest in the interpretation of cluster analyses than the extremes of 0 and 100%. A map in which successive similarity levels are shown as concentric rings is often useful for depicting stations groupings (see Chapter 3) and can be a valuable management tool.

Given the limited availability of polythetic divisive methods, agglomerative hierarchical linkage rules have gained predominance in ecology. One limitation of all space-dilating linkage methods (complete linkage, flexible sort) is that they are prone to misclassifications. The development of objective reallocation strategies may alleviate this complaint. Space contracting methods (centroid clustering) can cause reversals. Of the available methods, space conserving are therefore considered the most conservative, although they may not produce distinct

enough groups for some applications. Agreement of results analysed by several different methods can add confidence to the interpretation of results.

Since the purpose of this thesis is the description and classification of benthic assemblages, the methods to be used include a combination of a conservative dissimilarity measure (Bray-Curtis) and a linkage rule which utilizes the information available to the best advantage given the available methodology (agglomerative, hierarchical - unweighted pair group mean average sort). The intent is to obtain results which are readily interpretable and reasonably non-distorting, without data transformations.

One of the main disadvantages of classification methods has been the lack of objective criteria for determining the number of legitimate clusters. Until recently, most authors have arbitrarily selected a preferred optimum similarity level to determine the number of groups. The number of clusters must be sufficiently large so that the important differences in community structure are captured by the groupings, but not so large that the differences between clusters are comparable to those seen among the replicates drawn from each site. The availability of replicates is therefore an important factor in making subjective judgements about cluster groups.

Nemec and Brinkhurst (1988a) point out that parametric inferential methods often produce intractable results with classification analyses, so that a linear model is usually unsuitable. A relatively new nonparametric method known as the "bootstrap" (Efron 1982, Diaconis and Efron 1983, Efron and Gong 1983, Felsenstein 1985) has recently been applied to the problem of significance testing in cluster analyses. Nemec and Brinkhurst (1988a,b) describe a bootstrap method that can be used to assess the "statistical significance" of clusters, provided that replicate samples are available. The method tests the hypothesis that the two station groups that are joined at a particular linkage level are the same. A similar method has been used to compare two different dendrograms by testing the hypothesis that the two dendrograms are the same (i.e., the sample units from both clusters can collectively be considered replicates from a single community) at any given linkage

level (for applications of this method see Burd and Brinkhurst 1987, Brinkhurst 1987 and Brinkhurst *et al.* 1987). Strauss (1982) used a non-parametric approach based on a randomization method, which is suitable for the analysis of presence/absence data and compares the observed linkage levels with the linkage levels for the randomized data matrices to test for significant clusters. Raup and Crick (1979) have also defined a similarity measure for inferential testing of presence/absence data which is applicable in paleontology studies. They outline a probabilistic (counting) method for comparing two communities and placing a probability on their different structures. Smith *et al.* (1986) describe a bootstrap method for producing confidence intervals for the similarity between two algal communities. Clarke and Green (1988) discussed a randomization method for testing the significant differences between sites or sets of sit s in multispecies data. Unfortunately, these latter two methods are only valid for pairwise comparisons and may therefore suffer from multiple comparison problems.

Once the set of representative clusters has been decided upon, it is often desirable to determine which species, or groups of species a e useful for characterizing the clusters. Indicator species are often selected subjectively. An apparently objective method of identifying indicator species is to compare the mean (relative) abundance of each speci·s across the clusters, using a series of 1-way ANOVA F-tests (one for each species) or a set of "pseudo F-tests" (Mirza and Gray 1981). Those species that exhibit "significant" differences across the clusters are considered useful for discriminating between clusters (c.f. Shin 1982, Shin and Thompson 1982, Field *et al.* 1982). Some studies mention the potential pitfalls of such an approach (e.g., violation of the underlying normal assumptions, multiple comparisons problem using univariate tests). Field et. al. (op.cit.) also mention the use of an information statistic and Chi-square analysis for distinguishing important species.

R-mode (inverse) cluster analyses are sometimes used in concert with a Q-mode (station) cluster analysis. The species matrix is then physically rearranged so that the sites are aligned according to the results of the Q-mode analysis, and the species according to the R-mode

analysis. This is commonly referred to as a "Two-way coincidence table" or "Nodal analysis" (Boesch 1977), and can be useful for spotting misclassifications, which can occur during cluster analysis. An example of this is given in Smith *et al.* (1988). The rearranged data are visually examined for trends (c.f. Flint and Holland 1980, Smith and Greene 1976, Hughes and Thomas 1971a,b), but clear results are rare.

Ordination:

Each column (sample unit or station) of the data matrix corresponds to a point in a space with dimensions equal to the number of rows (species). If the columns can be represented as points in a space with considerably fewer dimensions, the representation is loosely referred to as an ordination. Each dimension in the reduced space then represents an "ordination coordinate". An ordination coordinate for a given sample unit may or may not be a simple (linear) transformation of the species abundances, depending on the method of ordination used. Like cluster analysis, ordination results in some information loss which is directly related to the extent to which the original number of dimensions is reduced. Hence the community structure of the sites will be described to a greater or lesser degree by the ordination coordinates. If the number of ordination coordinates is two or three, the relationship among the sites can be seen by plotting the sites in a plane or in 3-D space. If the community structure of the sites can be classified into discrete classes, the plot is expected to show a clustering of the sites. If the data form a continuum, the sites will be spread out over some region defined by the ordination.

Ordination can be used to examine data which are clustered into discrete communities, though the results are often more difficult to interpret than classification methods. However, if species data do not form discrete clusters but conform more to a continuous distribution, the data should be examined using ordination rather than classification methods. This occurs most commonly in nearshore and estuarine areas and some polluted areas with dominant physical factors.

Ordination methods include a variety of different types of analysis, some of which have been in common use in terrestrial ecological studies

for many years (see Whittaker 1967). There are two broad classes of ordination: metric multidimentional scaling and non-metric multidimentional (or ordinal) scaling. Metric dimensional scaling refers to any method in which the distance between data points can be approximated by Euclidean coordinates, i.e., it is assumed that the dissimilarities between any pair of objects can be approximated by a metric distance (in a lower dimensional space). It does not necessarily require that the distance or dissimilarity index itself be a metric (for assumptions see Chatfield and Collins 1980). Nonmetric methods do not attempt to approximate the actual dissimilarities between pairs of objects, but rather preserve only the agreement between the rank order of the pairwise dissimilarities.

Many of the common ordination methods utilize one of the standard dissimilarity measures described in the previous section. Shin (1982) points out that a "continuum" method such as ordination should only be applied to data sets that are relatively homogeneous (i.e. few zero records). Many authors use data reductions or primary transformations to satisfy this requirement (see section 2a), but in doing so may introduce problems of interpretation. Mills (1969) indicated that more effort in sampling and analysis is required to perform properly gradient or ordination than is required for classification analyses. As well, some ordination methods assume monotonicity of the response curve of the species with respect to environmental factors, or may even assume linearity.

Multidimensional scaling methods include: Principle Components Analysis (PcpA); Principle Coordinates Analysis (PcdA) or Gower's method of principal coordinates (Gower 1966) which was originally formulated by Torgerson (1952, 1958); non-metric multidimensional scaling; and Correspondence Analysis. Legendre and Legendre (1983) describe all of the above ordination methods, and provide examples. As well, a little-used somewhat subjective ordination method was described by Bray and Curtis (1957) and has been discussed further by Shepard (1980) and Beals (1984). Factor Analysis refers to a specific but different technique which is arguably a form of ordination. Unfortunately, "factor analysis" is often used in the benthic literature as a catch-all term for

ordination.

Principle components analysis is a specific application of "metric" multidimensional scaling (for assumptions of metric distance measures see Legendre and Legendre 1983). PcpA preserves the multivariate (Mahalanobis) Euclidean distances between the sites (Q-mode analysis) with the restriction that because this transformation is linear, the distances between sites may be distorted if the faunal data are not linear. In principle components analysis the ordination coordinates are linear combinations of individual species abundances. In q-mode analysis, each set of coordinates represents a sample unit. The percent of the variance that is explained by the first few principal components (or dimensions) is often used to assess the quality of the representation. If two or three components are sufficient to account for 50-90% of the variance, the representation may be acceptable. Legendre and Legendre (1983) discuss a number of misuses of principle components analysis, including the need to reduce or roll-up data (see section 2a) to avoid distortions of Euclidean distances that may result when there is a large number of "double-zero" pairs.

Some decisions made during PcpA are subjective, such as selection of a data transformation (see section 2a) or factor rotation. There are an infinite number of orthogonal and oblique factor rotations. There are various arguments for and against the use of different types of rotations, which are described by most multivariate statistical textbooks.

A good example of the application of principle components analysis is given in Lie (1974), who used both normal and inverse analyses. Some unusual but questionable applications have been evident in the literature. For example, Chester *et al.* (1983) applied a PcpA analysis to a data set combining assemblage data as well as environmental variables. Long and Lewis (1987) used a step-wise combined classification and ordination method which involved removing stable station groups at each step. The approach is not easy to follow, partly due to lack of clarity about the identification of the "stable groups" removed and confusion about how replicates were handled. The analytical method is also difficult to follow in the case of Stephensen *et al.*'s

(1972) reanalysis of Petersen's original community data, partly because of problems with the original data set.

Whereas principle components analysis attempts to explain the variances in the species abundances by producing weighted linear composites of observed variables, common factor analysis attempts to explain the covariances among the species abundances in terms of a small number of unobserved factors (which are often given some physical interpretation). The main problem with factor analysis is that it is indeterminate, i.e. there is not a unique solution for a particular model. For a short but enlightening discussion of the differences between principle components and factor analysis (as well as useful critique) refer to Wilkinson (1988 - SYSTAT software manual - pg. 408). For a more mathematical and in depth discussion of these differences refer to Reyment (1963). Gower's (1966) discussion of the relationship between PcpA, PcdA and factor analysis is particularly clear.

A more general form of Metric Multidimensional scaling (MDS) is Principle Coordinates Analysis (PcdA), introduced by Torgerson (1952, 1958) and described in a more generalized form by Gower (1966). PcdA differs from principle components and factor analysis in that it does not necessarily use a Euclidean distance measure. Principle coordinates analysis can use distances given by dimensionless similarity indices (such as Bray-Curtis, Canberra-Metric, etc.). The ordination coordinates are therefore dimensionless. Note that the use of a metric distance measure is sufficient to produce a solution, but not necessary (e.g. Bray-Curtis is non-metric). An equivalent solution to PcpA is found if the distance measure in Gower's method is Euclidean. Otherwise, PcdA suffers from the same interpretation problems as PcpA.

The aforementioned methods are all linear ordinations, which assume that the faunal data are linear with respect to the ordination dimensions imposed. Unfortunately, most species abundance and biomass data show a decline to 0 for both low and high values along any environmental or biological gradient. This non-monotonicity in assemblage data produces a "horsheshoe" shaped distribution of stations when plotted using linear ordination axes (see Pielou 1977).

Problems of non-linearity in ordinations applied to species

assemblage data are discussed by Austin and Noy-Meir (1971). Williamson (1978) and Smith *et al.* (1988) approach the problem from the perspective of the dissimilarity matrices used in ordination. In cases where the data set is diverse (i.e. dissimilarities approach 0 and 100%), the skewness in the dissimilarity distribution at these extremes produces the "horseshoe effect" on the ordination axes. The recommended "step-across" procedure (see section 2e) addresses this problem but can produce dissimilarities ¢100%. Therefore Smith *et al.* (op. cit.) recommend the use of the rank of the samples for the step-across dissimilarity matrix, rather than actual values. This produces the equivalent of a non-metric multidimentional scaling ordination, which may have the effect of eliminating the "horseshoe effect".

Non-linearity in the data can also be dealt with by the application of non-linear ordination methods. Non-linear ordinations such as non-metric Multi-Dimensional Scaling (for review see Kruskal and Wish 1978, or see Shepard 1980, Field *et al.* 1982, Ramsay 1982 and Kirkwood and Burton 1988) and Gaussian ordination may be useful for situations when continuous species data are being compared with environmental gradient data and it is not realistic to assume that the relationship is linear (for discussion see Green and Vascotto 1978). Non-metric MDS (proximity analysis) is a generalization of metric MDS. This has been used in benthic applications recently (see Clarke and Green 1988, Smith *et al.* 1988 and Field *et al.* 1982), but in practice there is no a priori reason to select a particular non-linear transformation, so the linear approach may be as reasonable as anything else. Gauch *et al.* (1974) discuss the use of Gaussian ordination as an alternative to linear and ranking forms. It assumes that species are distributed in bell-shaped patterns along environmental gradients, a pattern which is often obvious in direct gradient analysis.

Ordination is sometimes carried out in an R-mode fashion so that species are plotted as points in the ordination space. This causes problems of interpretation (especially with 200-300 species), as well as computational problems and is not commonly used. Smith *et al.* (1988) provide examples of such an analysis using data standardizations and tranformations.

Hill and Gauch (1980) pointed out problems with many commonly used ordination methods. They introduced Detrended Correspondence Analysis (DCA), which uses standard deviations of species abundances across ordination distances, instead of abundances. This method has not often been used, so that objective discussion is unavailable. The method may reduce the problem of disparity in abundances between rare and common species. Alongi (1986) used DCA in Q and R mode analyses sorted and analysed simultaneously, producing some interpretative challenges.

Multivariate comparisons with habitat factors:

Benthic community survey studies usually examine the effects of environmental factors on community structure. The effects of biotic factors on community structure are usually examined experimentally (exclusion and recolonization experiments) and are therefore outside the scope of this paper. There are a few examples of survey studies of biotic factors which utilize multivariate analyses. A good example is given by Smith (1981) who examined the influence of sand dollars on community structure in 10 beach areas. Smith's study is appealing because of the well-defined objective, which allowed an effective delineation of sample sites.

Unfortunately, studies of the effects of abiotic factors on community structure are rarely so well-defined. Commonly, the stated study objective is "to describe the effect of environmental factors on invertebrate infaunal community structure".

Because of the myriad of environmental factors potentially influencing an assemblage, and their interdependence (e.g., depth and sediment type), causal conclusions are difficult to make except where the effects are so profound and consistent that the resultant faunal patterns can be attributed to a single factor.

One approach to the problem is to select an assemblage in which the environmental factors can be reduced with reasonable confidence to one or two. An example of this is a rocky intertidal study in South Africa by Field and McFarlane (1968), in which wave exposure was the overwhelmingly dominant environmental factor, with all sample sites otherwise fairly uniform. The results were not statistically tested, but were so obvious as to require no further testing. Similar examples include hypoxic marine

habitats, where the overwhelming dominance of oxygen makes all other factors irrelevent (see Burd and Brinkhurst 1984), or in estuaries, where salinity overrides all other factors (see Chapman and Brinkhurst 1981). Such situations are not common, particularly in soft-bottom areas (see also Rosenberg 1980).

Factors which affect the distribution of undisturbed benthic communities include a range of sediment characteristics (for review see Gray 1974) such as particle size, structural complexity, organic content, ATP or chlorophylls content, clay size fractions, sulphide content, macrofloral (e.g. eelgrass) or microfloral composition. Other important factors include depth, or depth associated variables, which often cannot be considered independent of sediment characteristics. Water characteristics such as natural or stagnation-induced hypoxia are often related to depth (Burd and Brinkhurst 1984). Rosenberg (1980) suggested that natural stagnation causes more widespread defaunation than pollution-induced stagnation in the Baltic Sea. Salinity is depth-related, but is extreme only in nearshore or estuarine situations, or brackish seas such as the Baltic (for review of brackish water studies see Hedgpeth 1983). Sediment chemistry is often ignored in soft-bottom studies, because of the difficulties involved in sampling and analysis of interstitial waters. Interstitial salinity (Chapman and Brinkhurst 1981) and sediment oxygen/sulphide balance are more important that the water column chemistry, since the latter may not fluctuate to the same degree or in synchrony with interstitial water.

Pollution factors include a wide variety of organic and inorganic contaminants from sewage and pulp waste, as well as chemical toxins and heavy metals. Other forms of pollution are mainly related to disturbance, such as dredging. Gray *et al.* (1988) emphasize that the most common problem in benthic ecological surveys is that of separating natural and unnatural (pollution) environmental effects.

The analytical approach for comparing environmental factors with assemblage structure depends on the discreteness of the assemblage groups. If the data form discrete clusters, there are several effective statistical approaches for examining environmental effect. Analysis of variance (ANOVA) and multiple discriminant analysis are the two most commonly used methods.

ANOVA is used to determine whether or not the mean value of an environmental variable varies significantly across the clusters (c.f. Jones 1986). Many studies seem to test several environmental variables using a series of single factor ANOVA tests. If the number of tests is large, it is advisable to use a multivariate ANOVA or adjust for the multiple comparisons by using a studentized Newman Keuls test. If a large number of independent tests is performed at the 0.05 (p) level of significance, approximately 5% will reject the null hypothesis even when it is true.

ANOVA is a parametric test which assumes normality and independence of the sample units, and homogeneous variance for all variables, although the test is fairly robust with moderate departures from these assumptions. The Kruskal-Wallis test is a nonparametric version of the univariate 1-way ANOVA F-test, which can be used if the environmental variable does not have a normal distribution (it does not help if the independence or homogeneous variance assumptions fail, but will help if the distribution is skewed or otherwise non-normal). Another non-parametric test for comparing a cluster analysis with an independently determined "covariate" dendrogram (based on one or more environmental factors) is described by Nemec and Brinkhurst (1988b). It uses a Fowlkes-Mallows (Fowlkes and Mallows 1983) statistic, which is a measure of the degree of similarity between two dendrograms, to test the null hypothesis that the two dendrograms are unrelated. Examples of this method are in Burd and Brinkhurst (1987), Brinkhurst (1987) or Brinkhurst *et al.* (1987).

Green and Vascotto (1978) describe the use of multiple discriminant analysis (MDA) for examining multifactor effects on assemblages. Discriminant analysis can be thought of as a procedure for reducing the dimensionality of the environmental space rather than of the species data matrix. Multiple (clusters, not variables) discriminant analysis is used to construct a set of orthogonal "environmental axes" which correspond to linear combinations of environmental variables (discriminant functions) such that when the sites are plotted using these axes (using the values of the environmental variables at each site) there is a maximum separation of the clusters along each axis (see Green and Vascotto 1978). The first axis accounts for the greatest separation of axes, and therefore represents the environmental space which accounts for that maximal separation. Each

subsequent axis represents increasingly minor separations of the clusters. Since each axis, or discriminant function, is a combination of the environmental variables, it is often possible to determine which variables contribute the most to the cluster pattern. Green and Vascotto (op. cit.) point out that the advantage of this method is that it does not assume a linear relationship between the biotic variables (assemblage structure) and the environmental variables, but rather a linear relationship amongst the environmental variables (e.g. salinity vs temperature). In practice, certain environmental variables may require transformations (such as particle size percentages and pH) to produce linearity. If there are lots of environmental factors to consider simultaneously, a discriminant analysis might be easier to interpret than a multivariate ANOVA, provided that a small number of discriminant functions result in good separation of the groups. The drawback of MDA is that it is useful only when there are distinct clusters of samples.

Several examples of MDA are given by Smith *et al.* (1988). Shin (1982) also described an application of the MDA approach. His example is not ideal, however, because the clusters do not appear to be well-defined. The examples in Shin and Thompson (1982) and Green and Vascotto (1978) are more convincing. This type of analysis may be inferentially tested by a method such as Chi-square analysis (Shin 1982), although Green and Vascotto (op. cit.) suggest that the simple descriptive approach is more conservative.

If the data do not cluster into distinct groups or communities, a continuum method is appropriate. A standard approach for examining the role of environmental variables is to use multiple regression or correlation analysis to relate ordination coordinates derived from the species data to the environmental variables. The linearity assumption should always be assessed using regression diagnostics, such as scatterplots and residual plots. Simple linear regression is often used to investigate each environmental variable separately. The multiple comparisons problem arises here as well as with univariate ANOVA. A multiple regression approach is helpful for looking at the variables simultaneously. Smith and Greene (1976) use ridge regression to overcome the problem of the distortions that can arise when there are intercorrelations between the explanatory variables. An explanation of ridge regression is given by Marquadt and Snee

(1975), although this method has not been widely used in benthic ecological research. Smith *et al.* (1988) discuss several examples using multiple regression analysis to examine the relationship between combinations of environmental factors and assemblage factors.

Canonical correlation is sometimes used to examine the relationship between the biotic and environmental variables. Canonical correlation has been described by Legendre and Legendre (1983) as a generalization of multiple (linear) regression, which can be thought of as "a double principal components analysis followed by a rotation of the canonical axes in order to make them superimpose". Canonical correlation examines the (linear) relationship between two sets of variables. In the typical benthic application, the two sets of variables are the species data set and the environmental data set (see Chester *et al.* 1985, Penas and Gonzales 1983, Smith *et al.* 1988). A test of significance of the canonical variates is Bartlett's test (Penas and Gonzales 1983) which is a non-parametric method using contingency tables. Smith *et al.* (1988) suggest that canonical correlation provides no more useful data than such analyses as multiple regression analyses and can be more complex and difficult to interpret. Both assume linearity between community structure and environmental variables.

A univariate non-parametric method for examining the effects of environmental factors on assemblage structure has been proposed and involves comparison of ordination station loadings on a given axis and a chosen environmental factor using Spearman's rank correlation (described by Legendre and Legendre 1983). This ranking measure is similar in interpretation to a simple Pearson's r but is useful for examining the degree of monotonic relationship between two variables when the data are nonnormal, or the relationship is non-linear. Still, it must be accepted that a rank order transformation involves some loss of information. Such a method may be suitable when the ordination coordinates are suspected of being non-linearly related to the environmental variables (see Hughes and Thomas 1971a).

f. Time Series Analysis

Specific analytical methods have been used to compare large sets of temporal data. These methods are based on the same basic theory as the spatial surveys discussed in this review. Many benthic studies cover a long time period, but are not planned as detailed time-series analyses per se (see Chester *et al.* 1983, Govaere *et al.* 1980). An example of a relatively long-term benthic study is given by Beukema and Essink (1986), who correlated the abundance fluctuations of a series of tidal flat species over a 17 year period in order to separate global patterns of natural fluctuation from localized disturbances such as pollution. They found that 50% of the fluctuations were synchronized and correlated over wide areas. Williams and Stephensen (1973) discuss the three basic methods used for analysing time-series benthic data, the oldest and most common being to obtain a series of data matrices over time and compare them subjectively or in some inferential manner. They also suggest certain methods of combining species abundance, station and time data in two-dimensional or three-dimensional comparisons, the latter of which is problematical but may command more attention as consistent, long-term studies become more common.

Legendre *et al.* (1985) discuss the problem of mapping successional events in ecological communities. They propose a method that uses a "chronological clustering" of samples from a single station, where samples are replicated over time to identify discrete successional steps in the species composition. A non-parametric (randomization) procedure is used as a fusion criterion for the groups. An important component of the method is the exclusion of erratic or random singleton measurements which do not fit into the successional pattern. Unfortunately the method requires some subjective decisions which affect the power of the test, and it is not particularly effective for datasets in which a large number of the pairwise linkages join highly dissimilar groups. In their examples, Legendre *et al.* (1985) use relatively large significance levels (about 20%) to get viable results. This seems unacceptably high. The method of Nemec and Brinkhurst (1988a) would provide a similar type of test, without the problems mentioned above.

Other examples of time series analyses include spatial autocorrelation (Pielou 1977) and methods described by Barnard *et al.* (1986) which have potentially important applications in long-term environmental impact studies. However, the effective use of such methods usually requires a large number of identically treated temporal replicates (25 or more depending on sample design), which is rare in benthic studies. There will undoubtedly be greater emphasis on long-term analyses of assemblage structure in the future. As such surveys become more data intensive, with increased number of variables to consider, new graphical methods will be required to present and interpret this information. The recent development of GIS (Geographic Information Systems, Mounsley and Tomlinson 1988) in many disciplines offers a datamanagement and mapping tool which will be invaluable in large-scale ecological surveys.

4. Summary

Analytical and sampling methods in benthic survey studies have evolved from the original intuitive approach based on the indicator species (or group) concept, to objective univariate indices which provide a useful initial characterization of a community or spatial pattern. These univariate methods are being progressively replaced or enhanced by more rigorous descriptive and inferential multivariate methods. If anything can be concluded from the often contradictory opinions of different ecological authorities, it is that the analytical approach for handling multispecies data should be straightforward, avoiding the common trap of using a whole suite of complex (often uninterpretable) methods when one or two would be sufficient. If the dataset is "robust", the results will probably not be seriously affected by the use of questionable statistical methods. Much more attention should be paid to the biases and consistency of sampling methods and how they relate to assumptions inherent in statistical tests, to the validity of data transformations or reductions, and to the consistency and accuracy of taxonomic identifications.

A researcher may have reasonable confidence in the power of statistical inferential tests, due to the large sample sizes characteristic of most benthic studies. However, large sample sizes can lead to "trivial" but

statistically significant results, particularly if the sample area is insufficient. Therefore the effect size of interest should be carefully considered.

The use of biomass/size spectra to analyse trophic relationships and assemblage structure in benthos is an alternative approach which seems to be receiving some attention. The potential usefulness of combining taxonomic and biomass based studies has not been fully explored.

The appeal of non-parametric simulation or randomization methods for hypothesis testing is expected to increase, since these methods eliminate many of the problems encountered when attempting to fit aggregated, multi-species data to parametric models. Most researchers would agree that the introduction of reliable and flexible methods to simplify the often sing and frustrating process of data analysis would be welcome. To nd, more effort should be made to invent clear graphical methods for g complex statistical results, for the benefit of managers, public d political agencies with policy decisions to make.

ds and understanding of basic mechanisms affecting benthic improve, researchers seem to be attempting more ambitious ng-term data are now available in many areas, as well as the idespread sampling coverage and data-handling methods which may eventually encourage researchers to readdress broad community issues of the type raised originally by Petersen (1911-1915) and later by Thorson (1957,1966).

The methods selected for use in this thesis reflect the conclusions from the literature review. The data management approach incorporated both abundance and biomass faunal data, in an attempt to provide a detailed analysis of faunal patterns. The analytical classification approach used was simple to comprehend and familiar to all benthic ecologists, but has been enhanced by the use of non-parametric inferential methods to provide an objective means of identifying meaningful station groups, and comparing the results of two independently derived cluster dendrograms. Although the data were not originally collected with these methods in mind, the methods were selected because they seem to be the most flexible and sensible ones for the analysis of faunal distributions from a iety of habitats.

CHAPTER 2. METHODS

A. STUDY AREAS

The general survey areas are shown in Figs. 1 and 2. Site specific station maps were included in the separate chapters (3-8) detailing the results from these areas. Station names given at the times of surveys have been retained with slight modifications in this thesis, for consistency with the original technical reports. The naming protocol for stations is given in Appendix 1 and the introduction of each chapter. The survey areas in order of presentation included; four surveys taken over an eight year period in two northern mainland B.C. fjords, Alice Arm and Hastings Arm (chapter 3), one of which was affected by mine tailings; three seasonal surveys taken over one year in four disinct groundfish habitats of Hecate Strait, between the Queen Charlotte Islands and the B.C. mainland coast (chapter 4); two surveys taken on the mid-shelf region of the continental shelf off Barkley Sound on the west coast of Vancouver Island ("Shelf" -chapter 5); two surveys taken in Vancouver Harbour and Port Moody Arm on the southern mainland coast of B.C., in a heavily industrialized and populated inlet (chapter 6); one survey of Boundary Bay, a shallow, sandy beach area facing the open waters of Juan de Fuca Strait on the border between Canada and the U.S. (chapter 7); and a survey of a collection of stations from three fjords spanning the B.C. coast (chapter 8). Appendix 1 includes latitudes, longitudes, depths, sediment particle sizes, and replicates for all stations surveyed.

B. DATA SAMPLING AND PROCESSING

Since the data used herein were collected over a ten-year period, some variations in sampling procedure occurred (Table 1). However, identifications and sample processing was uniform for all surveys. The shallow sites (Boundary Bay, Vancouver Harbour) had to be sampled using a small Po· ($0.05m^2$) grab, whereas the other samples were all collected with a $0.25m^2$ Smith-McIntyre grab (shelf surveys) or a $0.1m^2$

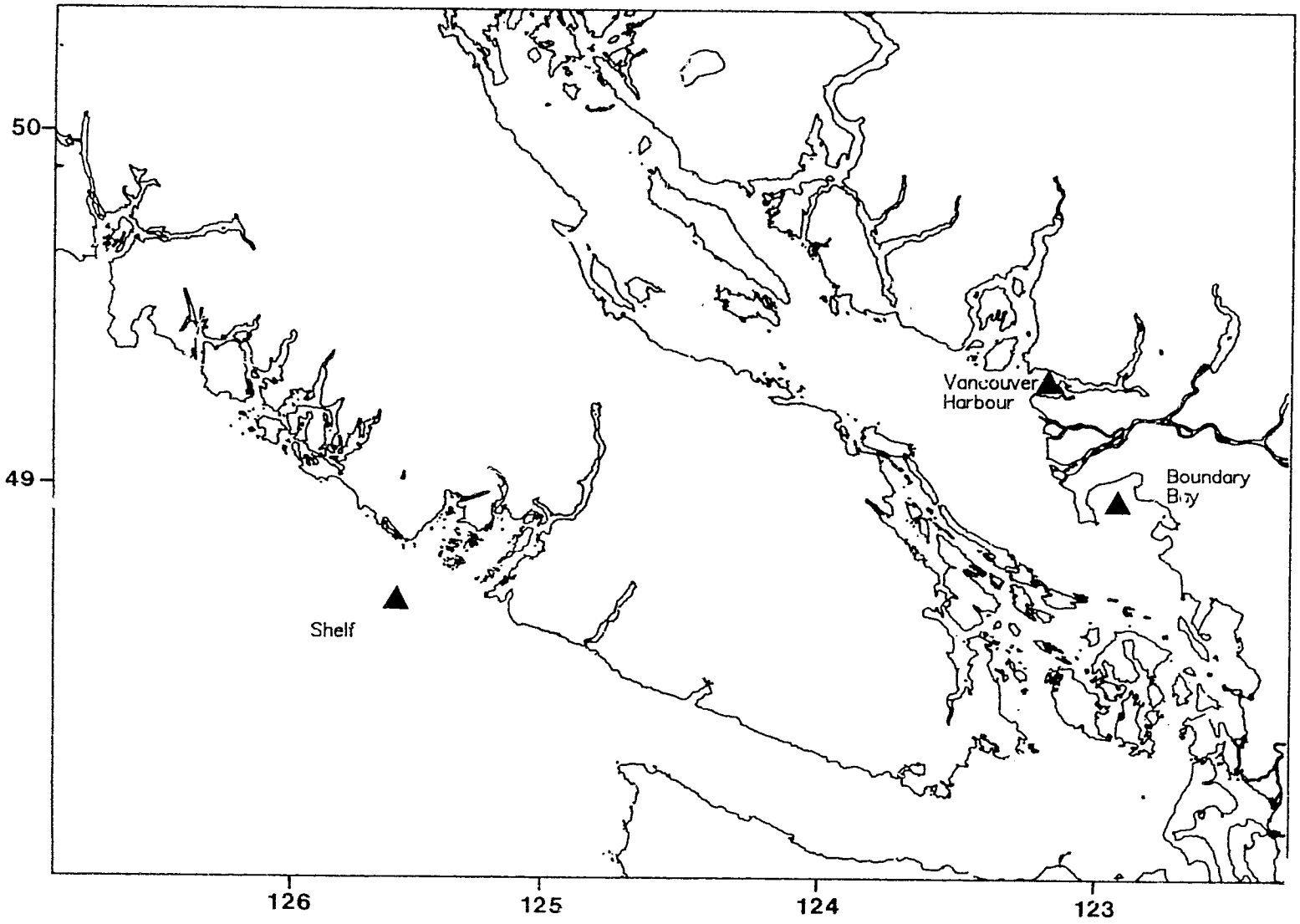

Figure 1. Map of British Columbia coastline showing general locations of the southern sampling areas.

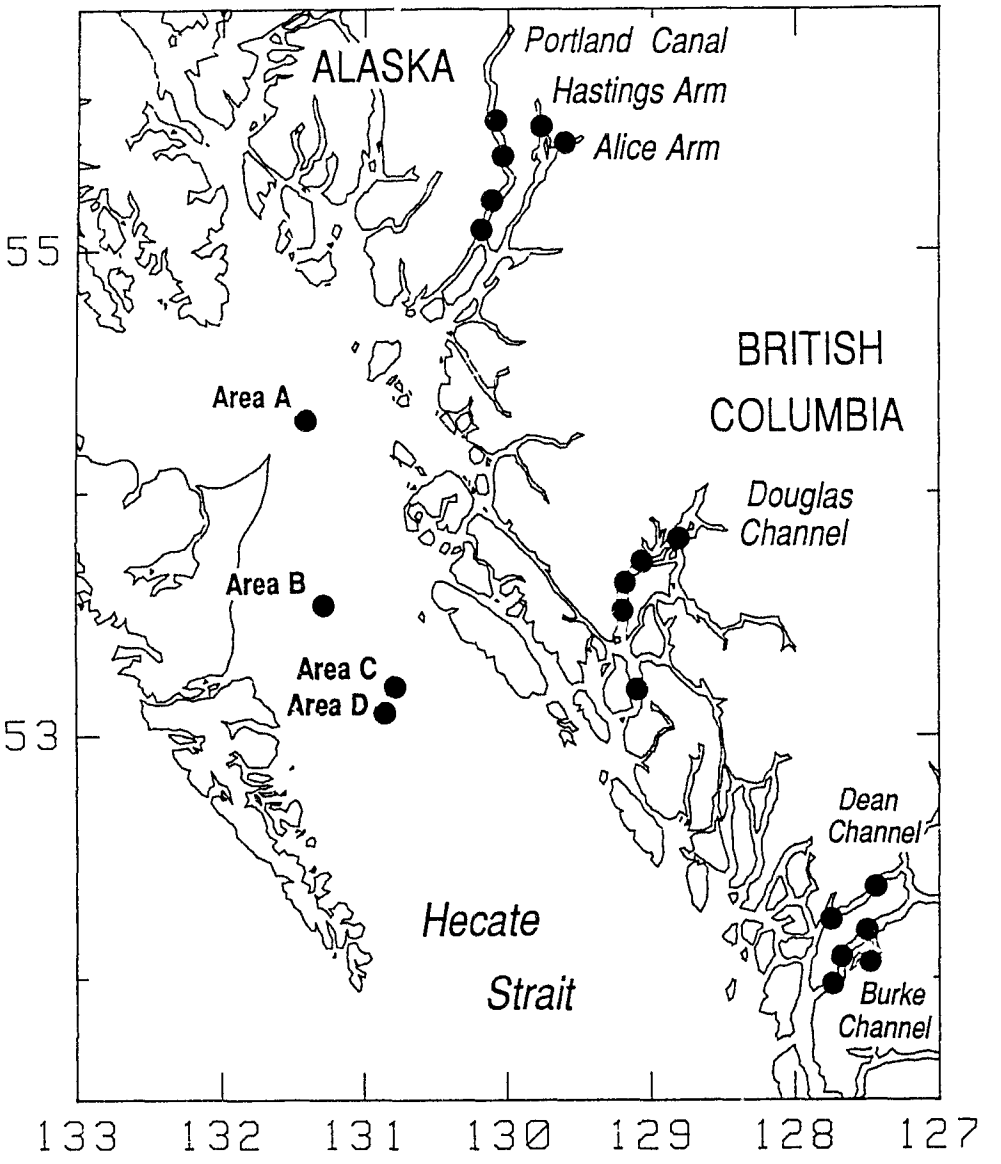

Figure 2. Map of British Columbia coastline showing general locations of sampling areas in the middle and northern coast. All sample stations for the fjords are shown, as well as the general sampling areas of Alice Arm and Hastings Arm (second northernmost fjord marked on the map). Sample areas for Hecate Strait are also included.

Smith-McIntyre grab (Hecate Strait, Alice Arm/Hastings Arm, fjords). Grab samples which were not at least half full were discarded and the cast repeated.

The organization of the Hecate Strait samples resulted in a total of 5 grab replicates per station (see Burd and Brinkhurst 1987), and three replicates per station were collected during the second Vancouver Harbour survey. The remaining stations from all surveys had two replicates each, except for station EM in Alice Arm in 1982, which was sampled only once.

Samples were processed aboard ship by carefully washing the grab material through a small diameter mesh screen, then preserving the retained material in 10% buffered, 10% rose bengal stained formalin. A small screen size was used in Boundary Bay (0.5mm) and Vancouver Harbour (0.3mm) surveys, whereas a large (1mm mesh) screen was used in the remaining surveys. The Shelf survey samples included a mixture of subsamples sieved with a screen as small as 0.25mm, as well as material processed with a 1mm screen. This occurred because one of the original purposes of the study was to examine size-related spatial distribution patterns within each sample replicate.

Fauna were sorted into their major taxonomic groups in the laboratory after washing through a 1mm screen, then preserved in 70% ethanol. Ten percent of the sorted residues were reexamined by an independent person to provide quality control. A five-percent error in total abundance was the maximum permitted. Taxonomic identifications were carried out a set of specialists for each taxonomic group (see acknowledgements). The shelf study, which was the first of the surveys, had different experts for identification of fauna at different stages of the project (Brinkhurst 1987). Counts of individuals for each species and each replicate were tabulated in a species by replicate table with each count standardized to $0.1m^2$ grab surface area (original technical reports are in the back pocket of the thesis). Taxonomic authorities were asked to produce a comprehensive reference collection of identified species. During the last four surveys in 1989, animals were sorted by species for mean biomass measurements. The collected specimens were

Table 1. Sampling parameters for the six survey areas. Sampling locations, depths and substrate types are detailed in Appendix 1.

Survey Area	Thesis Chapter	Grab size (m2)	Replicates per station	sieve size (mm)
Alice Arm/ Hastings Arm	3	0.1	2	1
Hecate Strait	4	0.1	5	1
Shelf	5	0.25	2	**0.25,1
Vancouver Harbour/ Burrard Inlet	6	0.05	*2,3	0.3
Boundary Bay	7	0.05	2	0.5
Other fjords	8	0.1	2	1

* Cruise 1 had 2 replicates, cruise 2 had three replicates
** half of each grab sample was processed with a 0.25mm sieve and the other half was processed with a 1mm sieve

archived at the Royal British Columbia Museum, the Royal Ontario Museum and the National Museum in Ottawa.

Dr. William Austin was contracted by the Ocean Ecology Department of IOS to produce a taxonomic checklist of the benthic fauna of B.C. with cross-references to pertinent synonymies and changes. This document (Austin 1985) became the cornerstone of the taxonomic structure of the databases developed during this study.

Obtaining mean biomass values for each species after identification and archiving of specimens was the most problematical part of the project. Since the specimens for all the surveys were archived in various museums, the first task was to recover these in order to weigh individual specimens. It soon became obvious that it would not be possible to retrieve all specimens, but all identified material that was available was retrieved. Fortunately, all the specimens from the 1989 surveys (Alice Arm, Vancouver Harbour) were available. Since there was considerable overlap in species among studies, all but 20 taxa from the entire set of surveys were obtained. In the more recent surveys (1989), there were often several hundred specimens of a given taxon available for weighing.

Specimens from each taxon were blotted dry and weighed to the nearest .01 mg. Mean wet weights were calculated from the total weight of all specimens divided by the number weighed (see Appendix 2). Species with mean weight less than 0.01 mg have a mean biomass of zero entered in Appendix 2, but have a positive value in the databases if there were sufficient of them in a given replicate to produce at least 0.01 mg of total estimated biomass. Copepods, which were eliminated because they were only processed from a few surveys, are also given values of zero in Appendix 2. In many cases, there was only one specimen of a given taxon found in the study or archived in the older reference collections. The weights used therefore only provided an estimate of the relative sizes of different taxa. The 20 species not recovered (indicated in Appendix 2) from archived material were all small, relatively low in abundance. Their mean wet weights were estimated based on congeneric species or values in the literature. In order to estimate total wet weight per species per $0.1m^2$ for each replicate, abundances were multiplied by the

mean species-specific wet weight. The main limitations of the mean wet weight measurements for each species were that they did not take into account the range or deviation from that weight for different animals within a given sample replicate or among different stations within a survey, and that differences in mean weight of a given species from one survey area or time might be different than for the same species from another survey. As well, there was no way to know what loss in organic weight occurred over the preservation time of the different samples (see Ellis 1987). Finally, total estimated biomass values for a given sample can be quite variable with the incidental inclusion or exclusion of rare, large megafauna. With these not inconsiderable problems it was obvious that the mean biomass data could only be interpreted as providing a rough weighting factor for relative weight per individual for each species, and as a relative rather than absolute measure of total biomass per unit area for a given station. Transformation of these weights into size classes on an octave scale was seriously considered as this method is used in biomass spectral analyses on both pelagic phytoplankton (Platt and Denman 1977, 1978) and benthic invertebrate communities (Schwinghamer 1981). However, to minimize information loss due to grouping of species into weight classes, the mean wet weights per individual were used directly for transformation of abundance data. The limitations in the sampling method (grab size and 1mm screens which reduced juvenile forms and captured very few larger mobile epifuana) produced surprisingly little size variation within taxa within a given survey. Large variation occurred in only a few species of polychaetes and a few bivalves.

Numerical abundance and biomass-weighted values are standardized to $0.1m^2$ surface area for all studies. The abundance data for each survey are presented in the original technical reports listed in the acknowledgements and will not be repeated in this thesis. Only the fjord dataset has not yet been published, but is included in a technical report to be submitted for publication late in 1991. The list of species used in the databases, as well as the mean wet weights of individuals of each species used to transform the species abundance datasets are included in Appendix 2.

C. SEDIMENT SAMPLE PROCESSING

A 100 ml core was inserted into each grab prior to extraction of the sample from the grab. The core sample was processed to determine percent gravel, silt and sand content of sediments, using the Wentworth method for sieving sediments (Wentworth 1922).

D. DATA MANAGEMENT AND DEFINITIONS

In this thesis, the term "abundance" meant numerical abundance of animals per unit area. The word "biomass" was used to denote the mean total biomass estimated for each station using the calculation described below. In contrast, the term "biomass-weighted" was used to indicate the weighting of numerical abundance data by the mean biomass for each species (given in Appendix 2).

All intact taxa except nematodes were identified to the specific level whenever possible. Because copepods were identified in only a few of the surveys, they were eliminated from the analyses. A few specimens and juveniles in each survey could not be identified to species and were left with genus or family designations only. To avoid placing different species from different surveys in the same category or row of the data matrix, the few taxa not identified to species were eliminated from the databases. Some genus and species designations have been changed over the years, and were communicated to me by the taxonomic specialists involved in identifications. Otherwise, taxonomic designations follow Austin (1985). The following changes are noted:

1) Alice Arm 1982: *Transenella tantilla* was misidentified and has since been corrected to *Psephidia lordi*.

2) synonymies such as *Mitrella carinata* = *Mitrella gausapata* were combined.

3) The cumacean species *Eudorella pacifica* and *Eudorella emarginata* are now considered probable synonymies and were combined.

Summary statistics were calculated for each station. Mean abundance was based on sums of animals for all replicates of a given station, divided by the number of replicates. Mean biomass for each

station was calculated by multiplying the mean wet weight (Appendix 2) by the abundance for each species, summing these values over all species and replicates for each station, and dividing by the number of replicates. Total taxa number was a sum of all taxa over all replicates for each station. Because of the elimination of some taxa from the analyses (see above), these values were considered estimates only, and were included to compare relative values between stations. Species dominant both in terms of abundance and biomass were described for each survey areas. Data were tabulated in a species by station matrix using the DOS program LOTUS 123. Individual matrices were then combined into a C program database designed especially for this dataset.

From the aforementioned data, two faunal data matrices were constructed. The first was a species by station matrix with abundance in numbers per 0.1 m^2. The second was a species by station matrix with biomass-weighted abundance in mg per 0.1 m^2. A third data matrix consisted of environmental data collected from all surveys. This database was a factor by station matrix including latitude, longitude (i.e. entries formatted as $123^{o}45.26'$ or $49^{o}12.10'$) as one row, station depth in meters as the second row, sediment silt content as percent in the third row, and finally sediment sand content in the fourth row.

E. STATISTICAL ANALYSES

For each survey, the data matrix was subjected to an agglomerative, hierarchical Q-mode cluster analysis using the Bray-Curtis coefficient of similarity (Bray and Curtis 1957) with unweighted pair group mean average linkage (Sneath and Sokal 1973). This first step was done with all replicates unaveraged, to see if most replicates clustered together. In the second step, the replicates were averaged, and a simultaneous Sigtree analysis was performed on the data matrix (Nemec and Brinkhurst 1988a). The results of these first two steps are given in Brinkhurst (1987), Brinkhurst et al. (1987), Burd et al. 1987, and Burd and Brinkhurst (1987, 1990a,b), and will only be discussed in context with the overall analysis (see below).

1. Sigtree

Sigtree tests the null hypothesis that the stations are grouped together by random chance (i.e. that the stations clustered within a given group can be considered to be derived from the same community). A thorough description of the method is given in Nemec and Brinkhurst (1988a). The method utilizes the variability within replicates for each station to generate many simulated replicates and tests the probability that the similarity between groups occurred by chance, based on the relative variance among replicates for within station and among station groups. This is known as a bootstrap technique. A low probability is used as a basis for rejecting the hypothesis and recognizing significantly distinct station groups. Only two replicates per station were available for many areas in this study, but more are generally preferable, particularly in areas with low numerical abundance of animals (Nemec, unpublished). The term "significantly homogeneous" refers only to those groups for which the linkage has a probability below the level for rejection of the hypothesis. The term "significantly distinct" will refer to those groups of stations which have been determined by the analysis to be distinct from each other at a given probability level, either because the linkage between the two groups has a probability below the level for rejection of the hypothesis, or because the group in question is not significantly homogeneous but is directly linked with a significantly homogeneous group.

2. Comtre

Unlike Sigree, the two Comtre methods do not utilize the species abundance information from the original data matrices. Rather, these methods compare the order of linkages between two dendrograms, ignoring the relative dissimilarity levels of those linkages. Comtre2 bootstraps the Fowlkes-Mallows statistic (Fowlkes and Mallows 1983). The Fowlkes-Mallows statistic tests the null hypothesis at any given linkage level, that two dendrograms are the same. Comtre1 utilizes the Fowlkes-Mallows

statistic to test the opposite hypothesis, that the two dendrograms being compared are different at any given linkage level. The use of this hypothesis is not conducive to bootstrapping (see Nemec and Brinkhurst 1988b).

These methods can be used to inferentially compare any two dendrograms based on data from the same stations. Therefore, one of the pair of "random" abundance dendrograms being compared can be substituted with a dendrogram representing environmental factors such as sediment type, depth, and geographic distance between stations to provide a statistical comparison of the two dendrograms.

3. Application of Statistical Methods

Sample replicates were combined for all surveys from a given area. The results for each area are presented in Chapters 3 to 8. In chapter 9, combined databases included all sample replicates from all areas. Cluster analyses and Sigtree tests were done on the combined data sets for species abundance data and for biomass-weighted species abundance data. The two faunal analyses were then compared to each other using Comtre2. In several time series studies, an environmental data matrix consisting of a combination of sediment particle size data (percent silt/clay and percent sand), depth and station location (latitude and longitude) was constructed. A cluster analysis was then performed on these data. The method Comtre1 was used to statistically compare the results of the faunal dendrograms and the environmental dendrogram linkage by linkage. This was not done for the Alice Arm time series because sediment data were not collected for 1982 and 1983 and because there was very little difference in sediment types between stations.

Statistical analyses were conducted for the combined dataset (chapter 9-all replicates from all sample areas) in the same manner as for individual survey areas.

F. POWER, SIGNIFICANCE AND ASSUMPTIONS OF STATISTICAL METHODS

There are a number of unknowns about the significance methods

outlined in section E. The first is the number of simulations required to provide confidence in the precision of the result, and the second is the power of the test (for a discussion of power, see chapter 1 section D3).

The first unknown is simple to address. Given the almost unlimited computer time available, the use of 500 simulations was feasible. This meant that the programs for the entire database required about 4 days of CPU time and 1-2 weeks of elapsed time on the IOS VAX mainframe computer.

The second issue is much more complicated and difficult. In fact, very few researchers bother to address the issue of type II (beta) error or its complement, power in statistical tests. Type II error indicates the probability of not rejecting the null hypothesis when it should be rejected (see chapter 1, section D3). The reliability or power of the test depends on a variety of often interdependent factors, the most important of which are:

1) Number of sample replicates
2) Overall abundance per replicate
3) Sieve size
4) Similarity between groups of stations
5) Significance level for rejection of hypothesis
6) "Effect size" (i.e. the amount of difference which it is ecologically meaningful to test)

The question of power is particularly difficult to address with multivariate inferential tests because the underlying distribution of the data is almost impossible to predict or determine. Therefore, power analyses which make no assumptions about the data distribution provide the only sensible solution. Using the bootstrap method and existing datasets, Nemec (1990 unpublished contractor reportto fisheries and oceans) ran preliminary Monte Carlo simulations of power analyses on a Sigtree analysis of the Hecate Strait data. Specifically, she examined the effects of 1,4 and 5 above. She found that using 4 or 5 replicates, a 1% significance level and similarities of 50% or less between groups, power was acceptable (probably between 60-80%) for abundances found in the Hecate Strait dataset. For only two replicates at the abundances

found in Hecate Strait, a significance level of 10% is required to provide reasonable power. In datasets such as the fjords and Alice Arm, abundances were similar to or lower than Hecate Strait, and only two replicates were taken. Therefore, a significance level of 10% is required for reasonable power. Unfortunately, when the total number of station groups (=linkages) being tested in Sigtree is more than just two or three, the overall significance of the analysis is lowered, because 10% of the linkages tested can be expected to incorrectly reject the null hypothesis. This is known as the multiple test problem. However, because this analysis is hierarchical (i.e. once a significant linkage is found, those linkages at a higher dissimilarity which are dependent upon the significant one must automatically define significantly distinct, but not necessarily significantly homogeneous groups - see Nemec and Brinkhurst 1988a), the overall significance of the entire analysis is improved and the multiple test problem is reduced. However the overall significance of the entire analysis cannot be determined easily.

In the Shelf surveys, only two replicates were used, but overall abundances were somewhat higher than in Hecate Strait (since a portion of each sample was sieved through a 0.25mm screen). As well, a larger grab ($0.25m^2$) was used, which would theoretically reduce the variability between replicates. With these improvements in the variability of the data, a conservative but realistic significance level of 2.5% could be used for the Shelf surveys. For the remaining nearshore surveys (Vancouver Harbour, Boundary Bay) the use of smaller sieve sizes and/or greater numbers of replicates produced much higher abundances at most stations than in the aforementioned surveys. Therefore 1 to 2% significance levels were used for these studies.

The significance testing of data from a large set of stations is a problem with Sigtree because of the multiple tests issue. For example, the overall analyses (chapter 9) consisted of a total of 190 linkages. Even if this problem is ignored, a suitable significance level for testing the linkages is difficult to determine because the dataset contained a mixture of surveys with different replicate numbers, sieve sizes and grab types.

Despite the overall significance problem, Sigtree can be very useful for another reason. The significance of linkages is independently determined at each linkage level (Nemec and Brinkhurst 1988a). Therefore, Sigtree provides an excellent indication of the within group versus between group variance at each linkage lev l. Significant linkages provide an indication of the relative homogeneity of groups, as well as their distinctness from other groups. Interpreted in this manner, Sigtree remains a useful statistical tool regardless of the number of linkages being tested and will be utilized in the overall analyses in Chapter 9.

Another issue of concern is the problem of effect size, or the magnitude of the effect being tested for (see Toft and Shea 1983). In a case where there are 5 or more replicates per station and abundances range in the thousands of individuals per station, it is conceivable that virtually every linkage would be significant even at a low probability level, based either on spurious or meaningless differences among stations. This problem could occur in overzealous sampling programs or when too many replicates are combined, but was not considered a problem in this study due to the low numbers of replicates per station (2-5). This effect size problem could be offset partially by the use of low probability levels ($\leq$1%) for rejection of the hypothesis.

In the two Comtre tests, the issue of power has not been addressed, although it is assumed for the sake of this study that it will be similar in magnitude and effect to that of Sigtree. One notable difference in Type I error is that each linkage test is not hierarchically dependent in Comtre, therefore the multiple-test problem is greater than in Sigtree. The overall significance of an analysis should be equivalent to the Bonferoni correction (see introductory statistics textbooks) based on the probability for rejection used at each linkage level, and the number of tests (linkages) conducted in a given analysis.

CHAPTER 3: ALICE ARM

A. INTRODUCTION

This chapter is included in the thesis because the data covers the longest time-span of any survey area, and represents an area affected by heavy depositions from an unnatural source. The Alice Arm surveys were conducted to examine the effects of mine tailings on the distribution of benthic infauna. In this chapter I examine differential effects of mine tailings and natural sedimentation on the distribution of small and large fauna, by comparing community analyses based on abundance and biomass-weighted data. Abundance data are in Kathman *et al.* (1983,1984), Brinkhurst *et al.* 1987 and Burd and Brinkhurst (1990a) in the back cover of the thesis.

Between April 1981 and November 1982, approximately four million tonnes of tailings from the AMAX molybdenum mine at Kitsault were discharged at a depth of about 50m into Alice Arm, a fjord located on the northwestern mainland coast of British Columbia. The mine was then shut down indefinitely because of a decline in world molybdenum prices. In October of 1982, a quantitative sampling survey of the benthic macroinfaunal communities in Alice Arm was conducted to assess the damage to the benthic community in the inlet. Three stations in the relatively undisturbed adjacent inlet, Hastings Arm, were also sampled to provide "clean" or "reference" data. Surveys were carried out again in October of 1983, 1986 and 1989, to examine the recovery of fauna following the cessation of mine tailings deposition.

Alice Arm and Hastings Arm are glacially fed, typically steep sided fjords with shallow sills at the mouth (20m in Alice Arm, 51m in Hastings Arm) separating them from external water bodies. The geomorphology of the runoff (glacial and riverine) sources for both inlets is similar (Losher 1985). Core data indicate that Alice Arm has a natural sedimentation rate of 1 to 2 cm per year (Losher 1985, Reimer 1989). Unfortunately, no core data are available to provide information on sedimentation rates for Hastings Arm. Dr. Brian Bornhold (Pacific Geoscience Centre, Sidney, B.C.) has commented that Hastings Arm is

subject to high turbidity and freshwater entrainment in bottom sediments from river delta destruction and variable glacial melt (see also Losher 1985). Rambold and Stucchi (1983) indicated that such runoff is not as extensive in Alice Arm in spring and summer as it is in Hastings Arm. Unpublished light attenuation data from the Institute of Ocean Sciences (R. Thomson, D. Stucchi) suggested that considerable surface turbidity ocurred in Hastings Arm between 1980 and 1982, with transmissivity values of 70-80% of baseline. All of these data suggest that Hastings Arm may be subject to frequent natural high sedimentation events.

Flushing rates, although particularly slow and restricted in Alice Arm, have produced partial or complete replacement of bottom water annually (Rambold and Stucchi 1983, Krauel 1981). Mining activities have ocurred in Alice Arm intermittently for many years prior to 1981 (for review see Losher 1985). Hastings Arm was the location of the ANYOX copper mine, which operated for approximately 30 years in the early 1900's.

Stations were located along a gradient from the outfall to the mouth of the inlet (Fig.3). Depths varied between about 214m to 400m in Alice Arm and 267 to 395m in Hastings Arm (Table 2). It should be noted that the depths of the Hastings Arm stations in 1989 were between 80-120m shallower than in previous years, due to a navigational error. As a result, the faunal composition of these stations is unique from previous years (see results). Two grab samples were taken at each of three stations per transect from the tailings outfall to the sill (transects C to E). The middle (M) station in each transect (CM, DM, D5M, EM respectively) was generally located within the deep, central trough of the inlet, whereas the north (N) and south (S) stations (CN, CS, DN, DS, etc.) were in the shallower, steep areas adjacent to the trough. An extra transect (D5) was added between transects D and E in 1983 and 1986 only. For construction of databases, station names for transect D5 have been shortened to transect "5" where relevent (i.e. A2D5M is indicated as A25M). A single transect of stations (Z) running from east to west (ZE, ZM, ZW) was sampled from the adjacent inlet, Hastings Arm. Station names were constructed as per the following example: A2DM where A=Alice Arm, 2=1982, D=transect D (second closest transect to the outfall),

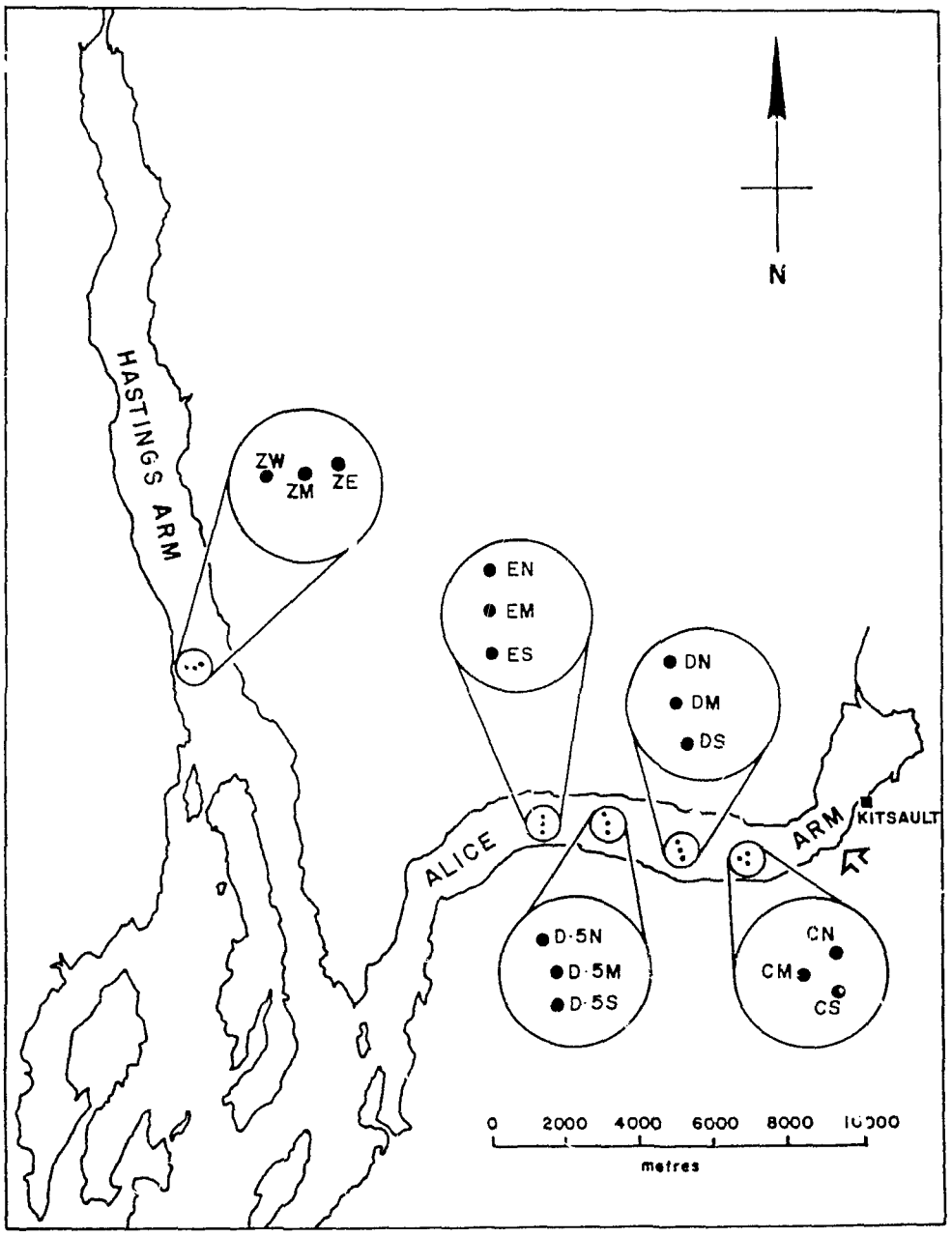

Figure 3. Alice Arm and Hastings Arm sampling transects. The outfall location (50m depth) is shown by the arrow. Transect D5 was sampled only in 1983 and 1986.

M=the middle station in the transect. Four transects (12 stations) were sampled in 1982 and 1989 and 5 transects (15 stations) were sampled in 1983 and 1986. Station A2EM had only one replicate. Therefore a total of 107 replicates were sampled for the entire study.

Sediment samples were taken from grabs in 1986 and 1989 (see section 2C). Sediments were silty for most stations, with some fine sand in a few (Table 2). Although sediment samples were not taken in 1982 and 1983, values were extrapolated from 1986 sediment data for the same stations, to complete the environmental dataset for the entire coast.

B. RESULTS

1. Summary Statistics

Abundance, species richness and estimated mean biomass values for each station are documented in Table 2. Visual inspection of these data is sufficient to identify several trends. Stations CN, CM and DM were in the direct path of the tailings plume (Burling *et al.* 1983). In 1982, abundance, biomass and species richness values were very low at stations CN, CM and DM; slightly higher in DS; higher but still low in CS and DN; and highest in transect E, furthest from the outfall (Table 2). In 1983, there was a decline in values for most stations (excluding EM abundance and biomass and DS species richness), whereas values for the previously impoverished stations (CN, CM, DM, DS) had increased somewhat. In 1986, abundance, richness and biomass were relatively high for all stations In 1989, abundance and species richness values were similar to values for 1983, and consistently lower than values for 1986. In contrast, biomass values in the C and D (but not E) transects in 1989 were comparable to those in 1986. In Hastings Arm (transect Z) abundance and species richness values were highest in 1982. Abundance declined by about 30% at most stations in 1983, did not change in 1986 and declined further in 1989 (Table 2). Estimated biomass values in Hastings Arm did not change from 1982 to 1983, rose slightly in 1986 and declined by about 50% in 1989.

Table 2. Mean biomass (wet weight in g/ $0.1m^2$), mean abundance (number/ m^2) and total taxa in all replicates for Alice Arm and Hastings Arm. Mean values were calculated from two replicates per station (A2EM had only 1 replicate).

	Mean Biomass g/$0.1m^2$	Mean Abundance No/$0.1m^2$	total taxa
1982			
A2CM	0.03	2	4
A2CN	0.01	2	3
A2CS	1.30	64	24
A2DM	0.00	2	4
A2DN	1.43	50	20
A2DS	0.08	11	10
A2EM	2.88	99	18
A2EN	3.94	289	37
A2ES	4.60	324	38
H2ZE	4.30	161	38
H2ZM	3.34	118	30
H2ZW	2.16	193	37

	Mean Biomass g/$0.1m^2$	Mean Abundance No/$0.1m^2$	total taxa
1983			
A3CM	0.13	7	7
A3CN	0.31	11	15
A3CS	0.26	21	17
A3DM	0.14	9	9
A3DN	0.46	17	14
A3DS	0.76	21	20
A35M	2.54	37	17
A35N	2.28	39	21
A35S	1.18	21	15
A3EM	3.40	119	20
A3EN	1.91	67	10
A3ES	3.34	166	23
H3ZE	3.56	80	31
H3ZM	2.97	74	32
H3ZW	2.52	97	32

	Mean Biomass g/$0.1m^2$	Mean Abundance No/$0.1m^2$	total taxa
1986			
A6CM	5.28	126	49
A6CN	4.62	117	35
A6CS	2.45	68	35
A6DM	4.95	184	42
A6DN	2.76	98	36
A6DS	4.31	124	38
A65M	4.95	89	34
A65N	4.19	73	41
A65S	4.45	78	33
A6EM	3.82	131	33
A6EN	5.18	144	41
A6ES	5.51	233	38
H6ZE	5.08	75	30
H6ZM	4.56	63	29
H6ZW	3.07	43	23

	Mean Biomass g/$0.1m^2$	Mean Abundance No/$0.1m^2$	total Taxa
1989			
A9CM	4.64	62	31
A9CN	4.28	53	25
A9CS	2.40	55	32
A9DM	3.00	53	34
A9DN	3.84	63	25
A9DS	2.30	78	39
A9EM	3.80	39	24
A9EN	3.70	47	26
A9ES	2.80	33	27
H9ZE	1.42	17	16
A9ZM	2.07	23	21
H9ZW	1.53	14	16

Table 3. Total abundance (numbers/ m^2) of major taxonomic groups in Alice Arm and Hastings Arm, B.C. Poly/Biv represents the ratio of polychaetes to bivalves.

Alice Arm

	1982	1983	1986	1989
Polychaeta	355	82	495	206
Bivalvia	466	280	533	147
Poly/Biv ratio	0.76	0.29	0.92	1.4
Gastropoda	7	5	6	38
Echinodermata	28	43	82	91
Crustacea	23	26	80	11

Hastings Arm

	1982	1983	1986	1989
Polychaeta	1183	83	76	76
Bivalvia	308	600	413	47
Poly/Biv ratio	3.8	0.13	0.18	1.6
Gastropoda	30	12	23	2
Echinodermata	23	18	27	20
Crustacea	9	22	27	12

The total abundance for taxoromic groups and the ratio of polychaetes to bivalves are listed for each year and each inlet in Table 3. Bivalves dominated the fauna in Alice Arm in all survey years except 1989, when polychaetes were dominant. Polychaete abundance was particularly low in Alice Arm in 1983 and highest in 1986. In Hastings Arm, polychaetes dominated overwhelmingly in 1982, dropped by 90% and remained at this level throughout the remainder of the survey period, though they were again dominant in 1989. Bivalves dominated in Hastings Arm in 1983 and 1986 then dropped by 90% in 1989. The ratio of polychaetes to bivalves was low in 1983 in both inlets, and in 1986 in Hastings Arm. The ratio was moderately low in 1982 in Alice Arm and close to 1 or greater in the remaining locations and years (Table 3). Echinoderm numbers increased steadily throughout the study in Alice Arm, but remained constant in Hastings Arm. Crustacean numbers were highest in 1983 and 1986 in both inlets.

In Alice Arm, the most abundant species in all years was the bivalve *Psephidia lordi* (misidentified as *Transenella tantilla* in Kathman *et al.* 1983 and Byers *et al.* 1984). The abundance patterns of *P. lordi* therefore strongly affected the overall patterns evident in Table 3. This species was rare at the C and DM stations in 1982, but abundant elsewhere. In 1983 it was missing from all the C and D stations. In 1986 it was present once more in C and D, missing in D5 and most abundant in E. In 1989 numbers had declined at all stations. Other species which were consistently dominant in terms of abundance included the bivalve *Nucula tenuis*, the polychaetes *Levinsenia (=Tauberia) gracilis*, *Galathowenia oculata*, *Prionospio steenstrupi*, the carnivorous polychaete *Nephtys cornuta cornuta*, and the holothuroid *Chiridota albatrossi*.

The increase in abundances at stations CN, CM and DM from 1983 to 1986 (Table 2) may be attributed largely to a dramatic increase in small polychaetes such as *Galathowenia oculata*, *Levinsenia gracilis*, *Sternaspis scutata* and *Prionospio steenstrupi*. Also particularly abundant in 1986 were the bivalves *Axinopsida serricata* (present only in 1986), the gastropod *Cylichna attonsa*, the cumacean *Eudorella pacifica* (=*E. emarginata*) and some ophiuroids. Species that increased steadily

in abundance from 1982 to 1989 include the holothuroid *Molpadia intermedia* and the mud star *Ctenodiscus crispatus*.

The biomass dominants included six species that were among the ten most dominant species in all years. These were the mud star *Ctenodiscus crispatus* (which was a particularly important biomass contributor in 1986 and 1989), the holothuroids *Molpadia intermedia* and *Chiridota albatrossi*, the bivalves *Psephidia lordi* and *Nucula tenuis*, the polychaete *Nephtys punctata*, and the crustacean *Paraphoxus oculatus*. The bivalve *Yoldia martyria* became a biomass dominant in 1986 and 1989, along with one other *Yoldia* species in each of these two years. Ophiuroids were dominant only in 1986 and 1989. The consistency in abundance of the echinoderms *Ctenodiscus crispatus*, *Chiridota albatrossi*, *Molpadia intermedia* and *Ophiura sarsi* from 1986 to 1989 accounts for the comparable biomass values between these two surveys (Table 3), in spite of the much lower overall faunal abundances in 1989. Slightly lower biomass values in the E stations in 1989 can be attributed to an overall reduction from 1986 in the numbers of the dominant bivalves *Yoldia martyria*, *Psephidia lordi* and *Nucula tenuis*.

In Hastings Arm, the most abundant species in 1982 was the carnivorous polychaete *Nephtys cornuta cornuta*, which was replaced thereafter by the bivalve *Nucula tenuis*. Other consistently dominant species included the polychaete *Levinsenia gracilis* and the bivalve *Psephidia lordi*.

Biomass dominants in all years in Hastings Arm included the bivalve *Nucula tenuis*, the polychaete *Nephtys punctata* and the echinoderms *Ctenodiscus crispatus* and *Chiridota albatrossi*. The remaining biomass dominants included a variety of bivalves of the genus *Yoldia*, the polychaete *Goniada annulata* (dominant in 1982 and 1983 only) and the anthozoan *Virgularia cystiferum* (present in 1989 only).

2. Statistical Analyses

The results of separate Sigtree analyses on the originally tabulated abundance data for each of the 1982, 1983 and 1986 sets of data are presented in Brinkhurst *et al.* (1987). In the current study, the data

from all four surveys from both Alice Arm and Hastings Arm were combined. Thus the set of data for abundance included a total of 107 replicates (from all four surveys) and 137 species. The abundance data were then weighted by the mean wet weight for each species (see Appendix 1), and a second database (biomass-weighted abundance) created. The results of Sigtree analyses on these two data matrices are shown in Figs. 4 to 7. Since abundance was not particularly high in this survey (see chapters 4-8) and only 2 replicates per station were sampled, the power of Sigtree would not be high with a probability of rejection of 1% or 5%. Therefore, significant linkages at the 7.5% level are given (for discussion of power see Chapter 2 section F).

a. Sigtree analysis of abundance data

The dendrogram resulting from the Sigtree analysis of the abundance data from all surveys (Fig. 4) emphasized the most abundant fauna and deemphasized the rare fauna. Seven station groupings can be identified as statistically significant and statistically homogeneous (Fig. 4; $p \leq 0.075$). By extrapolation, any groups which link onto the seven significant groups at a higher dissimilarity level must be significantly distinct from the aforementioned groups, although not significantly homogeneous (see Chapter 2 section E1). We can therefore discuss ten distinct groups in Fig. 4, plus the solitary stations A3EM, A3EN and A2CS. The station groups given in Fig. 4 are displayed geographically in Fig. 5 in such a way that both spatial and temporal comparisons can be easily made.

Three stations near the mine tailings outfall in 1982 are identified as group 2'. These three stations were distinct from and almost 100% dissimilar to all other stations, and represent the maximally defaunated stations near the outfall in 1982. The single station A2CS also had low abundance (Table 2), and was significantly distinct from all other stations. In 1983, the aforementioned four stations, plus all the remaining C and D stations, and the Hastings Arm stations from 1989 formed the second most impoverished group in terms of abundance (group 8). In 1986, the original three defaunated stations from 1982 again

formed a significantly distinct and homogeneous group (group 2; $p<5\%$) from the remaining C, D and D5 stations (group 3, also significantly homogeneous), even though abundance and species richness values were similar in the two groups. With the exception of one E station from 1982 (in group 4), the E stations from 1982, 1983 and 1986 were most similar to each other, but formed two distinct groups and two singletons ($p\leq 3\%$ - groups 5 and 6, and A3EN, A3EM - Fig. 4). In 1989, all of the Alice Arm stations (transects C to E) plus two D5 stations from 1983, formed a significant group that was non-homogeneous (group 1). Therefore, in terms of the most abundant fauna, the species composition was similar, but significantly distinct between 1986 and 1989. Group 4 consisted of one each of the D and E stations and all of the Hastings (Z) stations from 1982. The Hastings stations from 1983 and 1986 (except H6ZW) formed a significantly distinct and homogeneous group (group 7). In 1989, the Hastings stations were indistinct from the 1983 impoverished C and D stations (group 8), mainly because mean species richness and abundance values were similar (Table 2). However, the Hastings stations in 1989 were much shallower than any other year, indicating that samples were taken further up the inlet, where terrigenous and glacial sedimentation would be heavier.

In summary, the three defaunated Alice Arm stations were significantly distinct in 1982 (group 2'). Although abundance values were high compared to 1982, this group was again significantly distinct in 1986 (group 2). In 1983, the C and D Alice Arm stations were distinct and relatively low in abundance, whereas in 1986 these stations were also distinct (along with D5) but high in abundance. The faunal composition of the E stations (outer Alice Arm) was fairly similar from 1982 to 1986, and distinct from other Alice Arm stations. Faunal abundance and composition of Alice Arm stations in 1989 were similar to, but significantly distinct from the 1986 Alice Arm stations. The Hastings Arm stations clustered together in all years, but the 1989 stations were obviously located further up-inlet than in previous years.

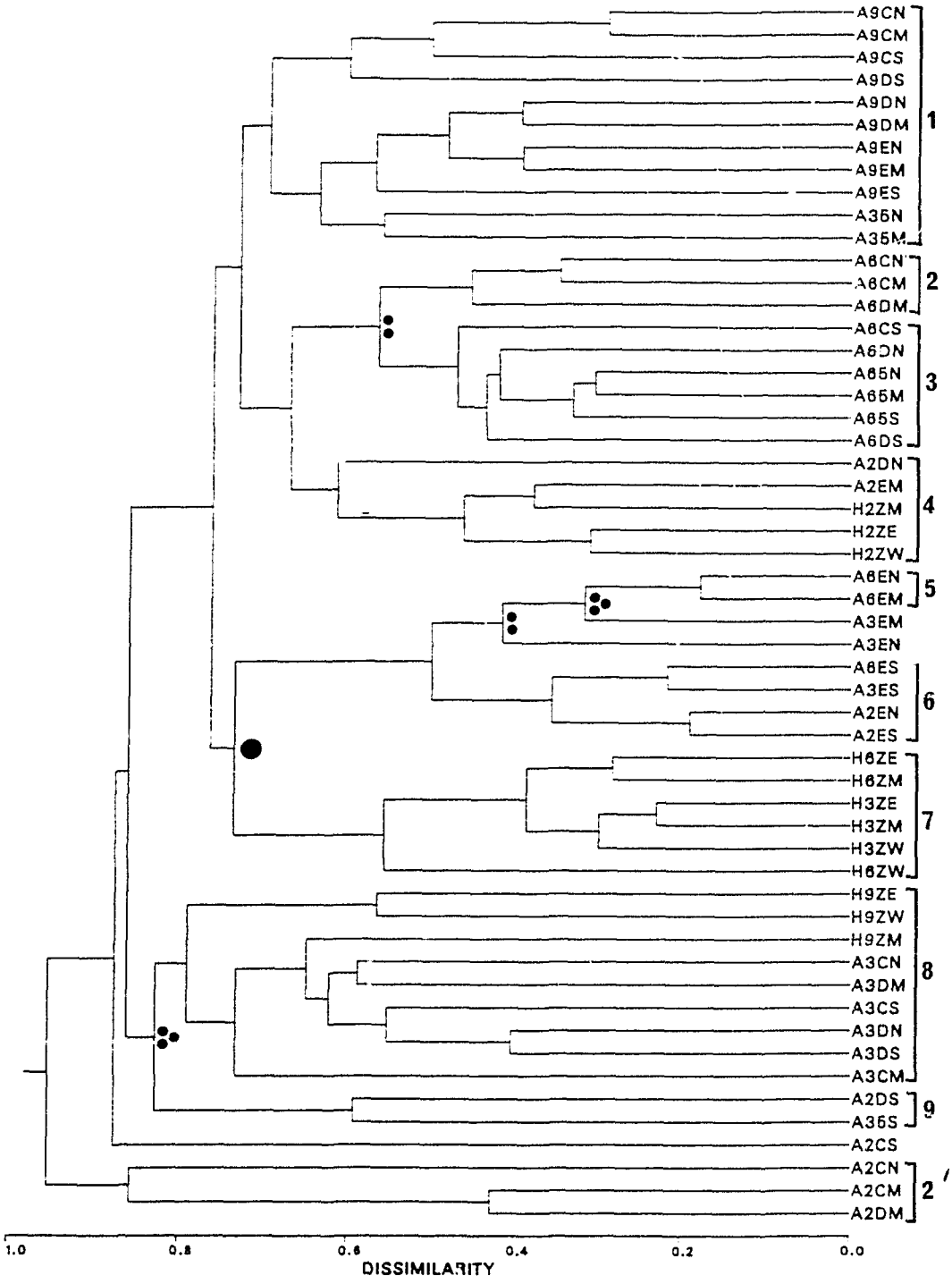

Figure 4. Cluster dendrogram for raw abundance data for all years from Alice Arm and Hastings Arm. Significances at the 1% level are indicated by the large dot, at the 5% level by two small dots and at 7.5% by three small dots. Significant (but not necessarily homogeneous) groups are indicated on the right hand margin. Note that transect D5 has been truncated to transect 5 for symmetry in the database.

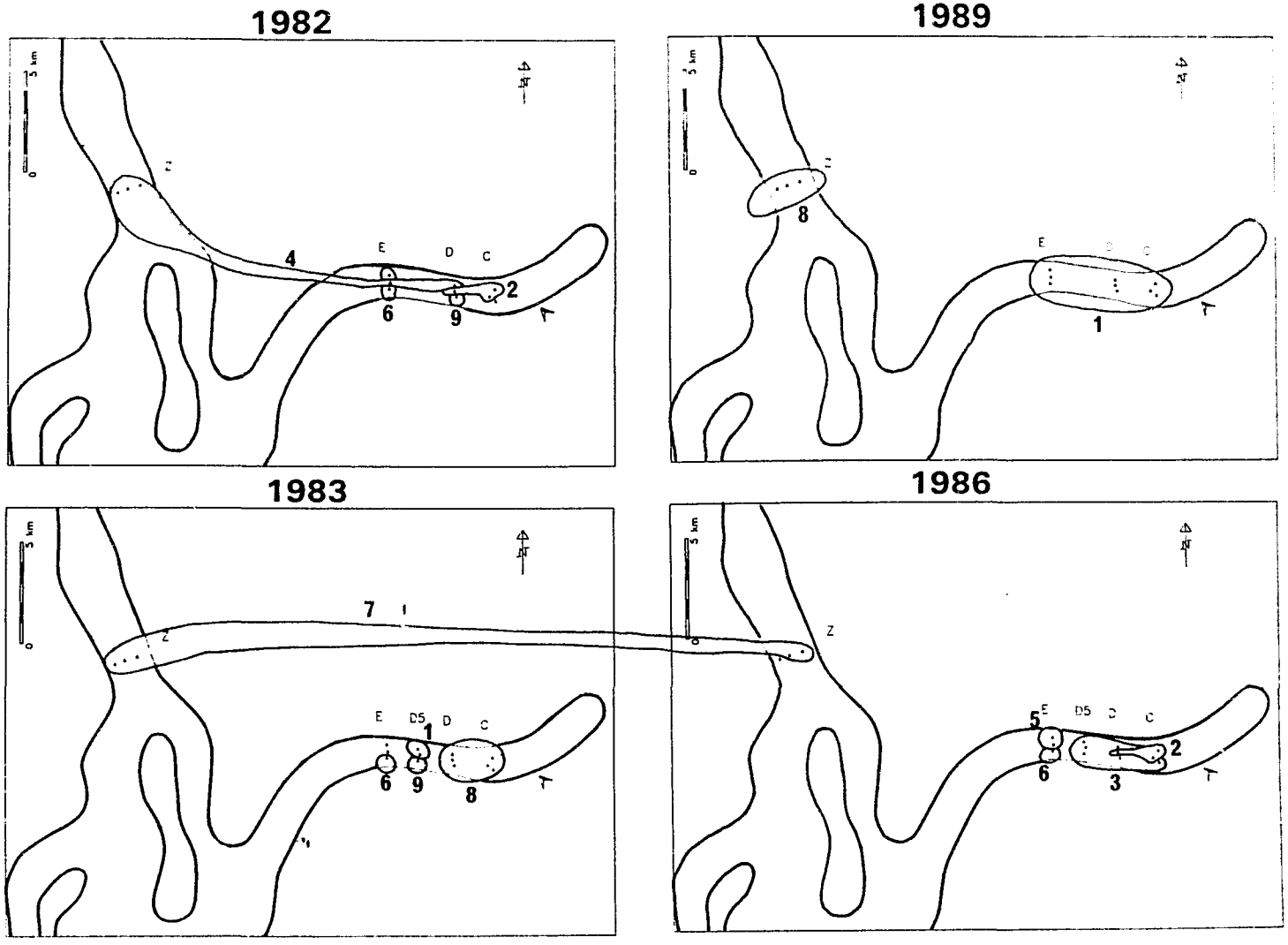

Figure 5. Station maps showing the significant groupings outlined in Fig. 4.

b. Sigtree analysis of biomass-weighted abundance data

The Sigtree analysis of biomass-weighted abundance data emphasized the largest species and deemphasized the very small fauna (Fig 6). There were no significant linkages at $p \leq 1\%$, 1 significant linkage at $p \leq 5\%$ and 1 significant linkage at $p \leq 7.5\%$. The 8 significantly distinct groups are displayed geographically in Fig. 7.

The most impoverished group in terms of large fauna (group 8) included two of the original three impoverished stations from 1982 (Table 2; CN,CM), plus A2DS, A3CM and A3DM. The third of the original impoverished stations (Table 2; A2DM) had the lowest estimated biomass of any station, and was significantly distinct from all other stations (Fig. 6). Group 7 included the remaining C and D stations from 1983 and A2CS, which were less impoverished than group 8, but still abnormally low in biomass (Table 2). All of the 1986 and 1989 Alice Arm stations (except A9DS), A35N, all the 1983 Hastings stations, two 1986 Hastings stations and one 1982 Hastings stations formed one distinct but non-homogeneous group (group 1).

The outermost Alice Arm (E) stations from 1982 and 1983, plus A35M were most similar to each other, but formed two significantly distinct groups plus two singletons ($p=5.6\%$ - groups 3,4, and A2ES, A3EN). An assortment of stations (A9DS, A35S, A9ZM, A6ZW) formed a distinct group (group 2) as did the remaining two Hastings stations from 1989 plus A2DN (group 6). The remaining two Hastings stations from 1982 formed group 5.

In summary, the results of the biomass-weighted Sigtree analysis (Figs. 6,7) indicated that the two groups of low biomass stations from 1982 and 1983 included the same stations that were low in abundance in 1982 and 1983 (Fig. 4). The composition of large fauna in Alice Arm (biomass-weighted Sigtree analysis) was not significantly distinct between 1986 and 1989, as it had been in terms of the small fauna (Fig. 4). As well, Fig. 7 shows that the species composition in terms of large fauna was relatively uniform throughout Alice Arm in 1986 and 1989, but not in 1982 and 1983.

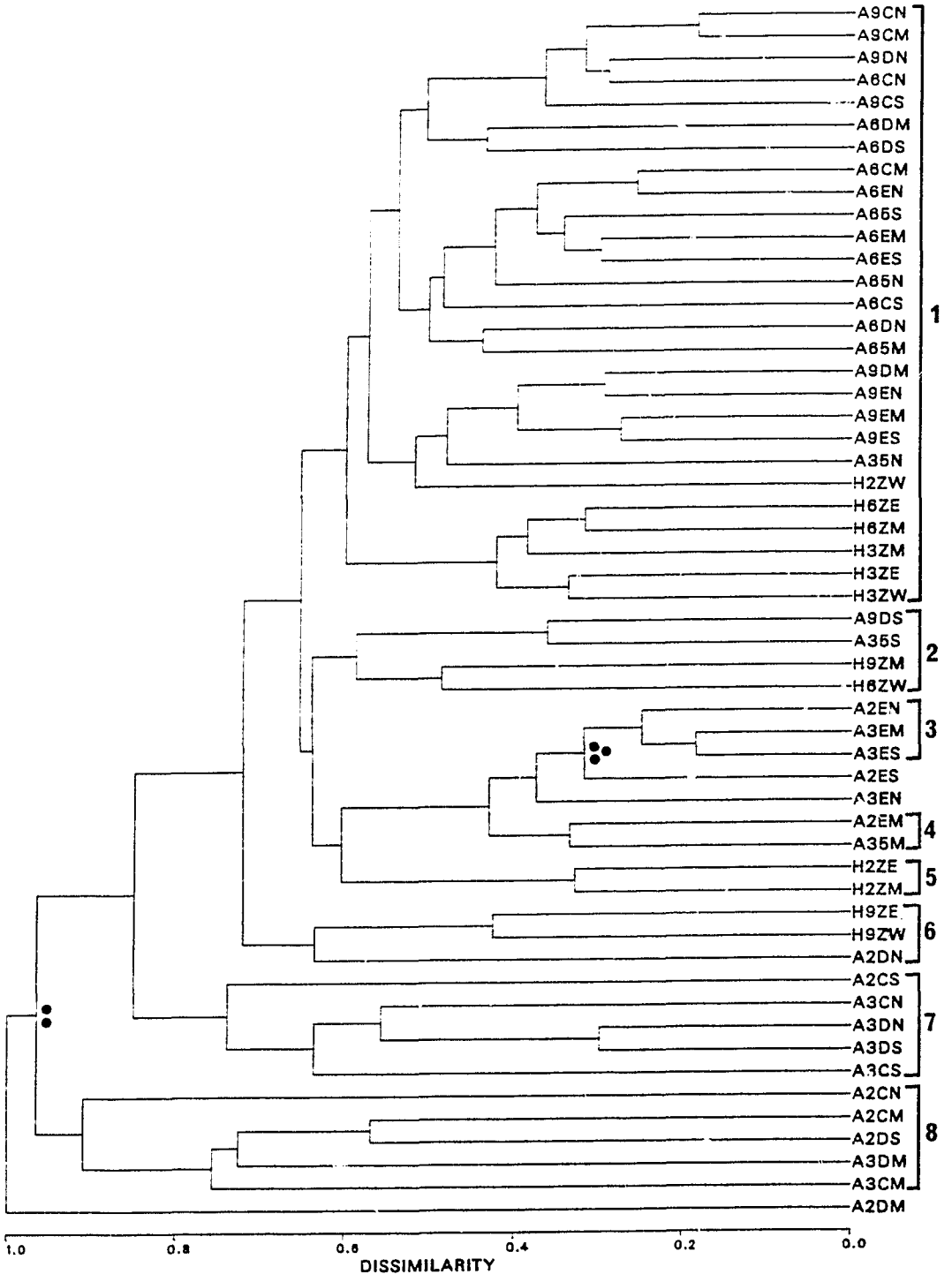

Figure 6. Cluster dendrogram for biomass weighted abundance data for all survey years from Alice Arm and Hastings Arm. Significances at the 5% level are indicated by two small dots and at 7.5% by three small dots. Significant groups are indicated on the right hand margin.

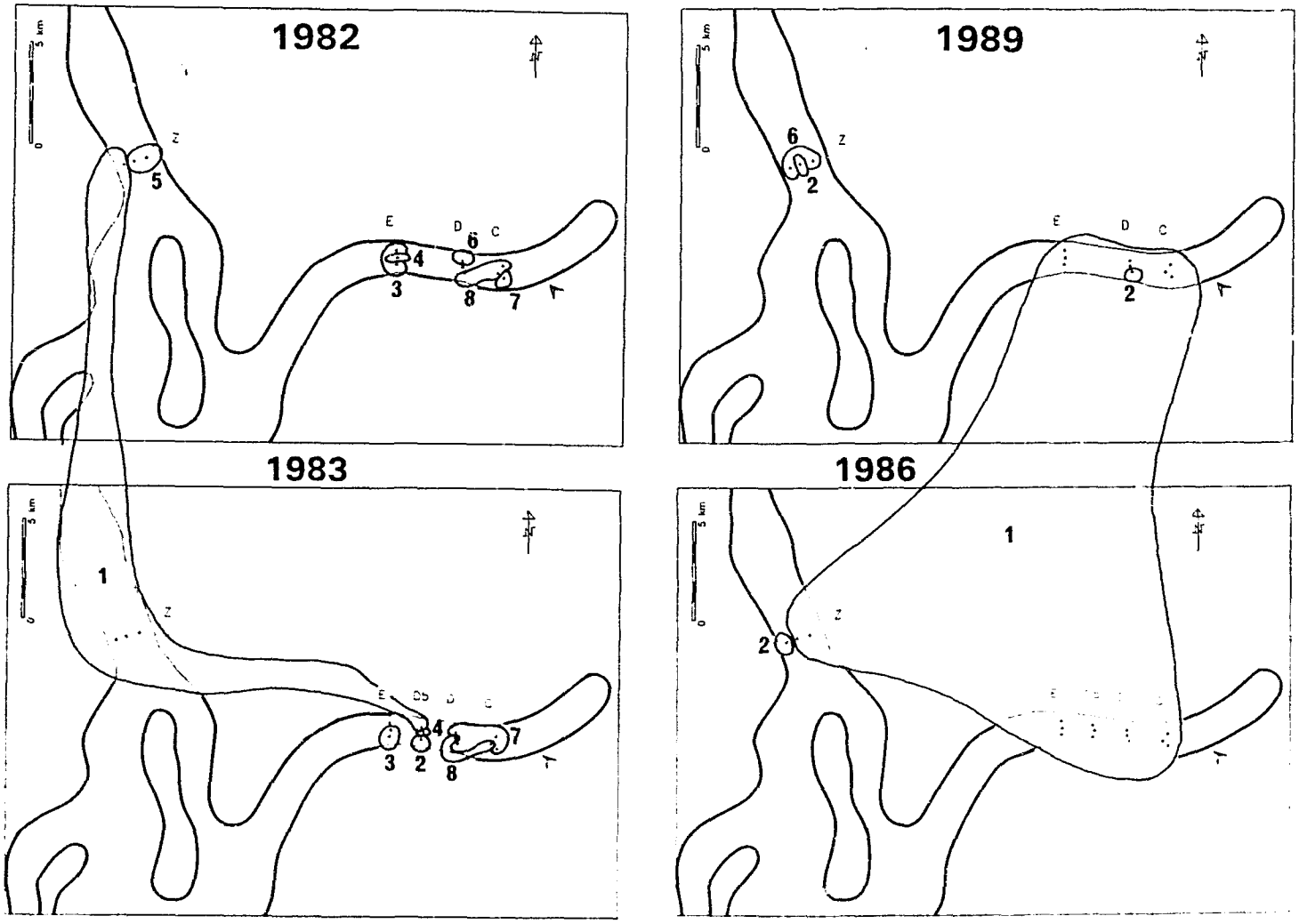

Figure 7. Station maps showing the significant groupings outlined in Fig. 6.

The Comtre2 comparison of the two faunal dendrograms (abundance and biomass-weighted abundance) tested the null hypothesis at each linkage level that the two dendrograms were the same. This analysis compares only group membership of the two dendrograms, and not the species complement which goes to make up the groups (see Chapter 2 section E2). The hypothesis was rejected at three linkages ($p \leq 7.5\%$ - Appendix 3a), suggesting that the station groupings based on abundance (small fauna) data were different from the groupings based on biomass-weighted abundance (large fauna) data.

3. Environmental Analysis

The similarity dendrogram representing environmental characters (depth, sediment type and geographic location - Fig. 8) clearly shows that there was very little difference in these characters among stations. The C stations grouped with one D5 station and the 1989 Hastings (Z) stations. The remaining D and D5 stations formed a group, as did the E and remaining Z stations. A small group of D stations (A3DN, A3DM, A6DN, A6DM) formed a group separate from the remaining D, D5, E and Z stations.

The Comtre1 comparison of the abundance dendrogram and the environmental dendrogram, which tests the null hypothesis that the two dendrograms are different, was rejected at 8 out of 53 linkages ($p \leq 7.5\%$). These rejections (see Appendix 3b) mainly reflect the tendency of the E and Z stations to group together within and among years. Therefore, the station groupings based on faunal abundance can be said to be partially related to environmental characters, particularly proximity and depth of stations (since sediment types were almost all the same). The Comtre1 comparison of the biomass-weighted abundance dendrogam with the environmental dendrogram (Appendix 3c), rejected 9 out of 53 linkages (Appendix 3c). As in the abundance comparison, the rejections mainly reflected the tendency of proximate stations to group together, particularly in the E and Z transects.

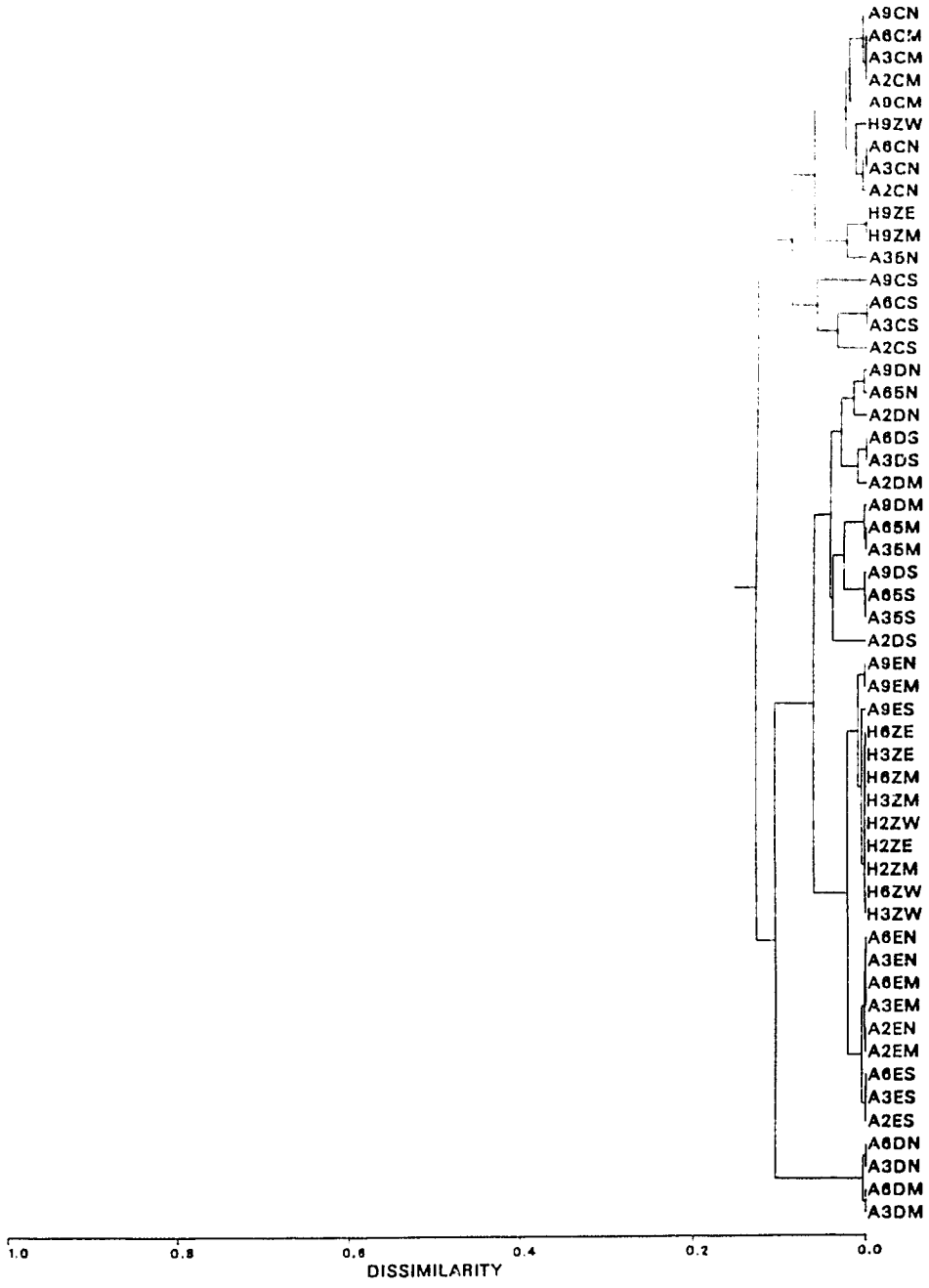

Figure 8. Environmental cluster dendrogram for Alice Arm and Hastings Arm. Variables in the analysis were depth, percent silt/clay, percent sand and geographic location.

C. DISCUSSION

In comparing the faunal distributions of Hastings Arm and Alice Arm, it must be kept in mind that although Alice Arm was subjected to an unnatural, heavy load of tailings sedimentation which did not occur in Hastings Arm, Hastings Arm has been known to experience high natural sedimentation events (B. Bornhold, Pacific Geoscience Center, Sidney, B.C. R. Thomson, D. Stucchi, IOS, Sidney, B.C., pers. comm.). In the ensuing discussion, I will examine the differences in faunal composition of the two inlets in light of the relative effects of natural versus tailings deposition, and how these differences are illustrated by the two different datamanagement methods (abundance versus biomass-weighted abundance Sigtree analsyes). The significant difference at three linkages between the abundance and biomass-weighted abundance patterns in the Comtre2 results suggests that there was a substantial difference in the distribution patterns of the large and small fauna from Alice Arm and Hastings Arm.

There is reason to assume that burial of benthic organisms is more likely than toxicity of tailings to cause faunal decimation (c.f. Harding 1983). Chemical analyses of tailings indicate that bioaccumulation and metal toxicity are minor concerns for commercial benthic species in Alice Arm (Reimer and Thompson 1988, Farrell and Nassichuk 1984). Smothering effects studied in tailings areas of Rupert Inlet, a fjord located on the northwestern side of Vancouver Island (Jones and Ellis 1975) substantiate this assumption. In laboratory experiments, Krantz (1974) found that certain forms of bivalves were unable to escape burial by natural sediment only 1cm thick if it was deposited too quickly. He concluded that a radical change from the native sediment could reduce burrowing ability, and burial in only 1 cm of an exotic sediment was often fatal. *In-situ* observations from a submersible following an earlier mining period in Alice Arm indicated that the number of burrows and castings from benthic animals declined in tailings areas compared to natural sediments in the same area (Goyette and Nelson 1977).

Reid and Baumann (1984) examined the specific effects of mine tailings burial in the laboratory on selected invertebrates from Alice Arm. They also reviewed pertinent literature on similar burial experiments using natural sediments. Their findings with respect to survival of bivalves and polychaetes is in line with similar studies in the literature, and strongly suggests that those animals which can best survive high sedimentation rates are (in decreasing order of survival): deposit feeding bivalves, filter feeding bivalves, errantiate polychaetes and sedentariate polychaetes. Burial experiments by Kranz (1974) also suggest that larger bivalves are better able to escape natural sediment burial than small ones. The aforementioned studies suggest specific patterns which may result from both tailings deposition and natural sedimentation.

1. Hastings Arm

Because the stations in Hastings Arm were originally used as "reference" sites for Alice Arm, the Hastings stations (Z transect) can be considered free from tailings or other anthropogenic effects. However, the effects of heavy natural sedimentation conditions on the fauna must be taken into consideration in comparing these stations with Alice Arm.

In Hastings Arm, abundances declined in 1983 and again in 1989 (Table 2). The abundance decline in 1983 was due mainly to a 90% decrease in polychaetes, with a simultaneous increase in bivalves over the previous year, resulting in similar estimated biomass values for stations from both years. Based on the results of Reid and Baumann (1984) described above, this pattern resembled a classic example of selective defaunation caused by high sedimentation. By 1989 there were few polychaetes and even fewer molluscs in Hastings Arm (Burd and Brinkhurst 1990a), however the obvious discrepancy in sample locations from previous years makes these data unreliable for temporal comparisons. The fact that the Z stations were located further up the inlet in 1989 than in previous years does provide an indication of what faunal patterns occur closer to the runoff source.

Much lower numbers of individuals were collected in samples from Hastings Arm in a 1977 study than were collected during the 1982 survey (see Kachman *et al.* 1983).

The dominant species in Hastings Arm were similar to those in Alice Arm. Unlike Alice Arm, the deposit feeding bivalve *Nucula tenuis* was consistently more abundant than *Psephidia lordi*. If the suspension feeding *P. lordi* has lower survival under high sedimentation conditions than the deposit feeding *Nucula tenuis*, as suggested by the results of Reid and Baumann (1984), the relative dominance of these two species in Hastings Arm supports the contention that Hastings Arm experiences higher natural sedimentation rates on a periodic basis than Alice Arm. *P. lordi* was also absent from the seriously impoverished C and D stations in Alice Arm in 1982 and 1983, which were presumably subject to heavy tailings settlement.

The Hastings Arm fauna was grouped with the fauna from the outermost Alice Arm stations in 1982, before the tailings had spread that far (see discussion on Alice Arm). This initially supported the contention that the Hastings stations would provide suitable reference data for observing changes in Alice Arm. After 1982, the Hastings stations were distinct from Alice Arm in terms of raw abundance data, but not in terms of biomass-weighted abundance (large fauna) data.

There was a strong similarity between the Hastings Arm stations in 1989 and the Alice Arm C and D stations in 1983 in the Sigtree abundance analysis. However, this pattern was not observed in the biomass-weighted analysis. A subsequent examination of biomass values in Table 2 clearly shows that the Hastings stations in 1989 had considerably larger fauna, and therefore higher biomass values than the tailings affected inner Alice Arm stations in 1983. Thus, an examination of abundance patterns alone would suggest that tailings deposition in the inner stations in Alice Arm produced a similar impact to some natural factor in Hastings Arm.

If the effects of tailings deposition and subsequent movement in Alice Arm are similar to natural sedimentation events such as those experienced in Hastings Arm, faunal patterns should be similar the two inlets. However, because of the difference in composition of

tailings to that of natural sediment, it is expected that the effects of tailings would be distinctive. In the next section, I examine the faunal patterns in Alice Arm, based on the assumption that natural sedimentation rates are low (Losher 1985, Reimer 1989), and that all other factors being similar in the two inlets, the major impact on fauna in Alice Arm is that of tailings deposition.

2. Alice Arm

Burling *et al.* (1983) described the development of a turbidity plume during mine tailings deposition, wherein sediment concentrations in the water exceeded 100 mg/l extending from the outfall down the deep central trench of Alice Arm. Such an event creates areas of unstable sediments where deposition rates are abnormally high, and the bottom is subject to slumping, causing turbidity and smothering of fauna. Brinkhurst *et al.* (1987) provide a general description of the faunal decimations and recoveries from 1982 to 1986. This description will be touched upon and modified based on the new, combined time-series analyses for all four survey years presented in this chapter. The turbidity plume from mine tailings in Alice Arm had catastrophic effects on the fauna of CN, CM and DM and slightly less impact on station DS in 1982, followed by a more widespread impact on D5S and all of the C and D stations in 1983. By 1986, the abundance, biomass and taxa numbers suggested that full recovery had occurred (Table 2). The subsequent decline in overall abundances in 1989 might at first glance suggest the occurrence of some event unrelated to tailings deposition.

The statistical analyses concur with the results from summary statistics, but reveal more detail on faunal distribution, particularly when the biomass-weighted results are examined. The results of the Sigtree analysis of abundance data confirmed the distinct nature of the group 2' stations in the direct path of the plume in 1982, and was sensitive enough to distinguish this group from all other stations in 1986, when the faunal numbers and biomass alone would indicate that recovery was complete. This long-term "signature" indicates that four to five years after cessation of tailings deposition, the overall species

composition at these three stations was still showing the after-effects of that tailings deposition event. The more widespread faunal declines in all C and D stations in 1983 was evident in results from both the abundance and biomass-weighted abundance Sigtree analyses.

The major difference in results between the abundance and biomass-weighted abundance Sigtree analyses was in the group membership for stations in 1986 and 1989. The distinct nature of group 2 in the 1986 Sigtree abundance analysis was not evident in the biomass-weighted analysis. Further, in the abundance analysis the 1986 stations were significantly distinct from the 1989 stations, because of the large difference in station abundance values for the two years (Table 2). In contrast, the biomass-weighted abundance analysis resulted in one significant group with 1986 and 1989 stations intermixed, as well as similar estimated biomass values for the two years (Table 2). Therefore, only the small, abundant components of the fauna were distinct between 1986 and 1989. This is not surprising, since the 1986 assemblage contained many small, opportunistic polychaete and bivalve species such as *Galathowenia oculata, Levinsenia gracilis* and *Axinopsida serricata*, which resembled a primary colonizing assemblage. Sometime between 1986 and 1989 many of these colonizers disappeared, reducing station abundances and leaving a community composed of relatively large animals.

Catastrophic burial by mine tailings accounted for the early, localized decimations in the stations nearest the outfall. Benthic fauna probably do not recolonize tailings as quickly as natural sediments (c.f. Taylor 1986), since they are tightly packed, low in oxygen, sulphate and organic carbon and high in Mo, Cd, Zn and As (Losher 1985, Reimer 1989, Reimer and Thompson 1988). Studies with artificial substrates near the tailings outfall from the Island Copper Mine in Rupert Inlet, B.C. indicate that colonization of tailings subtrates is slower than natural substrates (Taylor 1986). With a natural sedimentation rate of 1 to 2 cm per year (Losher 1985, Reimer 1989), it is not surprising that recolonization of these stations was still limited in 1983, one year after cessation of tailings. By 1985 and 1987, 6 and 9 cm respectively of sediment should have been deposited over the

tailings (Reimer op. cit.). This seems to have been sufficient to allow the considerable recolonization evident by 1986.

Unfortunately, the tailings did not remain immobile after initial settlement. Demill (1983) observed a slump edge of the tailings at 330m between the C and D transects in June of 1982. By 1987, tailings had sifted over the sill (Reimer 1989, Stukas 1983). This suggests that the unstable tailings continued to move considerable distances after mining operations ceased. The spread or resupension of tailings could account for the general faunal decline in all the C, D and D5 stations in Alice Arm in 1983.

An examination of some of the species changes in Alice Arm provides suggestive evidence that the faunal composition in Alice Arm may have been affected by shifting sedimentation patterns. Reid and Baumann (1984) concluded from experiments on the effects of mine tailings burial on benthic invertebrates, that polychaetes are less likely to survive burial than bivalves. This selective effect might explain the dominance of bivalves over polychaetes in Alice Arm in 1982 and 1983 (Table 3- polychaete/ bivalve = .76 and .29 respectively) when settlement of tailings was most intense, and the increase in relative dominance of polychaetes in 1986 and 1989 (ratio =.92 and 1.4 respectively). This is in direct contrast to findings from artificial substrates, that polychaetes dominate sterile tailings and natural substrates in the initial stages of undisturbed recolonization, and bivalves increase in dominance over time (for review see Taylor 1986). Abundance and biomass of all taxa declined drastically at those stations in the direct path of the tailings plume. Burling *et al.* (1983) hypothesized that particles with the greatest density would settle out nearest the outfall, with a gradual reduction in particle size and density down-inlet. Furthermore, Reid and Baumann (op. cit.) point out that some burial studies suggest that a change in particle size of settling sediments may have a much more devastating effect on all fauna than tailings of a similar size to that of the natural sediments. Therefore, the effects of deposition at the outermost Alice Arm transect (E) should have been different than at the C and D transects. The decline in numbers at the E transect from 1982 to 1983 was not accompanied by an overall decline in estimated

biomass. Many small polychaete species disappeared in 1983, whereas bivalve abundance increased (see Kathman *et al.* 1984). Based on the results of Reid and Baumann (op. cit.) this pattern suggests that a heavy sedimentation event(s) occurred at the E stations between 1982 and 1983, selectively damaging polychaetes more than bivalves. The faunal decline at the E stations was obviously not of the same character as at the stations nearest the outfall, and was probably related to the settlement of finer tailings particles farther from the outfall.

By 1989, a decline had ocurred in the small fauna of Alice Arm following the apparent recovery observed in 1986. This decline was considerably different in character from that caused in 1982 and 1983 by faunal burial from tailings deposition and movement, which resulted in low polychaete abundance relative to bivalves (Table 3). The relative polychaete to bivalve ratio actually increased from 1986 to 1989.

Reimer's (1989) core samples suggested no unusually high sedimentation rates from 1985 to 1987. Presumably, mixed tailings and natural sediment layers would be evident in the event of a later resuspension of tailings. However, during the 1989 survey of Alice Arm, a recent slump of trees and material from the steep walls of the fjord was noted adjacent to the south end of the D transect. A single fjord wall slump in Kitimat Arm, B.C. was documented to cover over 5 km of the bottom with a thickness of 10m at the leading edge (Prior *et al.* 1984), and was still active 11 years after it began. If the wall slump observed in Alice Arm, or some other factor introduced sufficient energy into the system, the unstable tailings and any sediment on the bottom may have been resuspended, causing widespread faunal effects. It is also possible that the 1989 decline in faunal abundance but not biomass may have been part of a natural successional change in the community. The information from this study is insufficient to do more than speculate on this issue.

D. SUMMARY

Results of both the abundance and biomass-weighted Sigtree analyses confirm and clearly delineate the spatial and temporal extent of

defaunation caused by mine tailings deposition, and suggest a somewhat different pattern caused by natural sedimentation events. Since there were no known anthropogenic factors affecting Hastings Arm during this period, and high sedimentation events have been observed in this inlet, the faunal pattern supports the hypothesis that heavy sedimentation tends to affect overall abundance but not biomass, partially by selectively decimating the small polychaete fauna and greatly reducing the polychaete to bivalve ratio (1983 and 1989). This represents the first "natural sedimentation" effect.

Faunal declines in the Alice Arm stations closest to the outfall in 1982 and 1983 were drastic for all taxa, decimating abundance and biomass values. This represents the second "tailings" effect. Conversely, the stations farthest from the outfall (transect E) seemed to show a selective decline in polychaetes relative to bivalves with little change in mean station biomass values, a pattern similar to that observed in the Hastings stations and referred to as the "natural sedimentation" effect. In the outer Alice Arm stations, the sedimentation was not natural, but produced a similar faunal impact.

The relatively high abundance values at stations in 1986 suggested that recovery was complete in Alice Arm, yet closer examination of species composition and estimated biomass of stations showed that the assemblage resembled a recolonization phase. Furthermore, in the three originally defaunated stations nearest the outfall, a long-term "residual" signature effect of the tailings was statistically distinct four years after cessation of tailings deposition. The 1989 abundance values in Alice Arm had declined considerably from 1986, and the Sigtree abundance analysis showed that faunal composition was significantly distinct ($p \leq 5\%$) between the two years. In contrast, estimated biomass values of stations and the biomass-weighted Sigtree analysis showed that there was no difference in faunal patterns between the two years. Superficially, this pattern resembled the natural sedimentation effect. However, in contrast to the effects of natural sedimentation, the polychaete to bivalve ratio in Alice Arm in 1989 increased from that in 1986. Therefore, the 1989 Alice Arm fauna was suggestive not of an assemblage impoverished in polychaetes, but rather a successionally

distinct one. This represents the third effect which I refer to as succesional.

Therefore, at least three types of faunal changes are postulated to have occurred in Alice Arm and Hastings Arm during the survey period. The most drastic change occurred as a result of direct tailings deposition, which decimated all fauna regardless of size. The sorted, less dense tailings which settled furthest from the source seemed to produce an effect similar to that of natural sedimentation, in that it selectively impoverished the smaller, less resistant polychaetes, reducing mean abundance per station, but not affecting biomass of stations. The third effect was distinct from the two depositional types described in that there was no major change in the polychaete to bivalve ratio or estimated biomass values, but a substantial change in overall abundance.

Although the descriptions of the aformentioned three faunal patterns are speculative, the comparative use of both abundance and biomass-weighted Sigtree analyses illustrates structural patterns within the Alice Arm and Hastings Arm fauna which would not be clearly evident using either approach individually. The numerical and biomass summary statistics alone hint at these patterns, but do not show significant similarities and differences in patterns of large and small fauna from year to year.

CHAPTER 4: HECATE STRAIT

A. INTRODUCTION

The Hecate Strait surveys represent a study which spans less than a year, but incorporates data collected in three different seasons. The Hecate Strait surveys were done to characterize benthic communities in several discrete fishing areas identified by fisheries researchers at the Pacific Biological Station, Nanaimo, B.C. Since the fish are present in these different areas in varying abundances seasonally, the benthos had to be sampled seasonally as well. The Hecate Strait benthic faunal study was therefore conducted as part of an interdisciplinary research project aimed at examining fisheries productivity in the area (see Tyler 1989). Abundance data are in Burd and Brinkhurst (1987) included in the back cover of this thesis.

Hecate Strait is a coastal strait separating the Queen Charlotte Islands from Mainland central B.C. The survey area has high current activity and frequent storms. The bottom is subject to high turbulence and strong currents (Crawford and Thomson 1991), particularly in shallow areas, where there is no thermocline and the entire water column is mixed year-round (AXYS 1991). The Strait is approximately 240 Km long by 110 km wide.

Hecate Strait is an important fishing area for benthic and pelagic fish, and contains spawning and nursery habitat for various commercial species. The bottom fishery takes place in selected areas and produces about 8000 to 12000 tonnes of mixed species landed annually (Fargo and Tyler 1991a). Research has been conducted on models for larval fish retention patterns in Hecate Strait (see Crawford *et al.* 1990), which suggest that the strong northward currents in winter (at the time of bottom fish spawning) would sweep many larval forms out of the Strait, but that a mid-strait southern current probably acts to retain some proportion of them. These patterns should pertain to some extent to benthic invertebrate larval forms as well.

Three benthic surveys were conducted from June 7-17, 1985 (cruise 1), Sept 23-Oct 4 1985 (cruise 2) and Jan. 27- Feb. 8, 1986 (cruise 3), in

conjunction with groundfish trawl surveys by personnel at the Pacific Biological Station. Three sample areas were initially selected by PBS personnel (areas A,B,C, Fig. 9) to include three previously identified fish species assemblage areas (Tyler 1986). Later a fourth area was added because the substrate of the third area was difficult to sample. The sampling pattern within each area is illustrated in Fig. 10. Five sample replicates were taken at stations 1 and 7 in each area, and only one replicate was taken at stations 2 to 6. Based on results of the initial data analyses in Burd and Brinkhurst (1987), stations 2 to 6 were combined as replicates to form one station (renamed station "2"). To avoid confusion, station 7 in each area was renamed station 3. Therefore a total of 5 replicates were analysed for each of three stations in three areas in cruise 1 and four areas in cruises 2 and 3. The stations were named as follows: H1C3 indicates H=Hecate Strait; 1=cruise 1; C=area C; 3=station 3, (formerly station 7 - see above).

Environmental characteristics are summarized along with all other survey areas in Appendix 1. Area A was located at the extreme north end of the survey, with B located more centrally and C and D quite close together at the south end of the survey location (Fig. 9). In general, area B had the highest sand and gravel contents in the sediments. In some stations of area B, much of the substrate was shell fragment. Area D had similar sediments to Area B, with finer sandy silt sediments in some replicates. Areas A and C had the highest silt content, with little gravel evident in Cruise 1, but more in cruises 2 and 3. Area A had more consistently fine sandy-silt sediments than area C, which had the most variable sediments of all areas. Area A had the deepest stations sampled during the Hecate Strait surveys, varying from 124-166 m. Area B had the shallowest depths (25-36 m). Area C depths were shallower than area A (78-148 m). Area D depths were intermediate between B and C (60-98 m).

B. RESULTS

1. Summary Statistics

Both abundance and biomass values ranged from 28 to 386 individuals per 0.1 m^2 and 1.3 to 5.2 g wet weight/0.1 m^2 respectively (Table 4). Unusually low biomass values were evident in station H1C3, and areas H2D and H3A. Abundance values were low in H1C3 and 2 of the 15 stations from H2D, but not in H3A. Species number per station also varied considerably. Generally, there were fewer species in area B stations than in stations from other areas. Low abundance stations also tended to have low numbers of species, but this was not consistent.

The relative abundances of the major taxonomic groups are given in Table 5. Abundance values have been presented separately for each area (A-D) and cruise. Polychaete abundance was high in areas A,B and C and lowest in D. Bivalves were the second most abundant taxa in areas A and C, area B from cruise 2 and area D from cruise 3, but were completely absent in area D from cruise 2. Bivalves were the predominant taxa in area B in two of the three cruises. The remaining taxa had relatively low abundance. Scaphopods were included in the summary statistics for Hecate Strait only, because of their high abundance in area C in 2 cruises, compared to the rest of the surveys in the thesis.

The most abundant species in area A in all cruises included the polychaetes *Lumbrineris luti*, *Prionospio steenstrupi*, *Spiophanes berkleyorum*, *Galathowenia oculata*, *Euclymene zonalis* and *Owenia fusiformis*. *Decamastus gracilis* was common in cruises 2 and 3 only, and *Polycirrus complex* was abundant in cruises 1 and 3. The bivalve *Axinopsida serricata* and the amphipod *Ampelisca macrocephala* were also common in all cruises. Biomass dominants in area A were the bivalves *Yoldia amygdalea*, *Macoma lipara*, *M. elimata* and *Axinopsida serricata*. Several polychaete species were also important in terms of biomass. These included *Artacama coniferi*, *Sternaspis scutata*, *Pista cristata* and *Glycera capitata*. The ophiuroids *Ophiura sarsi* and *O. leutkeni* also contributed a considerable portion to the estimated biomass in samples from area A.

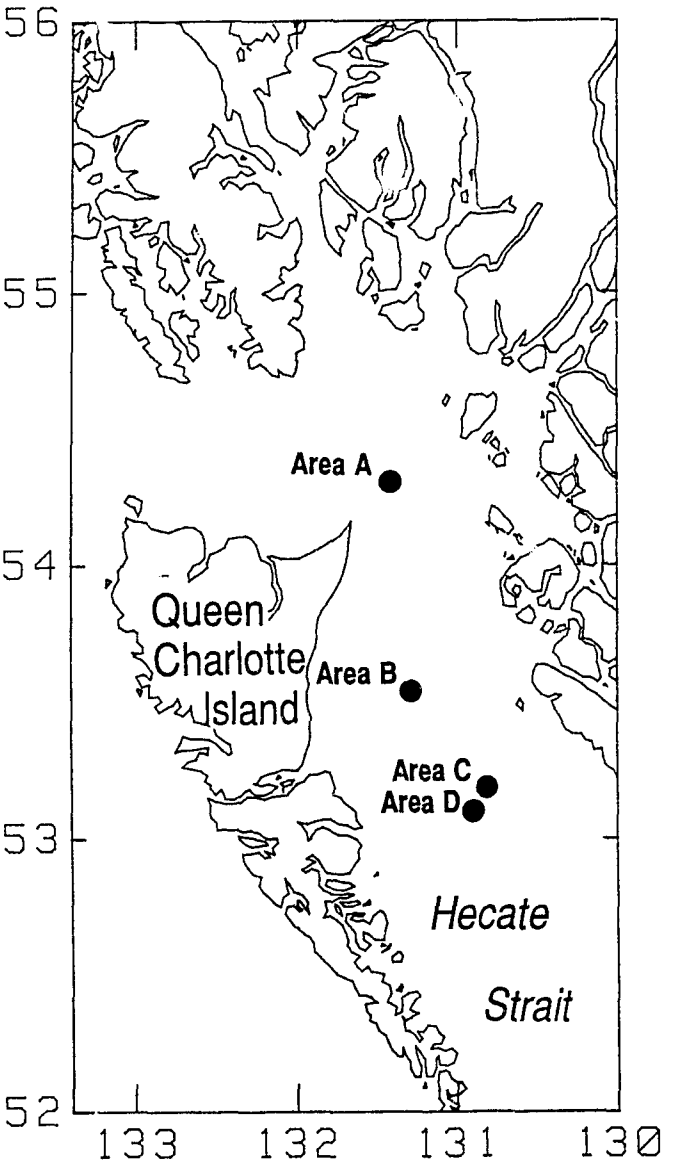

Figure 9. Map of sample areas in Hecate Strait. Areas A,B,C were sampled in all three cruises, and area D was sampled in the second and third cruise.

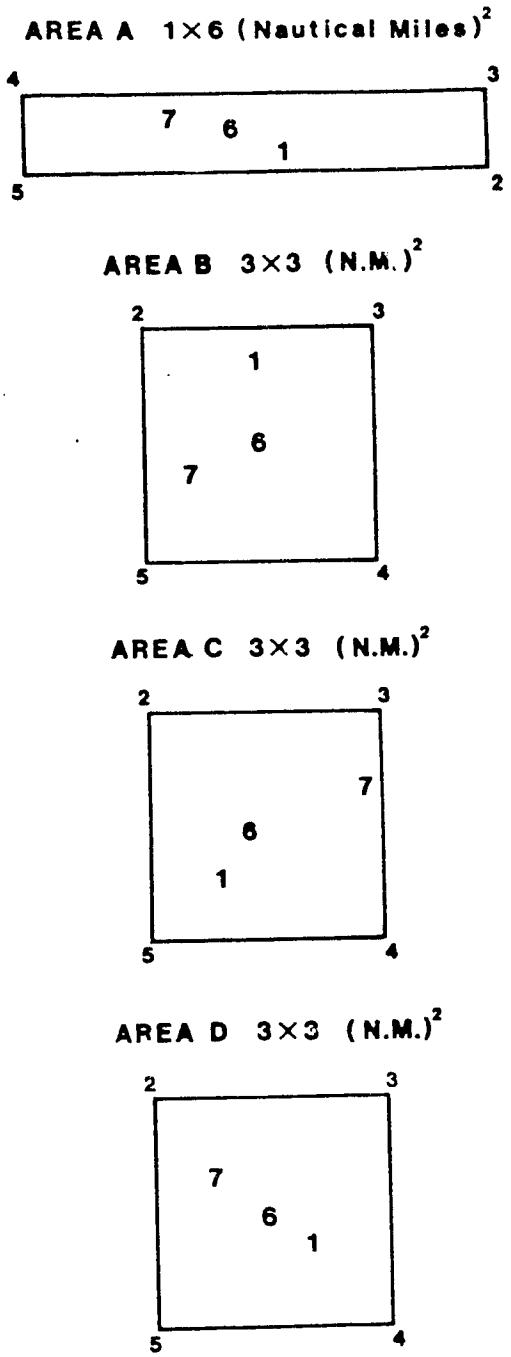

Figure 10. Diagram of sampling pattern within each area of Hecate Strait (from Burd and Brinkhurst 1987). The original pattern included a total of seven stations per area, with 5 replicates for stations 1 and 7 and 1 replicate each for stations 2 to 6. For statistical analyses, stations 2 to 6 were combined as replicates and renamed station "2" in each area. Station 7 on this figure has therefore been renamed "3" for subsequent analyses.

Table 4. Mean biomass (wet weight g/0.1 m^2), mean abundance (No/0.1 m^2) and total number of species for all grabs in each station from Hecate Strait. Values were calculated from 5 replicates per station.

	Cruise 1			Cruise 2			Cruise 3		
	Mean g/.1m^2	Mean No/.1m^2	Total Taxa	Mean g/.1m^2	Mean No/.1m^2	Total Taxa	Mean g/.1m2	Mean No/.1m2	Total Taxa
H1A1	5.23	228	78	H2A1	3.67	305	71	H3A1	0.74	253	71
H1A2	2.60	141	63	H2A2	3.65	248	72	H3A2	0.53	142	58
H1A3	2.76	137	61	H2A3	4.85	345	88	H3A3	0.29	172	56
H1B1	3.58	278	33	H2B1	2.27	351	32	H3B1	0.71	250	18
H1B2	1.59	298	31	H2B2	2.80	387	53	H3B2	2.17	386	38
H1B3	1.84	208	31	H2B3	2.47	436	33	H3B3	2.22	362	27
H1C1	3.63	215	93	H2C1	4.49	308	88	H3C1	4.38	298	75
H1C2	2.60	179	105	H2C2	3.92	219	74	H3C2	2.90	158	96
H1C3	0.73	28	33	H2C3	1.51	132	74	H3C3	1.45	122	68
				H2D1	0.0	53	40	H3D1	1.32	80	51
				H2D2	0.14	126	80	H3D2	3.36	195	113
				H2D3	0.04	35	32	H3D3	1.26	82	35

Table 5. Total abundance (Number/ m^2) for various taxonomic groups in the Hecate Strait samples. Values were presented separately for each survey area and time (cruises = 1,2,3; areas = A,B,C,D). Poly/Biv = ratio of polychaetes to bivalves.

Abundance (No/ m^2)

	H1A	H2A	H3A	H1B	H2B	H3B
Polychaeta	817	1713	1388	727	2103	940
Gastropoda	27	69	25	17	17	23
Scaphopoda	12	29	6	1	3	1
Bivalvia	621	818	301	1711	1431	2105
Echinodermata	35	73	19	45	73	145
Crustacea	95	207	39	91	93	59
Poly/Biv	1.3	2.1	4.6	.42	1.5	.45

Abundance (No/ m^2)

	H1C	H2C	H3C	H2D	H3D
Polychaeta	790	1181	1317	440	419
Gastropoda	42	53	23	33	51
Scaphopoda	13	105	69	14	7
Bivalvia	351	573	327	0	311
Echinodermata	10	47	27	3	15
Crustacea	103	85	85	81	173
Poly/Biv	2.3	2.1	4.0	N/A	1.3

The most abundant species in area B in all cruises was the bivalve *Tellina nuculoides*. Other abundant species included the polychaetes *Spiophanes bombyx* and *Hemipodus borealis*, the amphipod *Foxiphalus obtusidens*, and the echinoid *Dendraster excentricus*. All of these species except *Hemipodus borealis* were also biomass dominants. Other biomass dominants included the gastropod *Olivella baetica*, the barnacle *Balanus crenatus*, the bivalves *Spisula falcata* and *Ciliatocardium ciliatum*, and the polychaetes *Ophelina acuminata* and *Nephtys californiensis*.

In Area C the abundant species included a number of species also common in A, such as the polychaetes *Owenia fusiformis*, *Galathowenia oculata*, *Euclymene zonalis* and *Spiochaetopterus costarum*, and the amphipod *Ampelisca macrocephala*. Other abundant species included the scaphopod *Pulsellum salishorum*, and the ophiuroid *Amphioplus strongyloplax*. A number of the biomass dominants in C were the same as in area A, including *Ophiura leutkeni*, *Axinopsida serricata*, *Glycera capitata* and *Pista cristata* (see above). Biomass dominants common only in area C included the bivalves *Nemocardium centrifilosum*, *Psephidia lordi*, *Nucula tenuis* and *Tellina carpenteri*, the gastropod *Solariella peramabilis*, the polychaetes *Terebellides stroemi*, *Notoproctus pacificus*, *Ampharete finmarchica*, *Pista brevibranchiata* and *Galathowenia oculata* and the crustacean *Pandora bilirata*.

Abundance was low overall in area D in cruise 2. Common species in area D in cruise 3 included the bivalves *Psephidia lordi* and *Axinopsida serricata*, the polychaetes *Owenia fusiformis* and *Galathowenia oculata*. The polychaete *Spiophanes bombyx* and the amphipod *Foxiphalus obtusidens* were common in both cruises 2 and 3. The latter two species were also common in area B (see above). Area D had several biomass dominant species in common with its near neighbour, area C. These included *Ophiura leutkeni*, *Tellina carpenteri*, *Pandora bilirata*, *Axinopsida serricata* and *Pista brevibranchiata* (several of these were also biomass dominants in A area). Several biomass dominants were common to both B and D areas, including the gastropod *Olivella baetica*, the polychaete *Spiophanes bombyx* and the amphipod *Foxiphalus obtusidens*. Those species which were biomass dominants only in area D included the gastropod

Amphissa columbiana, the brachiopod *Laqueus californiensis* and the crustacean *Argis alaskensis*.

2. Statistical Analyses

The Sigtree analyses for Hecate Strait are assumed to have high statistical power, since 5 replicates per station were used (see Chapter 2 section F). Therefore, a probability of less than 1% was used to designate significant differences among groups. As discussed in chapter 1 section A1, the abundance analysis emphasized abundant (often small) fauna, whereas the biomass-weighted analysis emphasized large (often rare) fauna.

The Sigtree analysis of raw abundance data shows that most stations from a given area tended to group together spatially and temporally (Fig. 11). Areas A and C were most similar to each other, followed by area D. Area B was very dissimilar to the other areas. The Sigtree analysis produced two significant groups plus one singleton from area A stations. Additionally, there were three significant groups of C stations, 3 groups of D stations and 1 group of B stations. Each area was significantly distinct from the others at $p \leq .0001$. H1C3 was significantly distinct from all other stations.

The biomass-weighted abundance analysis also showed that the stations within a given area tended to group together over time and space (Fig. 12), with several important exceptions. As in the abundance analysis, area A stations from cruises 1 and 2 formed two significantly distinct groups. The A stations were significantly distinct from, but most similar to area C. The C stations formed one homogeneous group, except for station H1C3, which was significantly distinct from all other stations, and had particularly low estimated biomass and abundance.

There were some notable differences between the two Sigtree analyses. In the biomass-weighted analysis, station C3 was distinctive in all three cruises. Stations H2C3 and H3C3 were distinct from the other C stations at p=1.2% (Fig. 12 - not considered significant in this analysis, but a low probability nevertheless). Area A from cruise 3 formed a significantly distinct group separate from all the other A,C

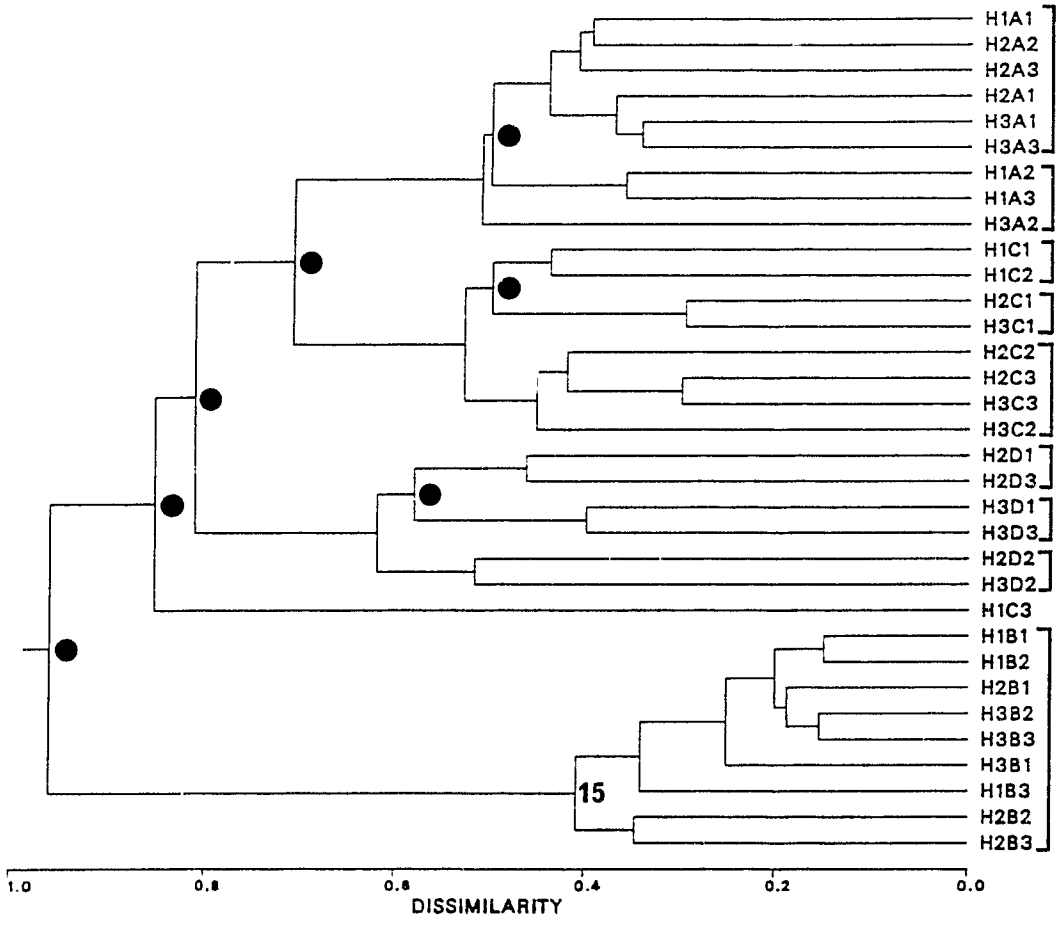

Figure 11. Cluster dendrogram for raw abundance data from Hecate Strait. Significances at the 1% level are indicated by the large dot. Linkage 15, which was significant in the Comtrel analysis, is indicated on the dendrogram.

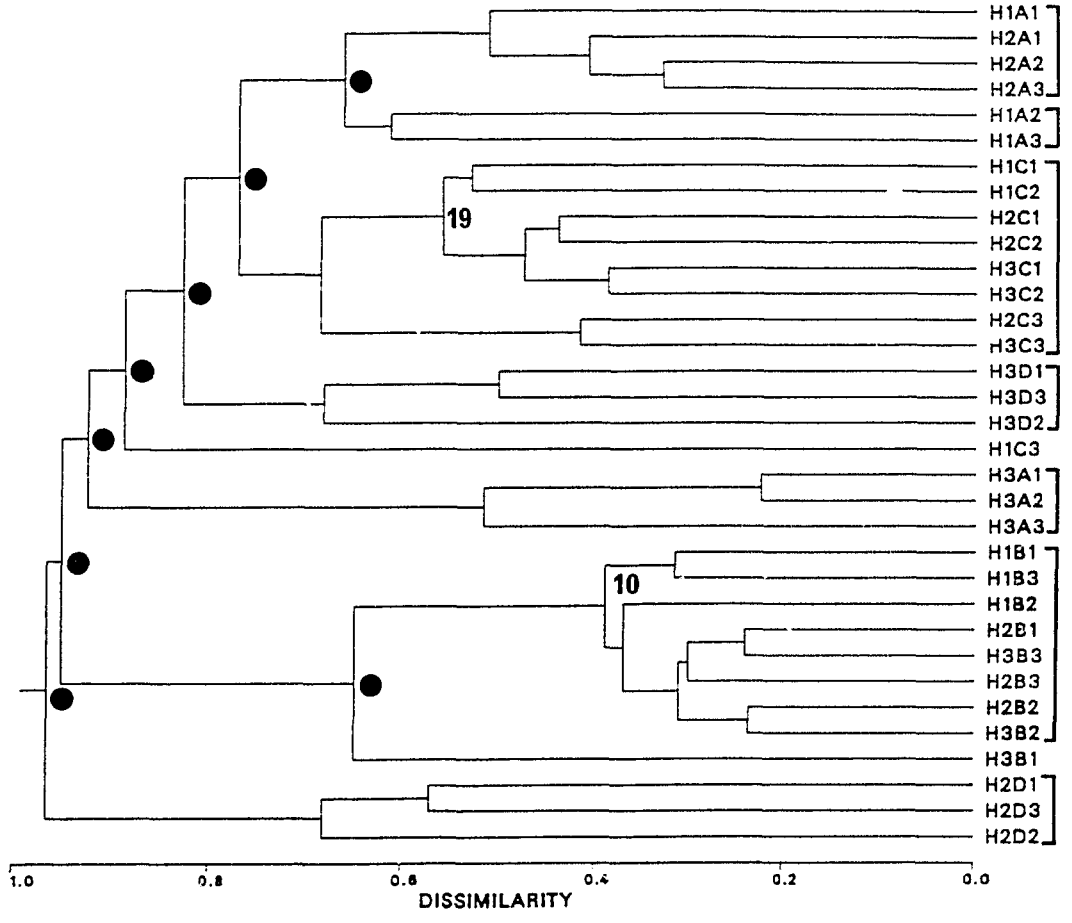

Figure 12. Cluster dendrogram for biomass weighted abundance data from Hecate Strait. Significances at the 1% level are indicated by the large dot. Linkages 10 and 19, which were significant in the Comtrel analysis, are indicated on the dendrogram.

and D stations, due to very low biomass (but not abundance). Area B stations grouped together and were significantly distinct from all other areas. However, station H3B1, which was characterized by low biomass and high abundance values relative to the other B stations, was significantly distinct from the remaining B stations. Finally, the area D stations from cruise 2 formed a significantly distinct group, highly dissimilar to all the other Hecate stations. This area was characterized by very low biomass and moderate abundance values, and was completely devoid of bivalves.

The Comtre2 analysis tested the null hypothesis that the two faunal dendrograms (abundance versus biomass-weighted) were the same at any given linkage level. The hypothesis that the two dendrograms were the same could not be rejected at any linkage (Appendix 3d).

3. Environmental comparison

The environmental dendrogram (Fig. 13) shows that areas A and C were generally indistinguishable from each other in terms of depth, substrate type and location. Area D was distinct from A and C but was more similar to these two areas than to B. Area B was very different in terms of environmental character from all other survey areas.

The Comtre1 comparison of the raw abundance and biomass-weighted abundance dendrograms with the environmental dendrogram showed that the environmental factors measured had little effect on species composition of either small or large fauna. The hypothesis that the two dendrograms were different could be rejected at linkage 15 in the raw abundance dendrogram (Appendix 3e) and linkages 10 and 19 in the biomass-weighted dendrogram (Appendix 3f). The pertinent linkage levels are marked on Figs. 11,12 and 13. The significant linkages partially reflect the close grouping of the B area stations in both the environmental and faunal patterns. Both faunal patterns agree on the distinct nature of the A and C stations, whereas the environmental pattern shows the stations from those areas intermixed. The environmental and faunal patterns all agree on the distinct nature of area D.

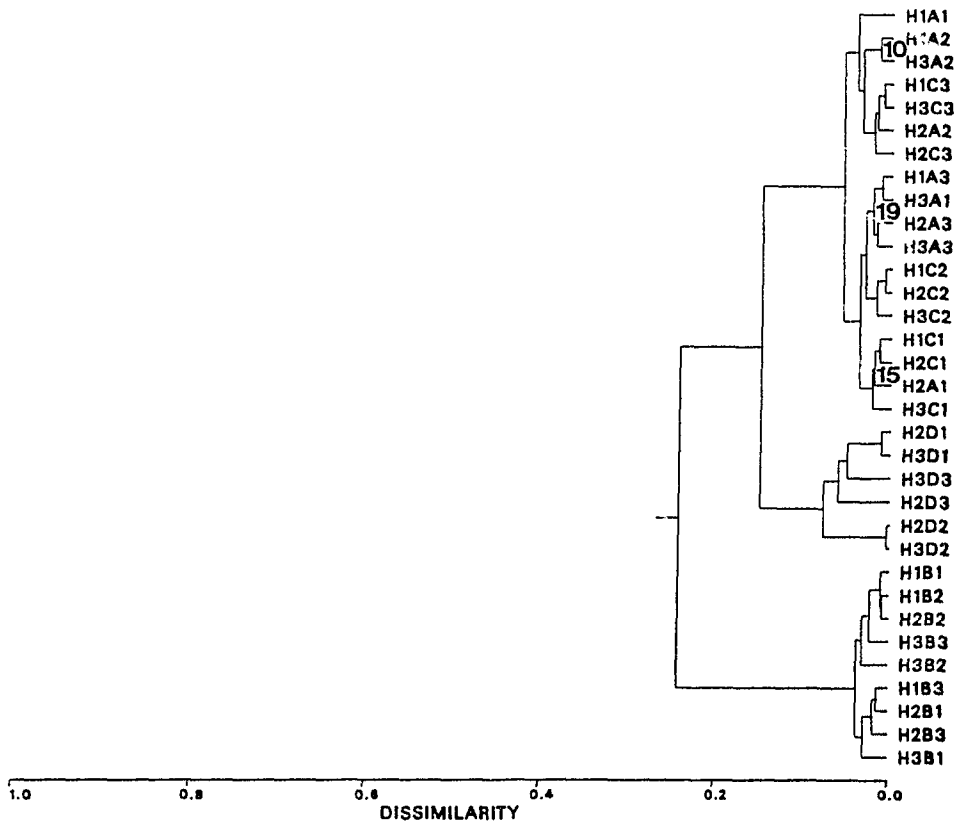

Figure 13. Environmental cluster dendrogram for Hecate Strait. Variables include depth, percent silt/clay, percent sand and geographic location. Linkages 10, 15 and 19, which were significant in the Comtrel analyses with the faunal dendrograms (Figs 11,12) are indicated on the dendrogram.

C. DISCUSSION

As expected from the benthic fish assemblage pattern determined prior to the Hecate Strait benthic study (Tyler 1986), the four sample areas all contained distinct faunal assemblages. However, based on Fargo and Tyler (1991a,b), only three distinct fish assemblages were recognized in the survey area, delimited partially by depth differences. Area A falls within the boundaries of the "Butterworth" assemblage, B in the "Reef Island" assemblage and C in the "Bonilla" assemblage. Fargo and Tyler (1991a) describe the fish species composition of these three areas. Area D falls on the boundary of the B and C assemblages, and might therefore be expected to display characteristics of both. Area D was also intermediate between C and B in terms of location and depth. Similarly, Fargo and Tyler (1991a) indicate that one of the major groundfish species, Rock Sole, occured with equal frequency in both areas B and D.

According to both the abundance and biomass-weighted abundance cluster patterns for Hecate Strait, area D was more similar to A and C than to B. However, the faunal assemblage of area D was significantly distinct from all other areas. Area D may in fact represent an intermediate position along a spectrum of faunal compositions in which B represents one extreme, and A represents another.

In this survey, the faunal composition of area B was characterized by a shallow subtidal, high energy, coarse substrate assemblage, consisting of suspension-feeding or scavenging species and mobile crustaceans, with no tube builders and few burrowers (for similar examples in Puget Sound, see the "exposed, unconsolidated sediment assemblage" DOC-EPA report 1982). Both the abundance and biomass-weighted analyses suggest that species composition of area B was unique in Hecate Strait. Biomass, abundance and taxa numbers were not unusual in area B compared to the other areas, despite the presumably lower organic content of sediments in B than in those areas with finer sediments. The mixing of the entire water column and strong current flow virtually all year round would ensure that nutrients from other areas and from the surface are readily available to the benthos in area B. Area B is known as the "shellground" because of the extensive shell debris and bivalve

fauna present. The species analyses suggest that this fauna is dominated numerically and in terms of biomass by the bivalve *Tellina nuculoides*, a species commonly found from Puget Sound in Washington to Alaska in shellground substrates (Lie 1969, Shevtsov 1964). Another biomass dominant was the gastropod *Olivella baetica*, which is often found on sheltered sandy beaches as well as subtidal sandy areas (Kozloff 1987) and is a grazing herbivore (Reid, U. Victoria, pers. comm.), thus suggesting that area B was shallow enough to permit algal growth. By contrast, areas A and C contained two distinct assemblages which had numerous polychaete species and burrowing or deposit feeding bivalves and burrowing ophiuroids. Current model patterns (Crawford *et al.* 1988, 1990) suggest that current speeds were low over both areas in winter and summer. Area D had environmental characteristics and species composition distinct from, but most similar to A and C. Areas B and D shared some biomass dominant species (such as *Olivella baetica*), and in the biomass-weighted comparison of all survey areas and times (see Chapter 9), areas B and D were most similar to each other. In the Hecate Strait analyses presented in this chapter, the faunal composition of area D is marginally more similar to that of areas A and C, rather than B for both small and large fauna.

It is evident from the Hecate Strait survey that low abundance stations may or may not be identifiable in the raw abundance dendrogram, whereas low biomass stations are distinct in the biomass-weighted dendrogram. Both analyses pinpointed the unusual paucity of animals of all sizes, and the significant distinction ($p \leq 1\%$) of station H1C3. However, only the biomass-weighted analysis suggested that C3 was unusual in all three years. The environmental data do not suggest any reason for the unusual nature of this station, except that it was the deepest station (148 m) in area C. The consistency of the result over time suggests that C3 faunal composition was affected by some factor which did not appear and disappear seasonally or over the time span of the 3 surveys.

The biomass-weighted analysis also clearly delineated the unusual features of area D in cruise 2 and area A in cruise 3 whereas the raw abundance analysis did not. Since this pattern occurred consistently in

15 replicates from each of the two areas, it is not incidental. However, the complete lack of bivalves from station H2D is very suspicious. In retracing the original taxonomic reports and data sets (prepared by EVS consultants in 1986), no record of the bivalves from cruise 2 can be found. A query to the taxonomic authority (Dr. R. Reid, U. Victoria) who originally identified the Hecate bivalves, and to the person originally in charge of the processing of samples by taxonomists did not succeed in solving the mystery of the missing bivalves. However, rough sort material and wet weights summarized in Burd and Brinkhurst (1987) suggest that there was a low biomass of bivalves present in area H2D. In fact, wet weights were low overall for this area, as in H3A. Regardless of the fate of the missing bivalves, the omission points out an important functional difference in the behaviour of the abundance versus the biomass-weighted cluster analysis. The abundance analysis provided no clue as to the unusual nature of either of the two biomass-impoverished areas, H2D and H3A. The stations from the aforementioned low biomass areas did cluster with stations from the same area in the raw abundance dendrogram, suggesting that the distribution of small species was not unusual. These two areas did not cluster with the other stations in the same areas, based on a paucity of the larger species. In area D, species which were abundant in cruise 3, such as the large gastropod *Olivella baetica* and the ophiuroid *Ophiura leutkeni*, were low in abundance and absent respectively in cruise 2. The species lacking in H3A were mainly the larger bivalves (*Yoldia, Macoma, Lucina*), large polychaetes (*Sternaspis scutata, Aratacama coniferi*) and the ophiuroid *Ophiura sarsi*. There are several possible reasons for the declines in large fauna, which are not evident from the surveys, but may be deduced in future from fish survey or stomach content data analysed by PBS personnel. Size related predation may be a factor, particularly for fish species which migrate or reproduce seasonally. The low bivalve abundance may also reflect the fact that flatfish such as English sole (*Parophyrs vetulus*) generally have 80-90% bivalves in their stomach contents, and can thus be considered very selective feeders (Reid, U. Victoria, unpublished data). As well, Fargo and Tyler (1991a), indicated that Big Skate (*Raja binoculata*) was found mainly in area A in winter, which may partially

account for the faunal decline in large benthic fauna in area H3A. Sediment disturbance is not likely the cause of the faunal decline in H3A since the small fauna were unaffected.

A dendrogram based on total wet weights for major taxonomic groups was produced during original data analyses (see Burd and Brinkhurst 1987). However, the cluster patterns showed all stations from all areas mixed together, illustrating that this type of data reduction produces poor discrimination of faunal patterns.

The Comtrel analyses suggest that the cluster pattern based on the combination of the three environmental factors did not explain the patterns of faunal composition. However, the environmental pattern did agree with both faunal patterns on the distinct nature of both areas B and D, and on the fact that D was more similar to AC than to B. The major difference between the faunal and environmental patterns was that the latter showed the A and C stations intermixed. Although there was considerable overlap in dominant species between areas A and C, these areas were significantly distinct from each other in terms of both abundance and biomass-weighted abundance analyses, and therefore in terms of small and large fauna. Faunal compositions of Areas A and C may be different because of the geographic distance between them and differences in larval recruitment based on circulation patterns in Hecate Strait (c.f. Crawford and Greisman 1987, Crawford *et al.* 1988). Based on a current model developed by C. Hannah (PhD thesis, University of British Columbia, in progress), many of the pelagic larval forms of the benthic fauna in area A in late winter through early summer may be swept east or west out of Hecate Strait. Alternatively, some larval forms in the Strait in late spring would be swept northward from area C up to the vicinity of area A.

Other than the mixing together of areas A and C stations based on faunal composition and the unusual nature of the low abundance station H1C3, the environmental pattern resembled the abundance cluster pattern. On the other hand, the environmental pattern was quite different from the biomass-weighted pattern, which emphasized the distribution of large fauna, and showed the A and D areas split apart based on widely disparate overall biomass values for different cruises. Despite this, the Comtrel

analyses suggested that the environmental pattern was more closely related to the biomass-weighted pattern than to the abundance pattern.

In summary, the biomass-weighted Sigtree analysis clearly showed a defaunation in the large fauna of two separate areas and times, which was not evident in the raw abundance pattern or the environmental pattern and could have an important effect on available food for bottom fish.

CHAPTER 5: SHELF STUDY

A. INTRODUCTION

The shelf surveys were conducted on the contintental shelf off the south-west coast of Vancouver Island. The shelf stations were sampled using the largest grab ($0.25m^2$) of all the survey areas, and the smallest screen mesh (0.25mm - used to process about 1/2 of each replicate sample). The shelf data therefore included some very small small macrofauna and meiofauna in the dataset and analyses, which were expected to dominate the abundance analysis but be ignored in the biomass-weighted analysis. Therefore, it was expected that the results of the raw abundance and biomass-weighted abundance Sigtree analyses would be very different if the small and large fauna responded differently to environmental conditions on the shelf.

This study was originally conducted to provide information on the distribution of macrobenthic infauna from the southwest coast of Vancouver Island, to complement oceanographic and sediment character studies of the area conducted by the Institute of Ocean Sciences and the Pacific Geoscience Center, Sidney, British Columbia. The combined studies were an effort to define and predict fisheries productivity in the area and link pelagic and benthic productivity. The original data for the benthic surveys was reported in O'Connell *et al.* (1983a,b), and again in revised form in Brinkhurst (1987 - in back cover of thesis).

Results of oceanographic studies (Denman *et al.* 1981, Freeland and Denman 1982, Mackas *et al.* 1980) indicate that the shelf off Barklay Sound is a highly productive area, maintained by two water masses: (a) a seaward moving mass of estuarine water from the Juan de Fuca Strait; and b) the upwelling California Undercurrent. The low oxygen, nutrient-rich California Undercurrent is deflected northwest along the continental margin, particularly in the region of the Juan de Fuca Canyon. This upwelling water is entrained into the seaward moving estuarine waters from Juan de Fuca strait in the southeast corner of Vancouver Island, which is also a region of high tidal mixing. The entrained, high-nutrient source moves along the shoreline, in a band some 65 km long and

approximately 20 km wide. Sampling areas were selected based on the aforementioned productivity patterns (Fig. 14). Stations in areas A and B were sampled because they were thought to be located under the nearshore Juan de Fuca front. Stations in area C were supposed to lie in the area outside the influence of the estuarine flow from Juan de Fuca.

The California Undercurrent abuts the shelf along its entire margin. This produces a weak upwelling, supplying nutrients to the surface water in the vicinity of outer canyons like Nitinat. This weak upwelling was thought to be responsible for maintaining the offshore front which parallels the 80 m contour some 35 km offshore. Stations in area D were selected because they were located within the influence of the upwelling front. The timing of the two cruises was related to the intrusion of low-oxygen water from the California Uncercurrent over the shelf, which produced bottom oxygen levels below 1.5 mL/L for several weeks in the summer of 1981 (Hill *et al.* 1982a, b). The first cruise took place in April of 1981 soon after predicted beginning of the intrusion. The second cruise was conducted in September 1981, 5 months after the predicted beginning of the intrusion.

Station locations and environmental variables for each sample replicate are listed in Appendix 1. Stations were named as follows: S1A3: S=Shelf; 1=cruise 1; A=area A; 3=station 3. Station locations with the same substrate type were selected, based on sediment chart data produced by the Pacific Geoscience Center, IOS. Despite this caution, two distinct substrate types appeared in the sediment samples, introducing an additional factor for consideration in describing faunal composition.

B. RESULTS

Results of faunal analyses were separated into two categories based on environmental factors (Appendix 1), a fine silt collection (A1-C2) and a fine sand group (C4-D4). Depths were greater in the silty stations than in the sand stations (about 120m versus 160m), and by extrapolation, bottom currents and turbidity were very different in the two areas.

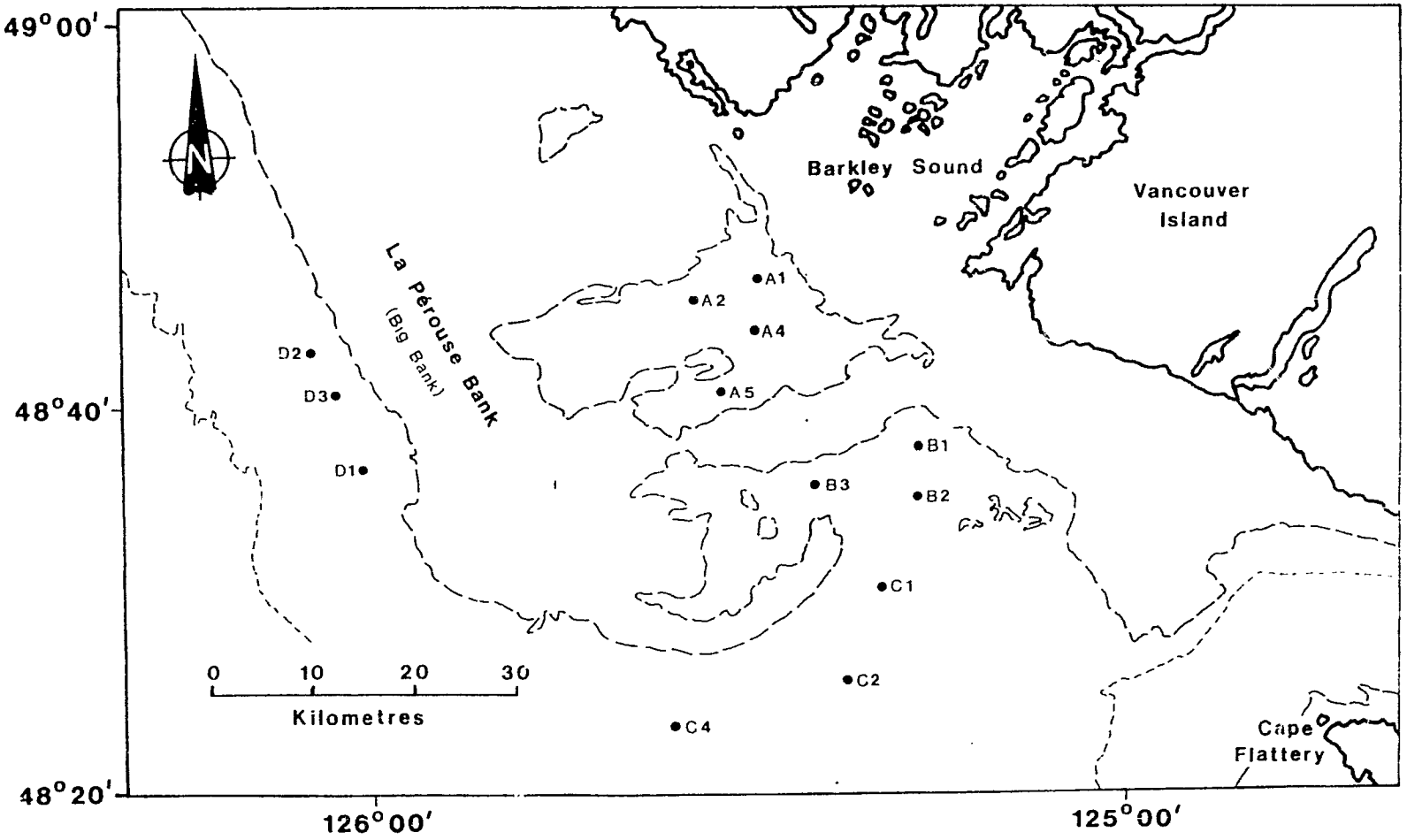

Figure 14. Station locations for the Shelf surveys (from Brinkhurst 1987). The 100 m contour is also shown.

1. Summary Statistics

Total faunal abundance was considerably lower than reported in Brinkhurst (1987) because of the elimination in the analysis of copepods and because some taxonomic groups were not identified to species in one or both cruises. For consistency, all unidentified taxa including ostracods, Aplacophora and nemerteans were eliminated from the dataset. As well, a number of miscellaneous taxa were not identified to species and thus had to be eliminated from the database. It is estimated that faunal eliminations were as high as 30-40% of original abundance.

Mean biomass, abundance and total taxa for each station are summarized in Table 6. No seriously defaunated stations were identified. Values were low at stations C1 and C2 from cruise 1 and at station D4 from cruise 2. In general, the values of biomass, abundance and taxa number were comparable to those for Alice Arm/Hastings Arm (Chapter 3) and Hecate Strait (Chapter 4). As well, biomass, abundance and taxa numbers varied little between cruises despite the difference in season of sampling, except for the decline in all three values at the sandy stations C4,D1,D2 and D4 in the second cruise, and the considerable increase in values at stations C1 and C2 in the second cruise.

The relative contribution of the major taxonomic groups in both the silty (A1-C2) and the sandy (C4-D4) stations for each of the two cruises is summarized in Table 7. Polychaetes predominated in both substrate types, followed by crustaceans and bivalves. Gastropods and echinoderms made up small portions of the total abundance in both sandy and silty stations. Bivalves were the only taxonomic group which did not decrease in abundance in the sandy stations between cruises 1 and 2, whereas crustaceans declined considerably. The abundance of all major groups increased in the silty stations between cruises 1 and 2.

The most abundant species in the silty stations in both cruises included the polychaetes *Galathowenia oculata*, *Levinsenia gracilis*, *Sternaspis scutata*, *Euchone incolor*, *Acesta lopezi*, *Cossura soyeri*, *Spio cirrifera*, *Allia ramosa*, *Prionospio steenstrupi* and *Decamastus gracilis*.

Table 6. Mean biomass (wet weight in g/0.1 m^2), mean abundance (number/0.1 m^2) and total taxa number for all grabs from each station in Barkley Sound, cruises 1 and 2. Values were calculated for two replicates per station.

	Cruise 1 (April/81)				Cruise 2 (Sept/81)		
	Mean Biomass g/.1m^2	Mean Abundance No/.1m^2	Total Taxa		Mean Biomass g/.1m^2	Mean Abundance No/.1m^2	Total Taxa
S1A1	4.13	344	91	S1A1	3.49	251	94
S1A2	3.06	291	83	S1A2	2.97	193	77
S1A4	3.27	287	85	S1A4	3.87	329	94
S1A5	3.13	259	75	S1A5	3.89	453	88
S1B1	3.91	348	95	S1B1	3.55	238	87
S1B2	3.28	247	81	S1B2	3.18	202	71
S1B3	1.77	150	68	S1B3	2.94	230	78
S1C1	1.53	92	63	S1C1	3.24	228	81
S1C2	1.25	97	59	S1C2	2.00	147	67
S1C4	3.19	278	91	S1C4	2.75	208	93
S1D1	3.62	257	115	S1D1	2.55	174	88
S1D2	3.46	229	103	S1D2	3.23	190	91
S1D4	3.76	210	112	S1D4	1.38	120	73

Table 7. Total abundance (number/ m^2) for all stations of major taxonomic groups for shelf cruises 1 (April 1981) and 2 (September 1981). Poly/Biv = ratio of polychaetes to bivalves.

Cruise 1

Abundance (No/ m^2)

Silty Stations A1-C2		Sandy Stations C4-D4	
Polychaeta	1326	Polychaeta	1507
Gastropoda	8	Gastropoda	5
Echinodermata	20	Echinodermata	38
Crustacea	148	Crustacea	350
Bivalvia	120	Bivalvia	313
Poly/Biv	11.1		4.8

Cruise 2

Abundance (No/ m^2)

Silty Stations A1-C2		Sandy Stations C4-D4	
Polychaeta	1582	Polychaeta	1052
Gastropoda	13	Gastropoda	5
Echinodermata	53	Echinodermata	18
Crustacea	190	Crustacea	83
Bivalvia	185	Bivalvia	333
Poly/Biv	8.6		3.2

Abundant crustaceans included the amphipod *Heterophoxus oculatus*, *Eudorella pacifica*, and the bivalves *Adontorhina cyclia* and *Yoldia scissurata*.

The most abundant species in the sandy stations included the polychaetes *Decamastus gracilis*, *Prionospio steenstrupi*, *Galathowenia oculata*, *Exogone lourei*, *Spiophanes berkeleyorum and Sphaerosyllis brandhorsti*, the bivalves *Adontorhina cyclia*, *Huxleyia munita*, *Lampropos triserrata* (cruise 2 only) and the amphipod *Photis pachydaccyla* (cruise 1 only).

Biomass dominants common both to the sandy and the silty stations included the polychaetes *Mediomastus ambiseta*, *Galathowenia oculata*, *Prionospio steenstrupi*, *Allia ramosa* and the bivalves *Axionopsida serricata*, *Adontorhina cyclia*, *Yoldia scissurata*, *Y. thraciaeformis*, *Macoma eliminata and M. carlottensis*. There was a strong commonality in species composition of bivalves between the sandy and silty stations. Biomass dominants found only in silty stations included the polychaetes *Levinsenia gracilis*, *Cossura soyeri*, *Euchone incolor*, *Acesta lopezi* and *Nephtys cornuta*, and the amphipod *Heterophoxus oculatus*. Dominants found only in sandy stations included the polychaetes *Spiophanes berkeleyorum*, *Glycera capitata*, *Sphaerosyllis brandhorsti* and *Tharyx secundus*, and the bivalves *Adontorhina cyclia*, *Huxleyia munita* and *Lampropos serrata* (cruise 2 only).

2. Statistical Analyses

Because a small screen size was used in the shelf surveys, the original faunal abundance values were relatively high (Brinkhurst 1987). The elimination of unidentified taxa in this study resulted in abundance values similar to those in many Hecate Strait stations. Abundance values standardized to $0.1m^2$ were presented in Table 6 to match other studies in this thesis, but the Sigtree analyses for this chapter are based on original abundances per $0.25m^2$. The effects of overall abundance or grab size on the statistical power of the Sigtree and Comtre tests were unknown, so that the appropriate rejection level for tests had to be estimated. A significance level of $p \leq 2\%$ was considered conservative to

reject the null hypothesis in each test and retain reasonable power (for discussion, see chapter 2 section F). The use of a lower probability was not considered reasonable because of the moderate abundance values and the availability of only two replicates per station. As discussed in Chapter 1, section A1, the Sigtree analysis of biomass-weighted data emphasized the large fauna, whereas the abundance analysis tended to emphasize the smaller fauna.

The abundance dendrogram for the combined data from both shelf cruises is shown in Fig. 15. There were no temporal distinctions evident in faunal distribution. Three significant groups of stations were evident at the 2% significance level, along with three singleton stations. The area A and area B silty stations formed one homogeneous group, with the C1 and C2 stations from both cruises forming one significant but non-homogeneous group and one singleton (S2C1). The sandy area D stations formed the final significant and homogeneous group, with each sandy C4 station significantly distinct.

The station pattern in the biomass-weighted analysis (Fig. 16) was slightly different from that of abundance analysis. All silty stations except three formed one significant and homogeneous group. Station S2C1 was significantly distinct from the remaining silty stations at $p \leq 2\%$. Stations S1C1 and S1C2 (the lowest abundance and biomass silty stations) formed a significantly distinct but non-homogeneous ($p \leq 4\%$) group from the remaining silty stations. By extrapolation, the sandy stations formed a significantly distinct but non-homogeneous ($p \leq 7\%$) group. The C4 stations were most similar to each other, but not significantly distinct from the D stations. The dissimilarity between the silty and sandy stations was therefore much less clear in the biomass-weighted analysis than in the raw abundance analysis.

The comparison of raw abundance and biomass-weighted abundance analyses using the method Comtre2 tested the null hypothesis at each linkage level that the two dendrograms were the same (Appendix 3g). There were no rejections at any linkage level and no probabilities below 60% on linkages. Therefore it cannot be concluded that the two dendrograms were different.

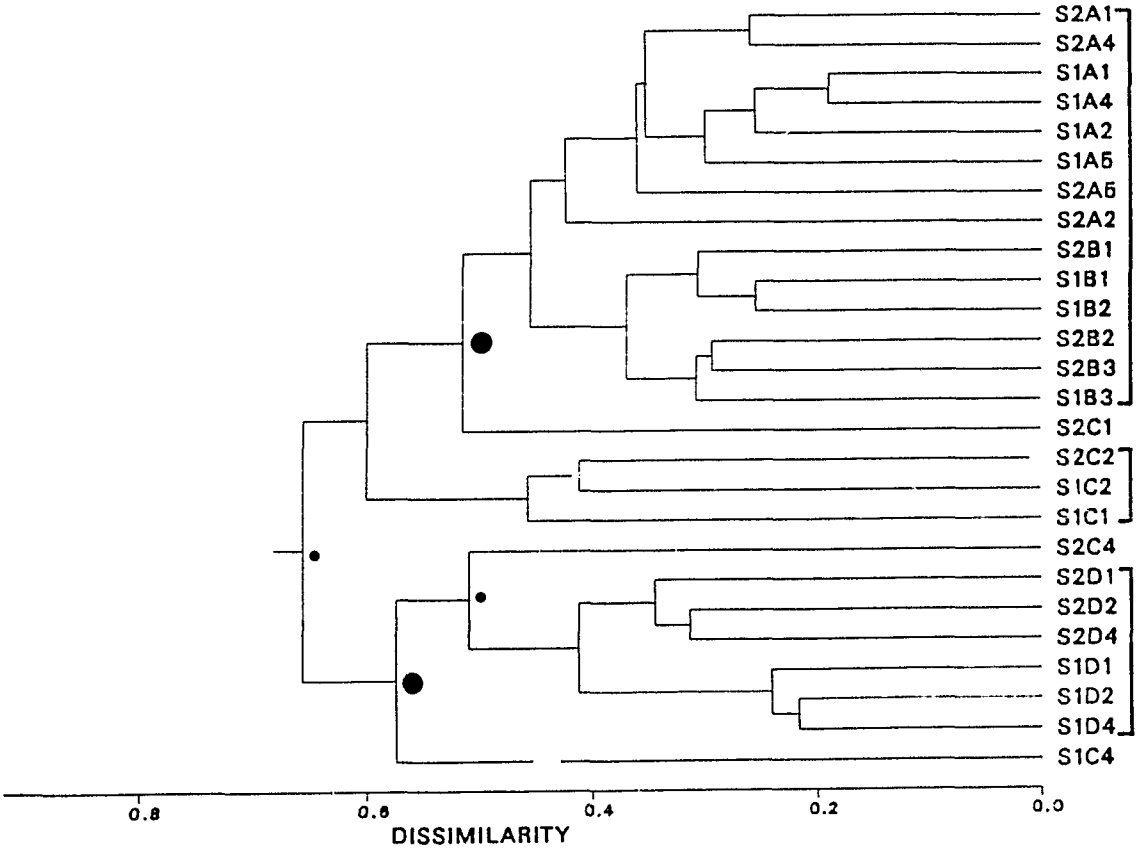

Figure 15. Cluster dendrogram for raw abundance data from the two Shelf surveys. Significances at the 1% level are indicated by the large dot, and at the 2% level by one small dot.

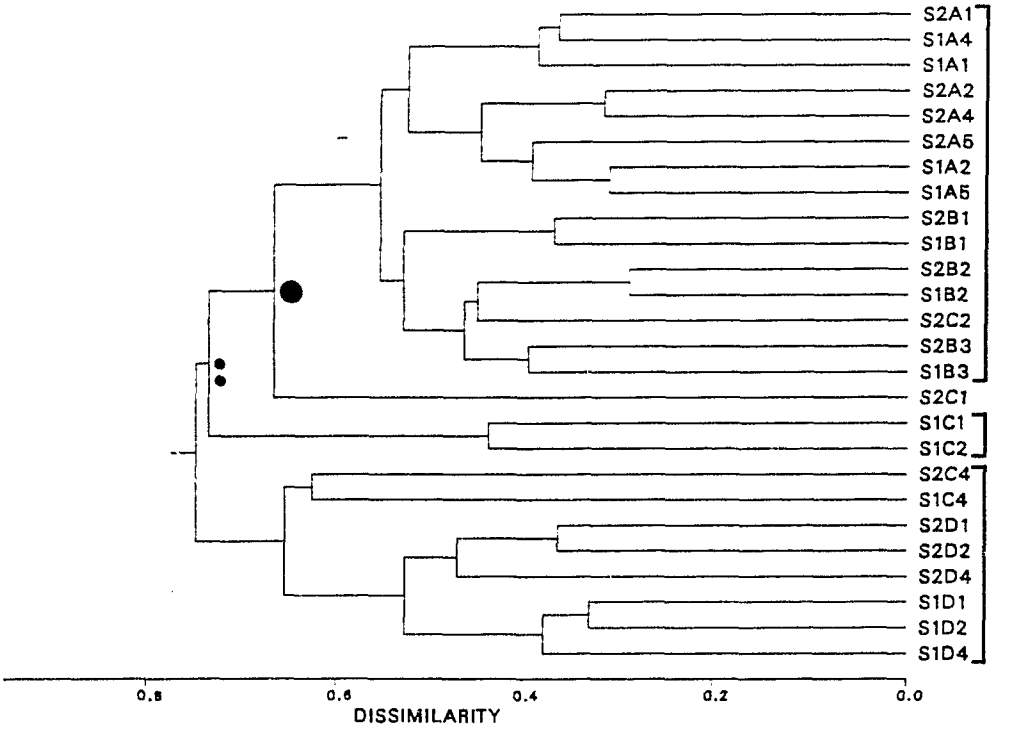

Figure 16. Cluster dendrogram for biomass weighted abundance data from the Shelf surveys. Significances at the 1% level are indicated by the large dot, and at the 2% level by one small dot.

3. Environmental Analyses

The environmental dendrogram (Fig. 17) clearly delineated the two groups of stations subjectively identified before the data analyses. Stations A1 to C2 comprised the silty, deep group, and stations C4 to D4 comprised the sandy, somewhat shallower, group of stations further offshore. The C4 stations from both surveys were somewhat distinct from the D stations. This result matches the pattern in both the raw abundance and biomass-weighted cluster analyses, in which the C4 species composition was fairly distinct from the other sandy stations. Station S1A5 was distinct in the environmental analysis, because it was about 15 m deeper than any surrounding stations (Appendix 1).

The Comtrel comparison of faunal dendrograms with the environmental dendrogram tested the null hypothesis in each case that the 2 dendrograms were different from each other at any given linkage level. The hypothesis was not rejected at $p \leq .025$ for any of the 25 linkages for the raw abundance dendrogram (Appendix 3h) or the biomass-weighted abundance dendrogram (Appendix 3i). Therefore, station patterns based on the measured environmental factors were not related to faunal patterns of small or large species. There were no unusual faunal characteristics in station A5 in cruise 1, despite the fact that it was unusually deep.

C. DISCUSSION

The purpose of this chapter in the thesis was to examine and compare results of small versus large species composition in a set of data collected using a large grab and mixed sieve sizes, and to examine faunal distributions in an open, coastal shelf habitat. The sampling resulted in a dataset with a broad size range in the fauna, as well as two very distinct sediment regimes. Unlike the Alice Arm study (Chapter 3), there is no evidence from the balance of polychaetes to bivalves, that heavy sedimentation events occured on the continental shelf off Barkley Sound. This provided an opportunity to examine the differential effects

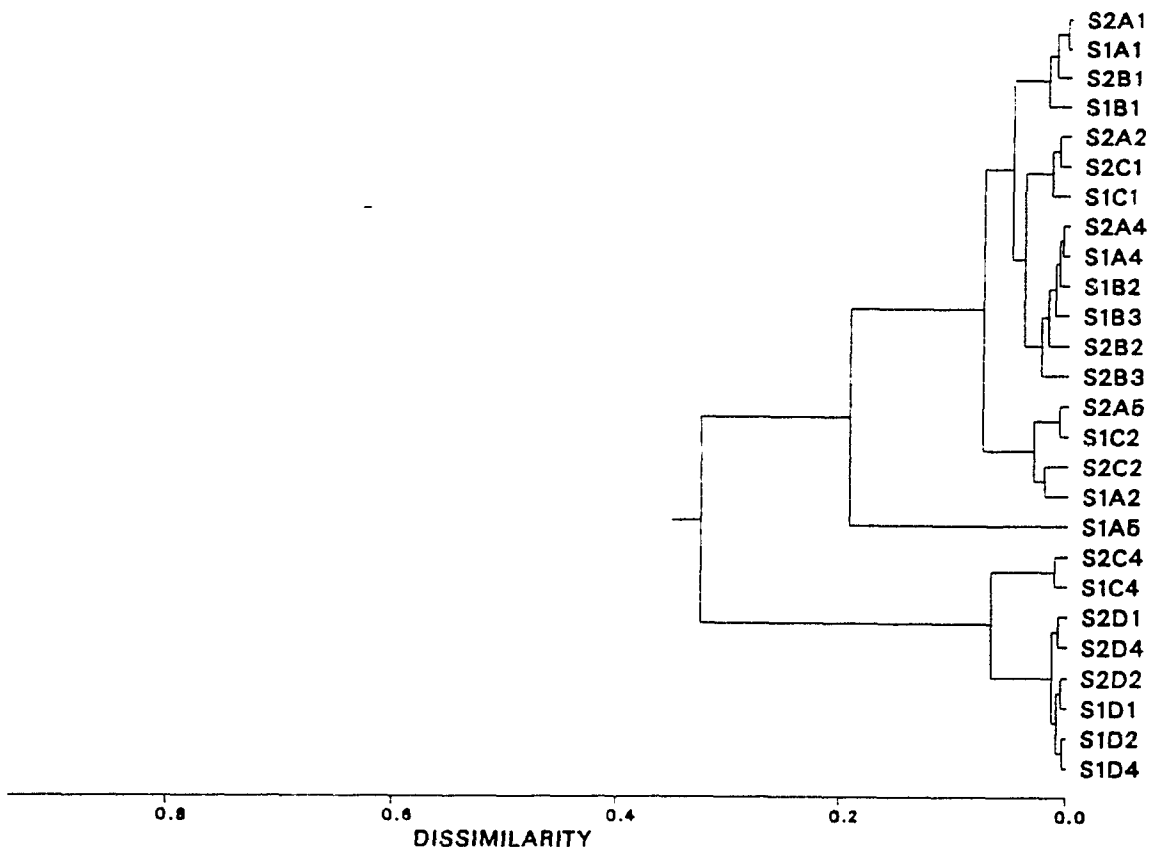

Figure 17. Cluster dendrogram based on environmental variables for the Shelf surveys. Variables in the analysis were depth, percent silt/clay, percent sand and geographic location.

of sediment type on the distribution patterns of small versus large fauna, without strong, complicating factors.

Clearly, the consistency in species composition of both large and small fauna in the two surveys suggested that there was considerable stability in the benthic faunal composition over the spring and summer season. Unfortunately, no further seasonal data were available. As well, the abundance Sigtree pattern was similar to those presented separately for each survey in Brinkhurst (1987), so the elimination of unidentified taxa prior to analysis did not greatly change the station pattern. Both the raw abundance and biomass-weighted abundance Sigtree analyses clearly showed that the composition of the silty stations was significantly distinct from that of the sandy stations. The results of the Comtre2 comparison of the two faunal dendrograms led to the conclusion that the raw abundance and biomass-weighted abundance cluster patterns could not be considered different. Therefore, both the small and large components of the fauna were distributed differently in fine silt and fine sand habitats. However, this distinction was less clear in the biomass-weighted analysis than in the raw abundance analysis. In the raw abundance pattern a significant distinction was evident between the C4 stations and the remaining sandy stations. This pattern was also suggested in the environmental pattern and the biomass-weighted pattern. Results of both the raw abundance and biomass-weighted abundance patterns agree as to the distinct nature of all the C stations in both cruises, whereas this was not evident in the environmental pattern. The fauna from C1 to C4 may have characterized a transition zone from a silty to sandy substrate.

Considering the clear distinction between the sandy and silty stations in the environmental and faunal dendrograms, it is somewhat surprising that there were not more significant linkages in the Comtre1 comparisons. Unmeasured factors such as sediment transport, which Jumars and Banse (1989) suggested was influencial to fauna distribution in coastal shelf habitats of the eastern Pacific, might have affected the shelf benthos more profoundly than sediment particle size and depth.

The original purpose of the study conducted by Dobrocky Seatech Ltd in 1981-1983, which was to try to relate euphotic zone productivity with

benthic productivity, was unsuccessful (Brinkhurst 1987). Later studies of the area suggested that most of the nutrient-rich waters of the euphotic zone in spring and summer derive mainly from Juan de Fuca Strait, whereas nutrients in bottom water derive from upwelling along shelf-break canyons (Crawford and Dewey 1989). Therefore, the pelagic and benthic communities are fueled by differing nutrient inputs with independent time-scales and rates of flux, and cannot be readily tied together. As well, recent studies by Mackas *et al.* (1987), and Crawford (1988) show that cross-shelf transport of water is considerable in this area, and the Juan de Fuca nutrient source is therefore not restricted to waters close to the western shore of Vancouver Island. Nor is the upwelling water from the California Current restricted to the offshore shelf-break area. Therefore there is no reason to assume that nutrient supplies are much different in the benthic areas A to D. The main difference between benthic areas is the amount of bottom turbulence and current, which produces silty substrates in the nearshore stations and sandy substrates further offshore. The sediment regime and geological history of the shelf area are described by Carter (1973). The sandy substrates off-shore are mainly glacial relic substrates, whereas the silty material nearshore is modern run-off material from land.

Jumars and Banse (1989) review the literature on continental shelf sediment transport/benthos interactions, with particular reference to the Pacific Northwest. They reiterate and discuss the general principle that continental shelf benthos communities are zoned by depth and correlated with sediment type. The results of the current study support this principle. However, it is interesting to note that the zonation off Barkley Sound is the reverse of the normal condition, with fine silt areas on the inner shelf and sandy substrates on the mid shelf.

Brinkhurst (1987) postulated that the decline in faunal abundance and estimated biomass in the sandy stations in the second cruise was related to the intrusion of dense, low oxygen water from the California Undercurrent in summer, since data from Freeland and Denman (1982, and Crawford and Dewey (1989) indicated that oxygen levels may be less than 1.5ml/l in that area for periods of time. However, under conditions of continuous water movement, this level would not likely affect infaunal

species, which often exist in lower oxygen regimes in reduced sediments, and tend to have reasonable tolerance for non-stagnant, low oxygen conditions. As well, CTD and bottom oxygen measurements (Crawford and Dewey 1989) suggest that the low oxygen area is over the silty stations, rather than the sandy stations. Yet the silty stations showed no decline in biomass or abundance values over the summer, whereas the sandy stations did. The fact that numerical abundance showed a much steeper decline than biomass in the sandy stations, with no concurrent change in species composition, suggested that the decline ocurred mainly in the smaller fauna. This result at least supported the contention that low oxygen affected the benthos. However, the increase in cruise 2 of mean abundance and biomass values for stations C1 and C2, which should have been in the path of the low oxygen intrusion (Crawford and Dewey 1989), belies the contention that low oxygen had a deleterious effect on benthos over the summer. A much more likely scenario related to the nutrient and bottom sediment transport processes on the shelf. The coastal upwelling responsible for the majority of nutrient flux on the bottom (see Crawford and Dewey 1989) is a summer event. By fall, this major source of input has ended. It is possible that in the silty sediment areas, there was little or delayed impact on the benthos because the fine, nutrient rich silts which settled in low-energy, silty areas during the summer upwelling season may have remained available for consumption by benthic deposit feeders long after deposition. However, in the sandy stations, finer silts may have been carried away by strong bottom currents, leaving less organic matter for consumption by the suspension feeders. If this scenario is true, the benthos in the sandy stations would have lower nutrient availability than their counterparts in the silty stations by the end of the summer season.

CHAPTER 6: VANCOUVER HARBOUR

A. INTRODUCTION

The interesting and unique aspect of the Vancouver Harbour and Port Moody Arm surveys is that they are areas subject to a complex mixture of point source and diffuse organic and inorganic pollutants. Therefore, in addition to the natural environmental factors measured, station patterns based on seven key pollutant factors were examined and compared with distributions of large and small fauna. This set of surveys included the consistent use of the smallest screen size (0.3mm) of all the surveys except the shelf (0.25mm). Because of the polluted nature of the inlet, some stations may contain only small fauna, which are sometimes more tolerant of pollution conditions than larger fauna (c.f. Pearson and Rosenberg 1978). The use of a small screen provided an opportunity to examine differences between station patterns based on very small fauna (Sigtree analysis of abundance) and on the large, rarer fauna (Sigtree analysis of biomass-weighted abundance), and how these relate to environmental factors.

Vancouver Harbour is a relatively well-flushed but shallow basin, with heavy industrial installations in many areas. Port Moody Arm is considerably shallower and less well flushed than Vancouver Harbour, with petrochemical installations, sewage and other sources of waste (D. Goyette, EPS Vancouver, pers. comm.), as well as bottom disturbance from dredging and the movement of large freighters and tankers. The physical oceanography of Vancouver Harbour and Port Moody Arm have been extensively studied by Davidson (1979) and R. Thomson, IOS (archived data).

The benthic surveys of Vancouver Harbour and Port Moody Arm were carried out in concert with an on-going Environment Canada assessment of the status and health of the area. Faunal samples were taken in areas already examined for sediment chemistry (Goyette and Boyd 1989). The surveys were conducted in October of 1987 and 1989. Results of the first benthic survey and sediment chemistry tests are presented in Burd and Brinkhurst (1990b). The abundance dataset for the second cruise is

presented in Cross and Brinkhurst (1991). Both of these reports are included in the back cover of the thesis. Biomass-weighted abundance, abundance, sediment chemistry and environmental data analyses for both cruises are presented in this chapter.

Stations were selected and named to conform with sampling patterns established by Environment Canada (Fig. 18). Station names were constructed as follows: Station V141B: V=Vancouver/ Port Moody; 1=cruise 1; 41B=station 41B: A second example, station V211= Vancouver Harbour cruise 2 station 11. Note that two replicates per station were taken in the first cruise, whereas 3 replicates were sampled in the second cruise.

Station locations, depths and sediment types are given in Appendix 1. Stations 1 to 25 were located in Vancouver Harbour in sandy-silt sediments from 13 to 67 m depth. Stations in Port Moody Arm (33-46) were shallower, with higher silt content. Fewer stations were sampled in cruise 2 than in cruise 1. Station 33 was sampled only in cruise 2. Station PEI, located outside the harbour itself, was considerably deeper than the other stations, and was sampled only in Cruise 1.

B. RESULTS

Because of the considerable difference in depth and sediment type of stations in Vancouver Harbour and Port Moody Arm, the results for these two areas were shown separately.

1. Summary statistics

Mean abundance, mean biomass and total taxa for each station are given in Table 8. Abundance values for most Vancouver Harbour stations were high relative to station abundances for Hecate Strait, Alice Arm and the shelf surveys. This is not surprising since the mesh size used for the Vancouver Harbour/Port Moody Arm studies was quite small (0.3mm). In the first survey, abundances were generally about 50-70% lower in Port Moody Arm than in Vancouver Harbour stations. In the second cruise, abundances were high in both areas. Abundances declined overall in

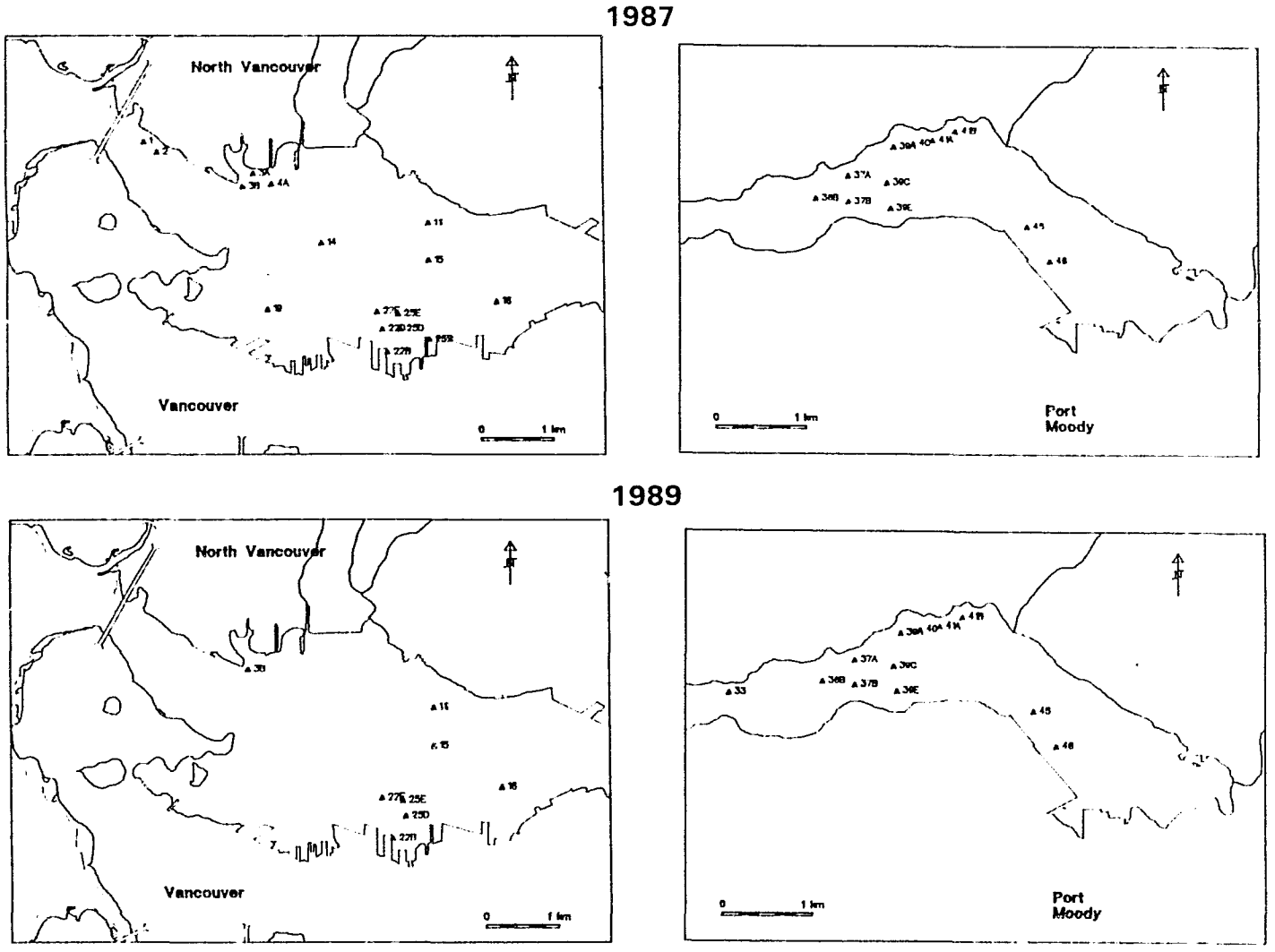

Figure 18. Station locations for Vancouver Harbour and Port Moody Arm in October 1987 (A) and 1989 (B). Station PEI is not shown, but was located outside the bridge at the narrowing of the harbour, off the dock of the Pacific Environmental Institute, West Vancouver, B.C.

Table 8. Mean biomass (wet weight in g /0.1 m^2), mean abundance (numbers/0.1 m^2) and total taxa for all grabs in a station, for Vancouver Harbour and Port Moody Arm in October 1987 and October 1989. Values were calculated from two replicates in 1987 and three replicates in 1989.

Vancouver Harbour

	1987			1989		
	Mean Biomass g/0.1m2	Mean Abundance No/0.1m2	Total Taxa	Mean Biomass g/0.1m2	Mean Abundance No/0.1m2	Total Taxa
V11	1.34	908	53	V21	1.03	756	22
V12	3.72	936	51	V211	4.87	844	48
V13A	2.70	542	34	V215	7.42	637	62
V13B	6.64	4711	70	V216	4.19	687	53
V14A	6.83	2566	69	V225E	8.79	919	61
V111	12.42	4033	65	V225D	1.41	705	32
V114	5.29	945	55	V222E	9.25	1277	62
V115	10.71	2137	70	V222D	3.11	676	65
V116	14.63	6713	50				
V119	8.18	2293	57				
V122B	14.75	3175	63				
V122D	11.23	1856	47				
V122E	12.30	2855	62				
V125B	6.05	2483	47				
V125D	13.44	3047	56				
V125E	13.02	2522	52				
V1PE	7.11	1023	57				

Port Moody Arm

	1987			1989		
	Mean Biomass g/0.1m2	Mean Abundance No/0.1m2	Total Taxa	Mean Biomass g/0.1m2	Mean Abundance No/0.1m2	Total Taxa
V136	3.33	391	29	V233	5.16	1105	45
V137A	2.06	345	29	V236	4.26	975	35
V137B	4.43	566	23	V237B	5.12	827	37
V139A	1.33	167	18	V237A	4.45	479	37
V139C	1.89	286	18	V239C	6.10	983	34
V139E	3.33	604	24	V239E	6.30	870	43
V140	3.03	1032	15	V240	2.97	573	44
V141A	1.86	332	19	V239A	5.60	788	27
V141B	0.05	19	8	V241A	3.28	268	19
V145	0.46	34	7	V241B	2.70	825	29
V146	0.04	72	1	V246	1.57	230	12
				V245	2.34	272	21

Table 9. Total abundance (number/ m^2) of major taxonomic groups for Vancouver Harbour and Port Moody Arm. Data were split to show results from Vancouver Harbour and Port Moody Arm. Poly/Biv = ratio of polychaetes to bivalves.

Cruise 1

	Vancouver Harbour	Port Moody Arm
	Abundance (No/ m^2)	
Polychaeta	11917	2966
Crustacea	1364	290
Echinodermata	22	0
Bivalvia	8367	988
Gastropoda	1936	149
Poly/Biv	1.42	3.00

Cruise 2

	Vancouver Harbour	Port Moody Arm
	Abundance (No/ m^2)	
Polychaeta	5156	3068
Crustacea	1010	1906
Echinodermata	3	4
Bivalvia	2534	1562
Gastropoda	359	227
Poly/Biv	2.03	1.96

Vancouver Harbour in cruise 2, and increased overall in Port Moody Arm. Numbers of taxa were not unusually high in Vancouver Harbour/Port Moody Arm, but were low in Port Moody Arm in cruise 1. In both cruises, estimated biomass values for stations were generally high in Vancouver Harbour and lower in Port Moody Arm. Stations which stand out include 41B, 45 and 46. These were almost defaunate in cruise 1, but had considerably more fauna in cruise 2. Station 46 was still distinctive in cruise two, with the lowest abundance and taxa number of any station. Biomass values were low at station 1 in cruise 1 (V11).

Faunal abundance was dominated in both cruises by polychaetes (Table 9). Bivalves were the next most abundant group at all sites in cruise 1 and in the Vancouver harbour stations from cruise 2. Gastropods and Crustaceans were particularly abundant in cruise 1, and less so in cruise 2. Echinoderms were low in abundance in both cruises. The polychaete to bivalve ratio did not change in Port Moody Arm between cruise 1 and 2, however, crustaceans increased dramatically.

Abundance dominants are considered separately for Vancouver Harbour and Port Moody Arm because of the geographic and depth differences between the two areas. In cruise 1, abundance dominants in both areas included the bivalves *Axinopsida serricata*, *Psephidia lordi*, the gastropod *Alvania compacta*, the polychaetes *Prionospio lighti*, *Nephtys cornuta franciscanum*, *Tharyx multifilis*, *Cossura longocirrata* and *Capitella capitata*. The gastropod *Philine polaris* and the cumacean *Eudorella pacifica* were abundant only in Port Moody Arm, whereas the polychaetes *Sphaerosyllis brandhorsti*, *Prionospio steenstrupi*, *Nephtys cornuta cornuta*, *Cossura modica* and *Exogone lourei* were common only in Vancouver Harbour.

In cruise 2, abundance dominants were similar to cruise 1, including the bivalves *Psephidia lordi* and *Axinopsida serricata*, the gastropod *Alvania compacta*, the polychaetes *Capitella capitata*, *Armandia brevis*, *Nephtys cornuta franciscanum*, *Tharyx multifilis*, *Cossura longocirrata*, *Lumbrineris luti*, *Prionospio lighti*, *P. steenstrupi* and *Pectinaria prudens*, the ostracods *Euphilomedes carcharodonta* and *E. producta*, and the amphipod *Protomedeia prudens*. Species abundant only in Vancouver Harbour included the bivalves *Thyasira gouldi* and *Acila castrensis*, the

polychaetes *Sphaerosyllis brandhorsti* and *Euchone incolor*. Species common only in Port Moody Arm included the polychaetes *Ophiodromus pugettensis* and *Trochochaeta multisetosus*.

The biomass dominants were fairly consistent between the two areas. Biomass was dominated overwhelmingly by bivalves in both cruises. Dominants included the bivalves *Axinopsida serricata, Psephidia lordi, Macoma carlottensis, Compsomyax subdiaphana, Lucina tenuisculpta* and *Acila castrensis*. *Macoma calcarea* was dominant only in cruise 1, whereas *Macoma eliminata* was common only in cruise 2. The dominant polychaete in both cruises was *Tharyx multifilis*. The polychaetes *Glycera capitata, Ophelina acuminata* and *Sternaspis scutata* were biomass dominants in cruise 1, whereas *Pectinaria californiensis* was dominant in cruise 2. The crustacean *Protomedeia prudens* was a biomass dominant only in cruise 2. Dominant echinoderms included *Molpadia intermedia* in cruise 1 and *Amphiodia urtica* in cruise 2.

2. Multivariate Statistical Analyses

Because a mesh size of 0.3mm was used in these surveys, abundance was high. However, the sampler size was small compared to the other surveys, and only two replicates per station were taken in the first cruise. Additionally, this was the only survey area in which different numbers of replicates per station were sampled in the 2 cruises. A significance level of $p \leq 0.01$ was considered conservative for rejection of hypotheses without unduly increasing the multiple comparisons problem for a total of 47 linkages. However, because of the small sampler and low number of replicates in one of the cruises, the power would probably be too low at 1%. Therefore, a significance level of 2% was considered more reasonable (for discussion of power - Chapter 2, section F).

The Sigtree analysis of abundance data for both cruises (Fig. 19) had 5 significant linkages which produced seven significantly distinct (but not necessarily homogeneous) groups and six singleton stations. The groups are illustrated spatially on Fig. 20. Although these groupings were not all spatially coherent, there are some generalizations which can be made. The Port Moody Arm stations in cruise 1 were

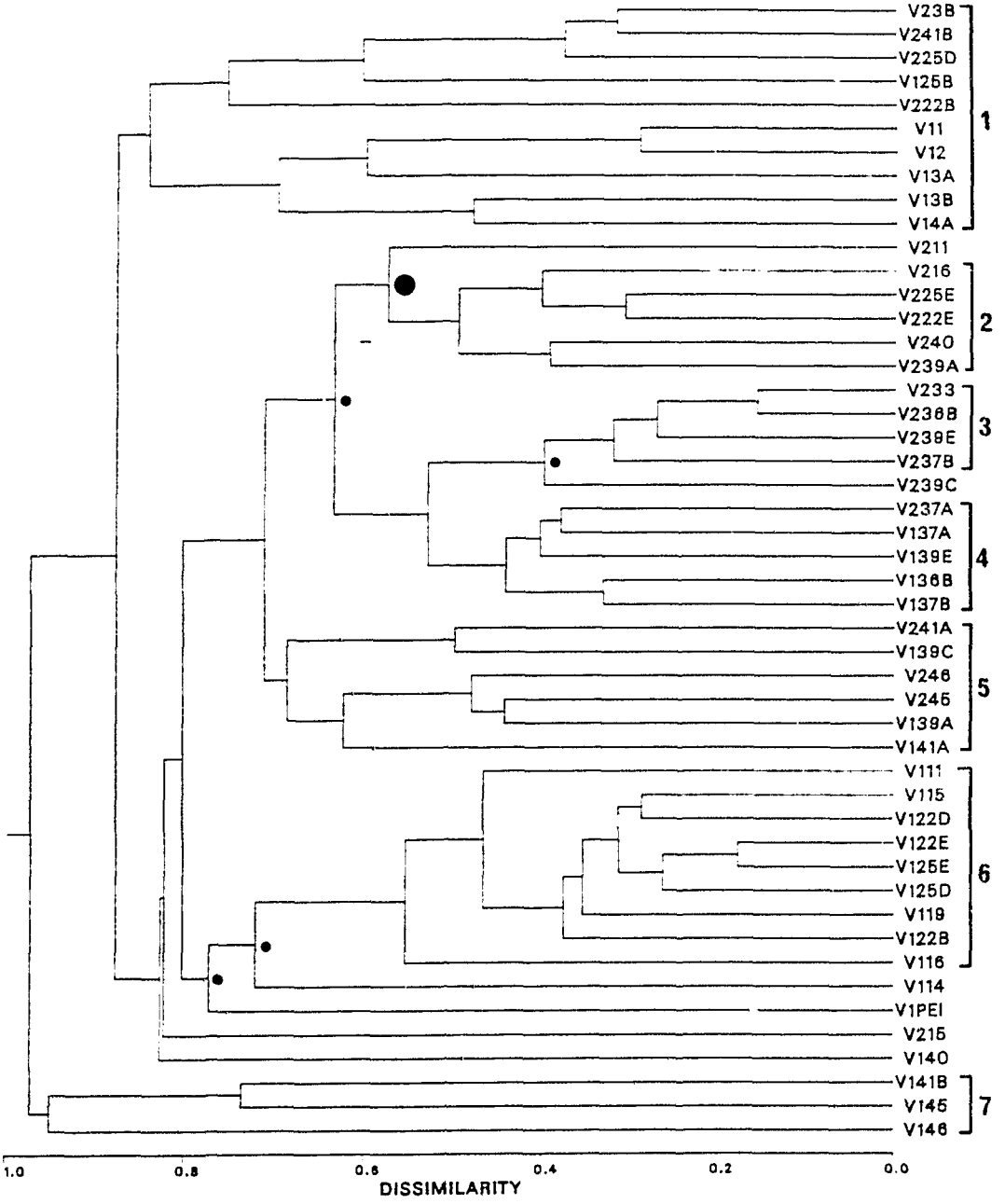

Figure 19. Cluster dendrogram for raw abundance data from Vancouver Harbour and Port Moody Arm. Significances at the 1% level are indicated by the large dot, at the 2% level by the small dots. Significant (but not necessarily homogeneous) groups are numbered on the right hand margin.

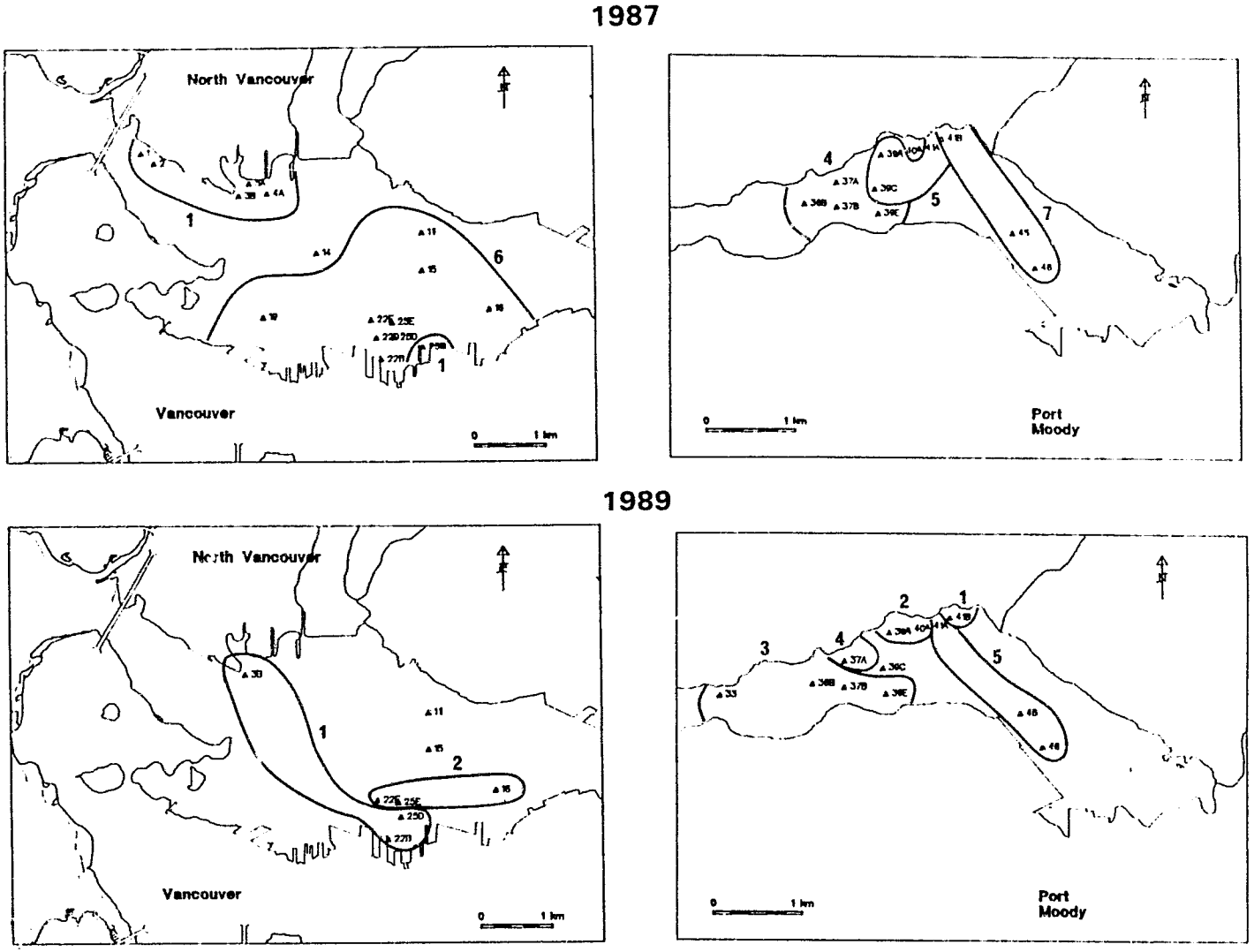

Figure 20. Station maps showing significant groupings for abundance sigtree analysis for Vancouver Harbour and Port Moody Arm (1987, 1989). Group numbers match those illustrated in Fig. 19.

distinctly separate from the Vancouver Harbour stations. In the second cruise, there was more overlap between the two areas (see groups 1,2). As well, there was considerable overlap in the Port Moody Arm stations from both cruises (groups 3,4,5). Group 1 included all of the stations closest to the mouth of Vancouver Harbour (stations 1-4A), as well as some inner Vancouver Harbour stations (22-25) and one Port Moody Arm and station (41B) from cruise 2. Groups 3-5 and 7 contained most of the Port Moody Arm stations from both cruises. Group 2 contained stations from both areas. The outermost station (PEI) had a species composition significantly distinct (at 1.2%) from both Vancouver Harbour and Port Moody Arm. As well, stations 14 and 40 from cruise 1 and 11 and 15 from cruise 2 were significantly distinct although similar in composition to other inner Vancouver Harbour stations. The three defaunate stations in cruise 1 (41B,45,46) were separate from all others, and formed a significantly distinct (but not homogeneous) group (group 7).

The biomass-weighted abundance (Fig. 21) and abundance patterns were similar with respect to the separation of Vancouver Harbour stations from Port Moody Arm stations. The spatial distribution of station groups is shown in Fig. 22. The first significant group contained most of the inner Vancouver harbour stations from cruise 1 and several from cruise 2. Stations PEI and 14 from cruise 1 were most similar to group 1, but significantly distinct as in the numerical abundance pattern. The remaining inner harbour stations from cruise 2 were singletons or a pair (group 7). Stations 11 and 15 from cruise 2 were significantly distinct. Station 1 from cruise 1 and 3B from cruise 2 were significantly distinct and very dissimilar to all other stations. Stations 2-4A from cruise 1 (outer Vancouver Harbour) formed part of a significant group (group 6) along with two Port Moody Arm stations from cruise 1. Groups 2,3,4 and 5 included only Port Moody Arm stations from both cruises. The defaunate stations in cruise 1 were distinctly separate from all other stations (group 8). Station 46 from both cruises was significantly distinct from all other stations.

The Comtre2 comparison of the raw abundance dendrogram with the biomass-weighted abundance dendrogram (Appendix 3j)

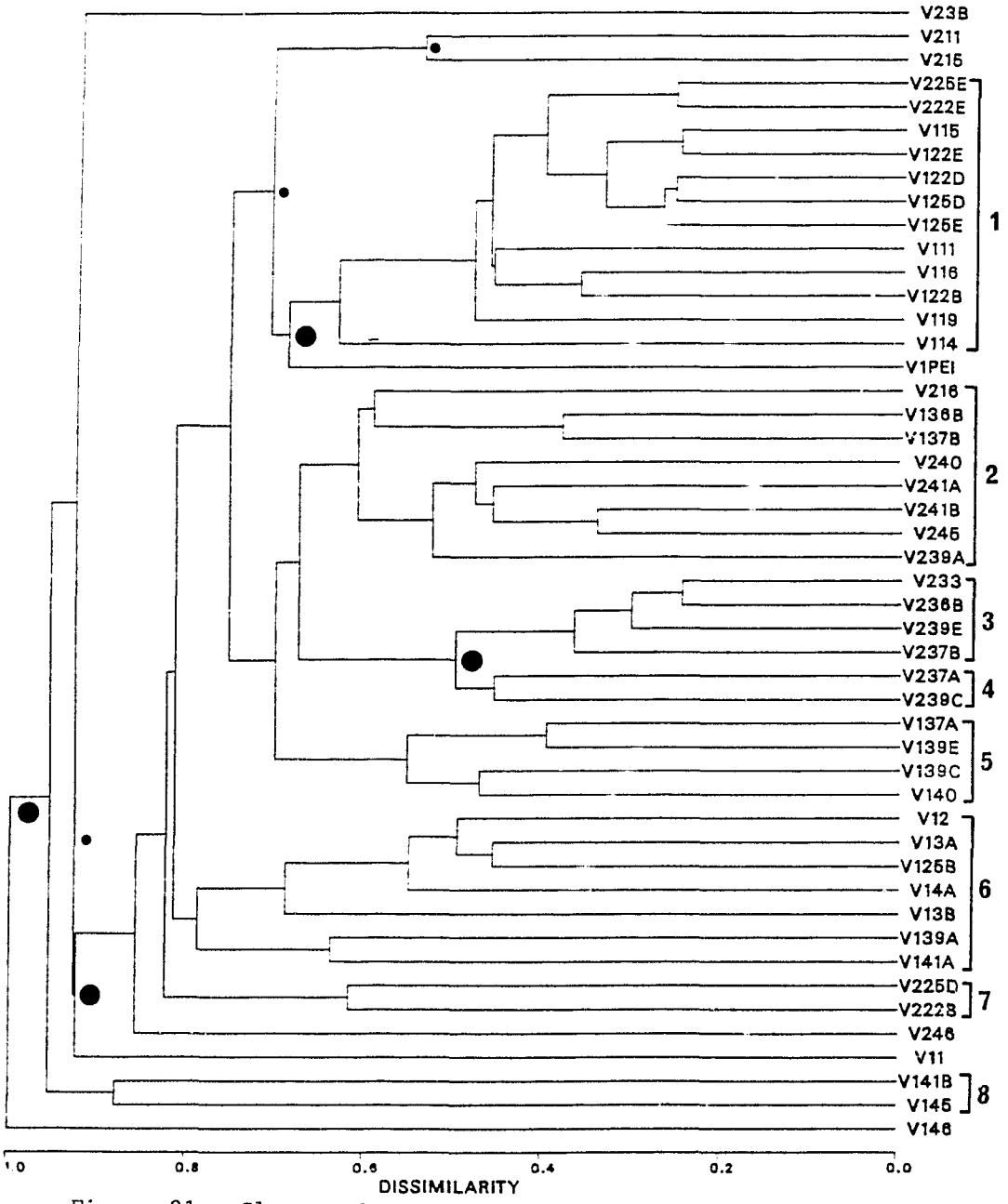

Figure 21. Cluster dendrogram for biomass-weighted abundance data from Vancouver Harbour and Port Moody Arm. Significances at the 1% level are indicated by the large dot, at the 2% level by the small dots. Significant groups are numbered on the right margin.

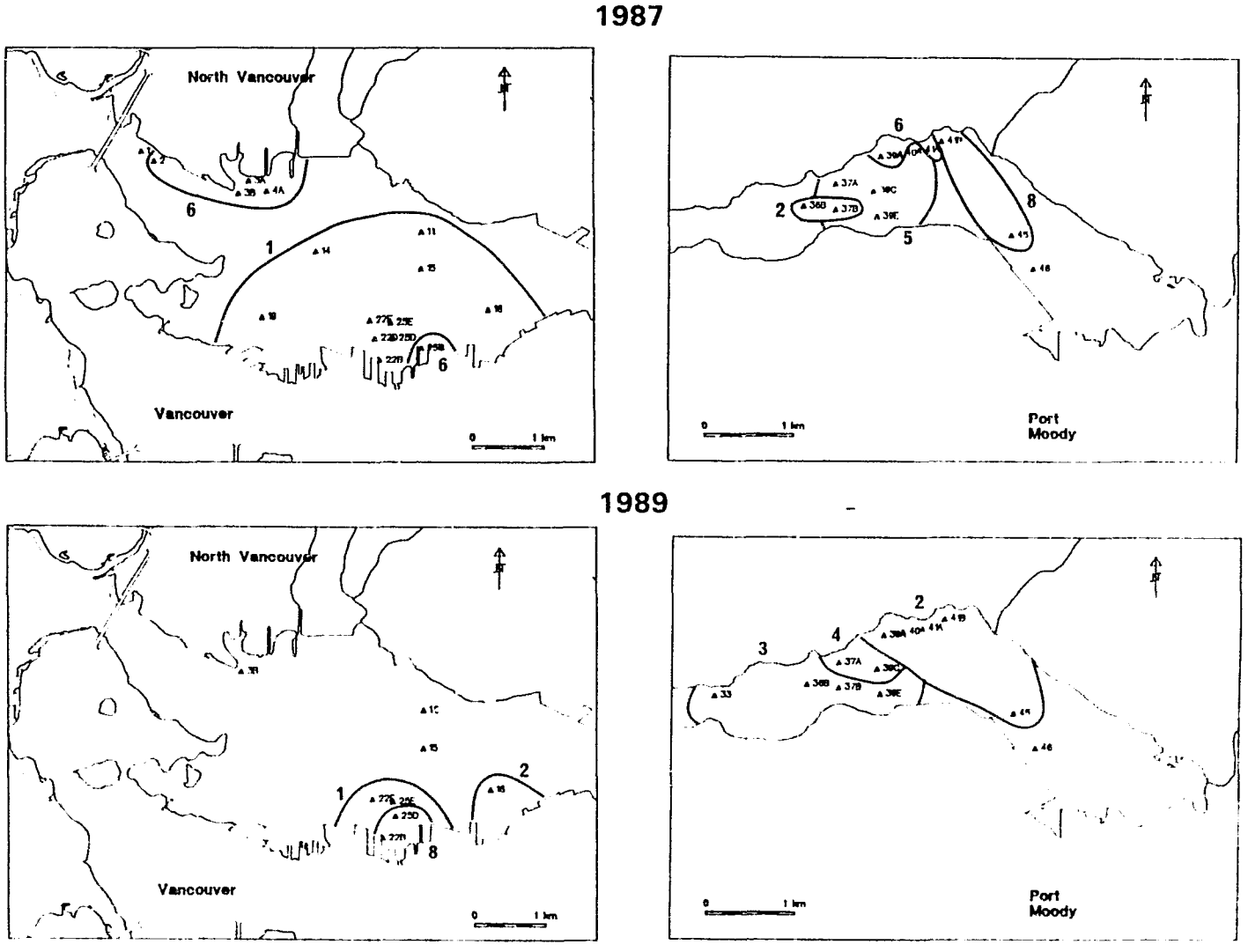

Figure 22. Station maps showing significant groupings for biomass-weighted cluster analysis for Vancouver Harbour and Port Moody Arm (1987, 1989). Group numbers match those illustrated in Fig. 21.

tested the null hypothesis at each linkage level that the two dendrograms were the same. The hypothesis could not be rejected at any linkage level. Therefore, the two faunal dendrograms cannot be considered statistically different.

3. Environmental Analyses

The cluster pattern based on depth, sediment type and geographic location of stations showed several distinct groupings (Fig. 23). The first grouping included all but one of the Port Moody Arm stations from both cruises, as well as many Vancouver Harbour stations with silty substrates. The second major group included stations from Vancouver Harbour with sediments composed of about 50% sand and 50% silt. Station PEI was dissimilar to all of the aforementioned stations and formed a separate group. The 5 sandy stations from Vancouver Harbour (very low silt content) formed the final group.

The Comtrel comparisons of the environmental dendrogram with the two faunal dendrograms (Appendices 3k,3l) tested the null hypothesis that the compared trees were different at each linkage level. For the comparison of the raw abundance dendrogram with the environmental dendrogram, the hypothesis could be rejected at one linkage at the 1% level, and one further linkage at the 2% level. For the comparison of the biomass-weighted pattern with the environmental pattern there were two rejections at the 1% level, and two further rejections at the 2% level. In summary, the environmental dendrogram was more closely related to the biomass-weighted dendrogram than to the abundance dendrogram.

4. Sediment Chemistry Analyses

The cluster pattern of stations based on seven sediment chemistry factors is shown in Fig. 24. The sediment chemistry data were obtained from Goyette and Boyd (1989), and D. Goyette, Environment Canada, Vancouver, B.C. (pers. comm.). The factors used in the cluster analysis were Cd, Cr, Cu, Pb, Zn, total hydrocarbon and PCB (Table 10). Some of the values used for the 1987 cruise were taken in late 1985 (see Burd

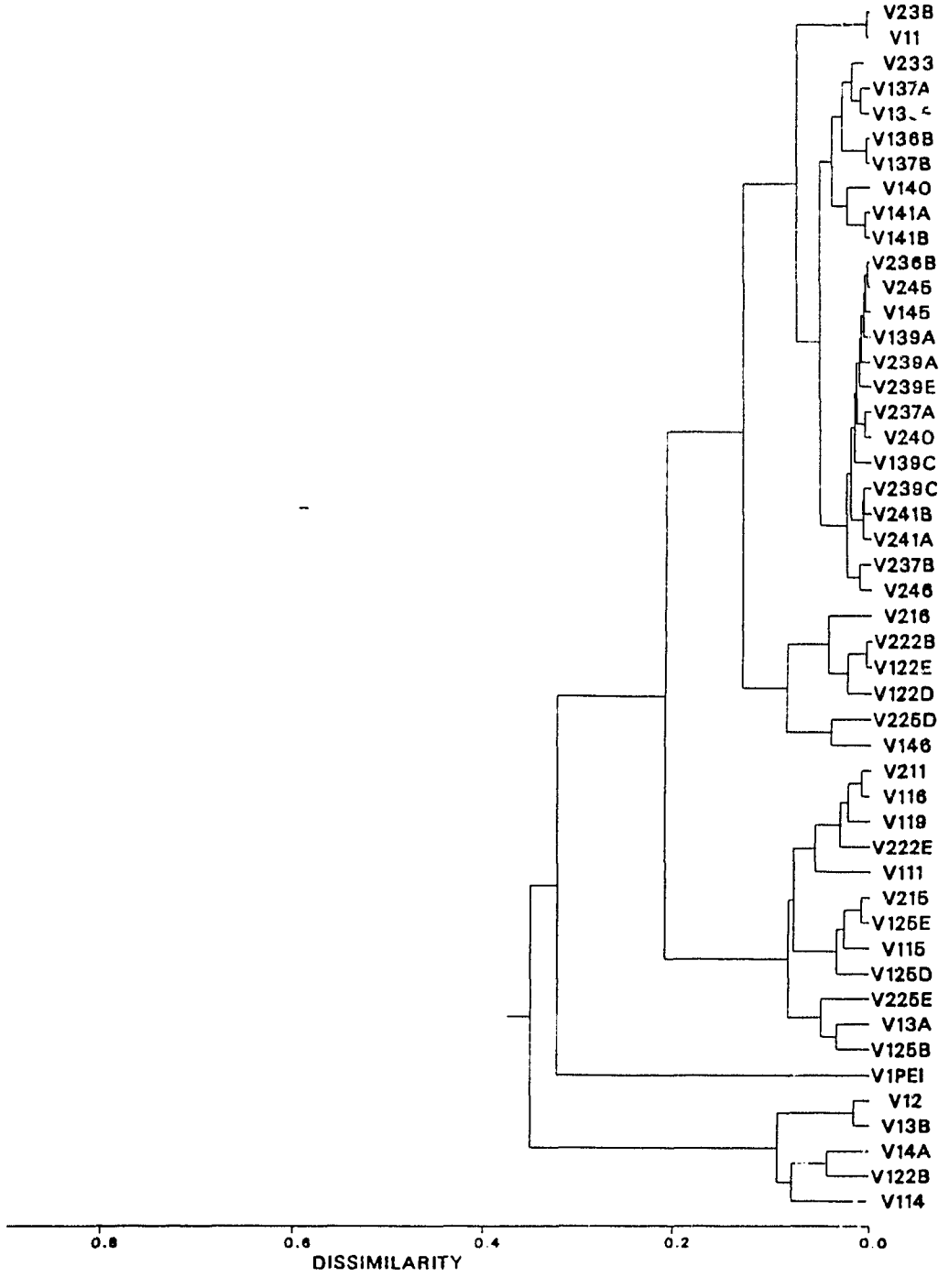

Figure 23. Environmental cluster dendrogram for Vancouver Harbour and Port Moody Arm. Variables include depth, percent silt/clay, percent sand and geographic location.

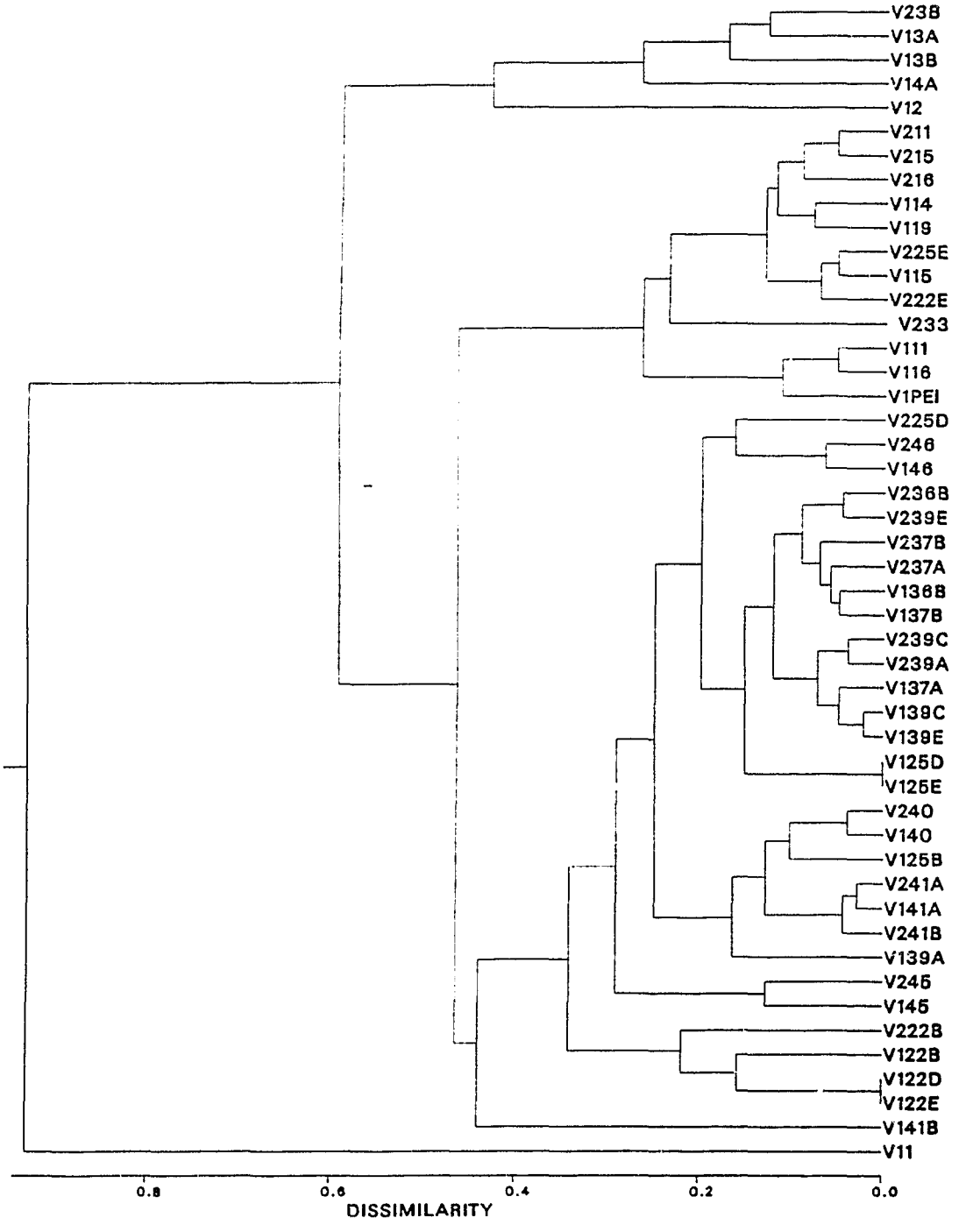

Figure 24. Sediment chemistry dendrogram for Vancouver Harbour and Port Moody Arm. Variables include 7 key metal and organic pollutants (see text).

Table 10. Sediment chemistry factors from Vancouver Harbour and Port Moody Arm (from Goyette and Boyd 1989). Values are transformed to ratios of expected baseline levels (D. Goyette, EPS, Vancouver, B.C.).

Station	Cadmium	Chromium	Copper	Lead	Zinc	HC	PCB
V1PEI	1.3	1.1	2.8	2.2	1.3	3.0	0.1
V11	17.2	0.3	62.8	642.5	19.7	6.6	0.0
V12	8.5	1.2	67.0	24.4	5.7	9.6	0.0
V13A	24.8	1.0	18.3	10.6	11.1	13.4	0.1
V13B	22.0	0.9	30.3	10.9	11.0	2.2	0.0
V14A	9.1	1.5	18.6	6.8	18.5	3.1	0.2
V111	1.5	0.5	2.8	2.0	1.0	2.2	0.2
V114	1.9	0.7	5.1	2.7	1.3	3.2	0.0
V115	2.3	0.8	6.1	3.4	1.8	4.2	0.1
V116	1.5	0.5	2.9	2.0	1.2	1.6	0.1
V119	2.1	0.8	4.4	3.4	1.3	2.6	0.0
V122B	5.0	0.8	12.9	5.0	3.2	17.7	0.3
V122D	2.7	0.8	13.2	4.0	2.1	10.3	0.1
V122E	2.7	0.8	13.2	4.0	2.1	10.3	0.1
V125B	4.4	0.6	5.1	10.0	2.2	24.5	0.4
V125D	3.0	0.9	6.7	5.6	2.1	14.2	0.2
V125E	3.0	0.9	6.7	5.6	2.1	14.2	0.2
V136B	3.1	1.3	3.7	4.0	1.7	14.8	0.1
V137A	4.2	1.5	2.5	4.6	1.8	19.2	0.2
V137B	3.8	1.2	2.3	3.9	1.8	14.6	0.2
V139A	5.9	1.6	2.3	5.6	1.9	35.5	0.2
V139C	4.7	1.6	2.1	3.9	1.8	18.2	0.2
V139E	4.7	1.3	2.2	3.9	1.3	18.0	0.0
V140	6.2	1.9	2.1	12.4	2.6	24.0	0.1
V141A	6.6	2.6	2.2	5.0	2.1	26.2	0.3
V141B	39.3	2.2	2.1	4.6	2.1	24.4	0.1
V145	5.6	0.9	0.9	0.8	1.1	9.9	0.1
V146	8.5	1.3	1.6	2.7	2.2	19.5	0.1

Cruise 2

Station	Cadmium	Chromium	Copper	Lead	Zinc	HC	PCB
V21	15.7	0.9	21.6	10.4	8.4	9.9	0.1
V211	2.8	0.7	5.9	2.3	1.6	2.4	0.0
V215	2.8	0.7	6.1	2.5	1.6	3.5	0.0
V216	2.8	0.7	5.1	2.5	1.7	4.9	0.0
V225E	2.1	0.8	7.0	2.9	1.8	4.5	0.0
V225B	9.3	0.9	6.1	8.0	2.8	17.0	0.2
V222E	2.0	1.0	6.8	3.4	2.0	5.8	0.0
V222B	6.3	0.9	20.6	5.1	3.6	7.5	0.0
V29	2.1	1.1	3.2	3.6	1.9	8.4	0.0

Table 10. (continued)

Station	Cadmium	Chromium	Copper	Lead	Zinc	HC	PCB
V236B	2.1	1.3	2.6	4.5	2.0	11.9	0.1
V237E	2.0	1.1	2.2	3.5	1.8	14.0	0.0
V237A	3.0	1.6	2.6	4.7	2.2	14.3	0.0
V239C	2.9	1.2	2.2	4.6	1.9	16.3	0.0
V239E	3.6	1.4	2.4	4.4	2.2	12.2	0.0
V240	6.0	1.7	2.1	10.8	2.6	22.5	0.0
V239A	2.8	1.1	1.9	4.5	1 9	17.9	0.1
V241A	6.5	2.1	2.0	5.7	2.5	26.5	0.1
V241B	6.7	1.9	1.9	4.2	2.3	24.9	0.1
V246	8.6	1.3	1.6	3.4	2.4	16.1	0.0
V245	6.3	1.2	1.4	2.5	1.9	11.4	0.0

and Brinkhurst 1990b), but the 1989 values were taken concurrently with the benthic faunal samples. Chemistry values were standardized by taking the ratio of the measured value to baseline (= expected background levels provided by D. Goyette, EPS). This was necessary since the scale of contaminants measured varied considerably.

In the Comtrel comparison of the abundance dendrogram with the chemistry dendrogram (Appendix 3m), the hypothesis that the two dendrograms were different could be rejected at 3 linkages at the 1% level, and an additional 2 linkages at the 2% level. For the comparison between the biomass-weighted abundance dendrogram and the chemistry dendrogram (Appendix 3n), the hypothesis was rejected at 5 linkages at the 1% level, and 5 more linkages at the 2% level. Several stations stand out in Fig. 24 because of unusual sediment chemistry. Station 1 in cruise 1 (V11) had particularly high cadmium, chromium, lead and zinc levels (Burd and Brinkhurst 1990b). Stations V141B and V145, two of the three severely defaunated stations, had high cadmium and hydrocarbon levels. The outer Vancouver Harbour stations (1-4a, both cruises) had high levels of all contaminants measured except total hydrocarbon. All stations in Port Moody Arm (33-46) had high hydrocarbon contents (Burd and Brinkhurst 1990b, EPS, unpublished data). The station groupings on sediment chemistry were very similar to those found in the faunal dendrograms, particularly the biomass-weighted pattern.

C. DISCUSSION

The temporal differences in abundance, estimated biomass and total taxa for stations were not seasonal, since both cruises occurred in October. The overall abundance and biomass values changed considerably over the two year sampling period, decreasing in Vancouver Harbour and increasing in Port Moody Arm. Such changes suggest that benthic fauna in the area may undergo considerable fluctuations in abundance over time. Natural conditions such as tidal flux could cause such widespread changes, although it is difficult to imagine that the impact from human activities does not have some significant effect on benthic faunal composition and abundance.

Considering the small screen used for the two surveys, the pattern of station groupings based on the abundance and biomass-weighted abundance analyses were surprisingly similar. The Comtre2 comparison of the two analyses indicated that the abundance and biomass-weighted patterns could not be considered different.

The intermixing of stations from the two survey years in both the abundance and biomass-weighted Sigtree analyses indicated that there was some similarity in species composition of Vancouver Harbour and Port Moody Arm over the two year span of the study. However, the biomass-weighted analysis showed considerably more heterogeneity in the species composition of Vancouver Harbour stations in cruise 2 than in cruise 1.

Of the two faunal cluster patterns, the biomass-weighted abundance dendrogram was most closely related to the environmental dendrogram. It was not surprising that the Comtre1 relationship between environmental and faunal dendrograms was not particularly strong in either analysis, since there were many sources of pollution in Vancouver Harbour and Port Moody Arm which undoubtedly affected local benthic comunities in complex ways. The relationship with faunal distributions was considerably stronger for sediment chemistry than for environmental factors. Furthermore, the comparison of the sediment chemistry dendrogram with the biomass-weighted dendrogram had twice as many significant linkages (10 versus 5) as the comparison with the abundance dendrogram. A finding of 10 significant linkages out of 47 without selective manipulation of the linkages being compared in the Comtre1 analysis is suggestive of a strong correlation. Therefore, it can be concluded that sediment pollutants affect faunal composition much more strongly than the natural environmental factors measured. More close correlations and informative patterns relating faunal composition and sediment chemistry could possibly be discerned using the analytical methods outlined in this thesis, by manipulating the specific cluster groups being compared in each dendrogram. In particular, the biomass-weighted abundance analyses appeared to provide more useful information than the abundance analysis for comparison with anthropogenic effects. In particular, large fauna were more seriously affected by sediment chemistry than small fauna.

Cross *et al.* (1990) used log-transformed abundance data from the second Vancouver Harbour cruise to show a gradient of community composition changes from the mouth of Port Moody Arm to to the mouth of Vancouver Harbour. The problem with this type of analysis is that the log transformed results cannot be interpreted easily. In general, the analyses in this thesis agree that there is a fundamental difference in species composition between station PEI (outside Vancouver Harbour), the outer Vancouver Harbour stations (1-4a), the inner Vancouver Harbour stations (11-25) and the Port Moody Arm stations (33-46). However, this gradient of faunal composition from Port Moody Arm out to station PEI was complicated by the mixing of a few stations from the different areas, suggesting that unnatural factors may have a strong influence on species composition. The log-transformed analysis of Cross *et al.* (op. cit.) did not suggest this.

CHAPTER 7: BOUNDARY BAY

A. INTRODUCTION

The Boundary Bay survey was incorporated into the thesis because it included the only intertidal and shallow, subtidal environment sampled during the course of the benthic program. As such, the distribution of small versus large fauna was of interest for comparison with deeper areas (see Chapter 9). The study utilized a screen size (0.5mm) intermediate to that used for the other surveys.

Boundary Bay, located on the Canadian/US border, was sampled as part of a cooperative investigation coordinated by Environment Canada to analyse the impact of 45000 L of 2% Sodium tetra/penta-chlorophenate (4CP/5CP), which spilled on March 4, 1984 into Hyland Creek, which empties into the Serpentine River and thus into Boundary and Mud Bays. The spill was of concern because of the known toxicity of low concentrations of chlorophenols to a variety of aquatic organisms. Immediately following the spill more than 5000 juvenile salmonids and other fish were reported killed in Hyland Creek (Colodey 1986). Colodey (1986) did not detect any chemical toxicity in sediments of Boundary Bay after the spill.

The benthic survey of Boundary Bay provided no real information on the long-term effects of the spill on macrofauna in the area, but did ultimately provide background information on the benthic fauna of a nearshore, shallow area which is influenced by waters of both Puget Sound and Georgia Strait.

A Sigtree analysis of the original Boundary Bay numerical abundance data was reported in Burd *et al.* (1987), which is included in the back cover of the thesis. However, no biomass estimates or environmental data were done at that time. The intertidal designation of some stations is somewhat arbitrary (Fig. 25). The chart datum (Can. Hydrogr. Service chart L/C-3463) indicates that stations deeper than 2 m were subtidal. Stations between 2 m and 0 m (chart datum) may have periodic exposure (W. Crawford, IOS, Sidney, B.C.). For the purposes of this study, those stations shallower than 2m will be called low intertidal.

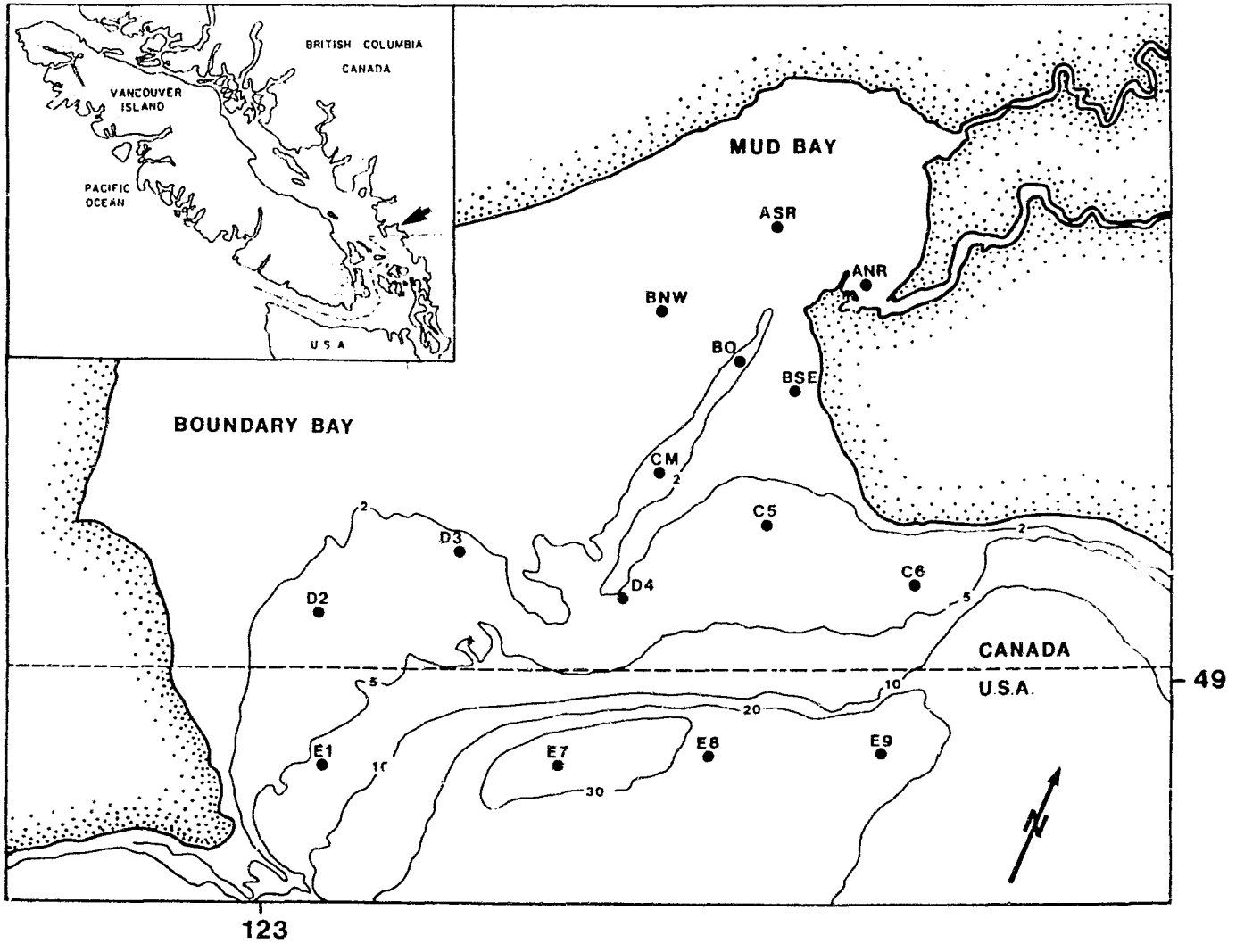

Figure 25. Station locations for Boundary Bay (from Burd et al 1987).

The station locations, depths and sediment types are included in Appendix 1. Two Ponar grab samples (0.05 m^2) per station were taken from a small launch on November 14, 1985. Several distinct station types were evident, including intertidal sand stations with some gravel (ASR,BNW,BSE), high subtidal sandy stations with considerable shell debris (ANR, BO, CM, C5, C6, D2, D3, D4) and subtidal, sandy silt stations (E7, E8, E9).

B. RESULTS

1. Summary Statistics

Mean abundance, estimated biomass and total species per station are included in Table 11. Numerical abundance was higher than Alice Arm, Hecate Strait or Shelf surveys (Chapters 3,4,5) and comparable to those in Vancouver Harbour (Chapter 6). Biomass values were comparable to other surveys, and relatively low in a few stations (ASR, BO, D2). In spite of the high abundance values, the number of total taxa per station was not high compared to other surveys. Station D2 was the only evidently impoverished station in terms of all three variables.

Based on the sediment types (see above), the description of abundant species and taxonomic groups has been presented separately for two station groups, including the shallower, sandy (ASR-E1) and the deep, silty stations (E7-E9). Table 12 shows the mean total abundance per square meter of the major taxonomic groups. Crustaceans dominated the shallow, sandy stations, followed by bivalves and polychaetes, with minor contributions from gastropods and echinoderms. In the deeper, silty stations, polychaetes and crustaceans were equally abundant. As well, there were many echinoderms (mostly the ophiuroid *Amphiodia urtica*) but few bivalves and gastropods. As an illustration of the contrast evident between abundance and estimated biomass patterns, a similar breakdown of mean biomass per square meter is included in Table 12.

Bivalves dominated the biomass in both the sandy, shallow and the deep, silty stations, despite the low abundance in the latter, followed by polychaetes and crustaceans in the sandy areas, and echinoderms

Table 11. Mean biomass (wet weight in g/0.1 m^2), mean abundance (number/ 0.1 m^2) and total taxa for all grabs in each station, for Boundary Bay. Values were calculated from two replicates per station.

	Mean Biomass g/0.1m^2	Mean Abundance No/0.1m^2	Total Taxa
BANR	4.9952	1299	70
BASR	1.0321	752	40
BBNW	2.7901	343	55
BBO	1.0386	162	43
BBSE	5.8036	2545	41
BC5	2.4092	1223	46
BC6	2.4733	1366	41
BCM	5.2206	1563	59
BD2	0.8292	106	20
BD3	2.5136	376	45
BD4	6.5686	3166	60
BE1	3.3779	1011	56
BE7	3.1569	309	41
BE8	3.1262	509	43
BE9	2.839	292	43

Table 12. Total abundance (numbers/ m^2) and biomass (wet weight in g/ m^2) for major taxonomic groups in Boundary Bay. Values have been split into two groups which are; Group 1 = the sandy, shallow stations (ASR-E1) and; Group 2 = the deeper, silty stations (E7-E9).

	Abundance (#/m^2)		Biomass (g/m^2)	
Taxon	Group 1	Group 2	Group 1	Group 2
Polychaeta	1814	1277	7.5	5.3
Bivalvia	3396	470	14.6	13.4
Crustaceana	5624	1203	4.2	4.1
Echinodermata	38	600	0.7	6.7
Gastropoda	349	140	3.2	2.6
Poly/Biv	0.5	2.7	jp1	

and polychaetes in the silty area.

A description of abundance dominants for Boundary Bay is given in Burd *et al.* (1987) and is repeated here for convenience. In the shallow, sandy group (ASR-E1) the abundance dominants included the bivalves *Mysella tumida*, *Mytilus edulis*, *Psephidia lordi*, *Nutricola tantilla* and *Tellina carpenteri*, the amphipods *Ampelisca agassizi*, *Corophium ascherusicum* and *Photis brevipes*, the tanaids *Sinelobus stanfordi* and *Leptochelia dubia*, the cumacean *Cumella vulgaris*, the ostracod *Euphilomedes carcharodonta* and the polychaetes *Armandia brevis* and *Owenia fusiformis*.

Dominants in the deeper, silty stations (E7-E9) included the echinoderms *Amphiodia urtica* and *Pentamera sp.*, the cumacean *Eudorella pacifica*, the amphipod *Heterophoxus oculatus*, the polychaetes *Levinsenia gracilis*, *Nephtys cornuta franciscanum* and *Prionospio cirrifera*, the bivalves *Acila castrensis*, *Mysella tumida*, *Axinopsida serricata* and *Nucula tenuis* and the gastropods *Solariella varicosa* and *Gastropteron pacificum*.

Biomass dominants in the shallow, sandy group included the bivalves *Psephidia lordi*, *Tellina carpenteri*, *Mysella tumida*, *Mytilus edulis*, *Tapes philippinarum*, *Protothaca staminea*, *Macoma inconspicua* and *Mya arenaria*, the gastropod *Polinices pallidus*, the polychaetes *Nephtys californiensis*, *Owenia fusiformis*, and *Platynereis bicanaliculata*, the ophiuroid *Dendraster excentricus* and the amphipods *Ampelisca agassizi* and *Photis brevipes*. In the deep, silty stations, the biomass dominants included the ophiuroid *Amphiodia urtica*, the bivalves *Acila Castrensis*, *Psephidia lordi*, *Nucula tenuis*, *Tellina carpenteri*, *Compsomyax subdiaphana* and *Mysella tumida*, the gastropod *Polinices pallidus*, the amphipod *Ampelisca agassizi*, the cumacean *Eudorella pacifica*, and the polychaetes *Goniada brunnea*, *Pholoe minuta* and *Nephtys californiensis*.

2. Multivariate Statistical Analyses

Since the sieve size used was moderately small (0.5mm) for this study, and abundances were relatively high, a significance level of 2% was used to determine meaningful clusters in the Sigtree analysis. The

small grab size (0.05 m^2) precluded the use of lower probabilities. Generally, the rationale for significance levels was similar to that used for Vancouver Harbour (Chapter 6).

In the Sigtree analysis of abundance data, two significant groups of stations were evident at the 2% level (Fig. 26). The spatial distribution of significant station groups is illustrated in Fig. 27. Group 1 included all the shallow, intertidal and high subtidal sandy stations (ASR-E1), and group 2 included the three subtidal, silty stations (E7,E8,E9).

The pattern of stations for the Sigtree analysis of biomass-weighted data (Fig. 28) was similar to that for the raw abundance pattern. The spatial pattern of stations is illustrated in Fig. 29. As before, the shallow, sandy group and the subtidal silty group were significantly distinct, but at a much lower probability ($\leq$0.5% versus 2%) than the raw abundance pattern. Additionally, the shallow group was split into two significant groups at p=2%. The first included the shallowest (low intertidal) stations (ASR,BNW,BSE) as well as the deeper station located in a channel right at the mouth of the Nikomekl River (ANR). This group was located inshore around Mud Bay, mainly in eel-grass beds. In both faunal analyses, the dissimilarity amongst these four stations was quite high. The second group included the high subtidal, sandy stations below chart datum (2m). This separation was also evident at the 4% level for the raw abundance pattern.

The Comtre2 comparison of the raw abundance and biomass-weighted abundance analyses tested the null hypothesis that the two dendrograms were the same. The hypothesis could not be rejected at any linkage level (Appendix 3o).

3. Environmental Analyses

The dendrogram representing the clustering of stations based on depth, sediment type and location (Fig. 30) shows a clear separation between the intertidal and high subtidal sandy stations and the subtidal, sandy-silt stations, with very low dissimilarity within groups. The

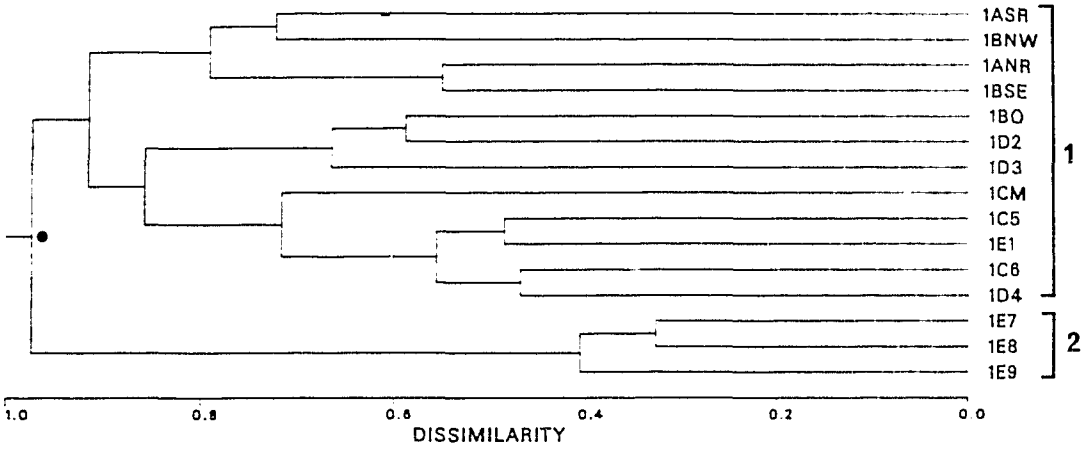

Figure 26. Cluster dendrogram for raw abundance data from Boundary Bay. Significances at the 2.5% level are indicated by one small dot.

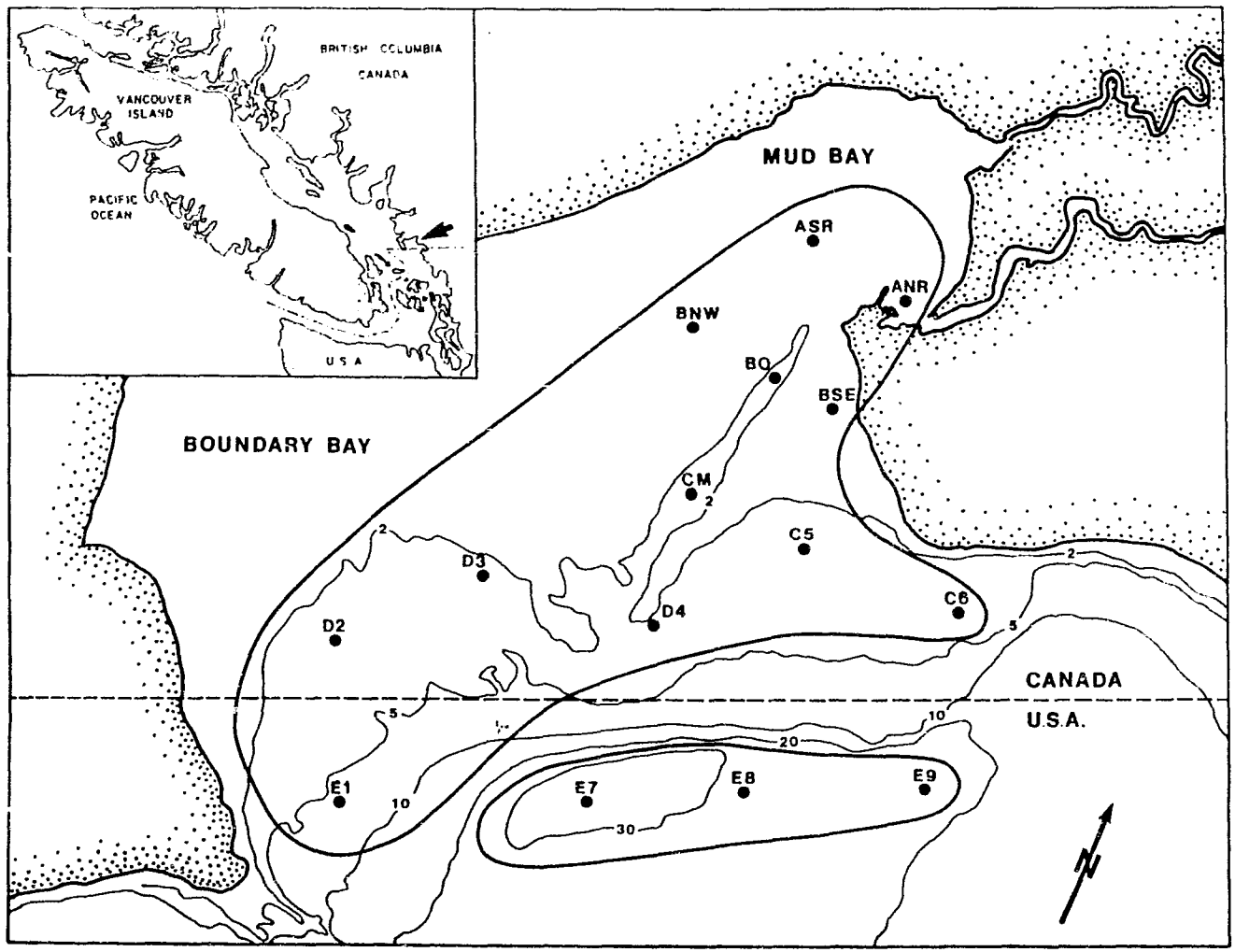

Figure 27. Station maps showing significant groupings for abundance sigtree analysis for Boundary Bay. Groups numbers match those illustrated in Fig. 26.

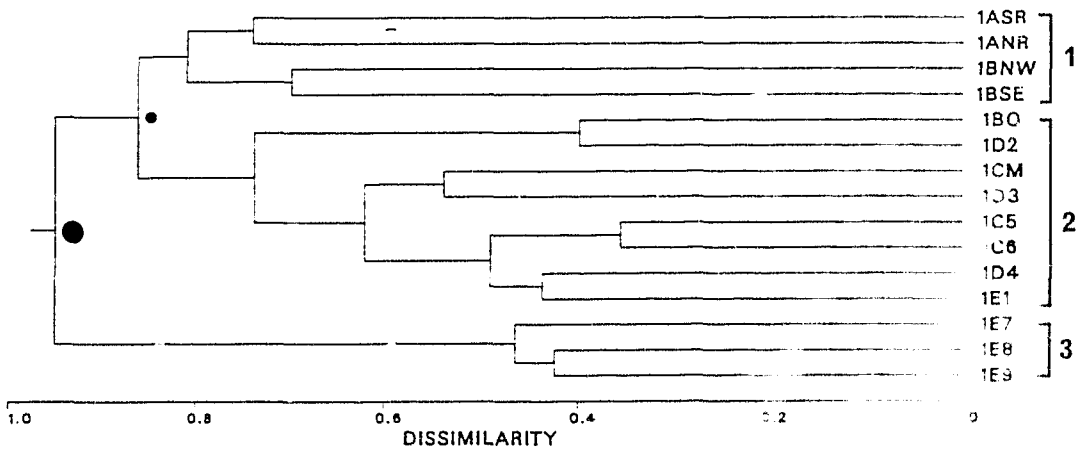

Figure 28. Cluster dendrogram for biomass weighted [illegible] Boundary Bay. Significances at the 1% level are ind[illegible] dot, and at the 2.5% level by one small dot.

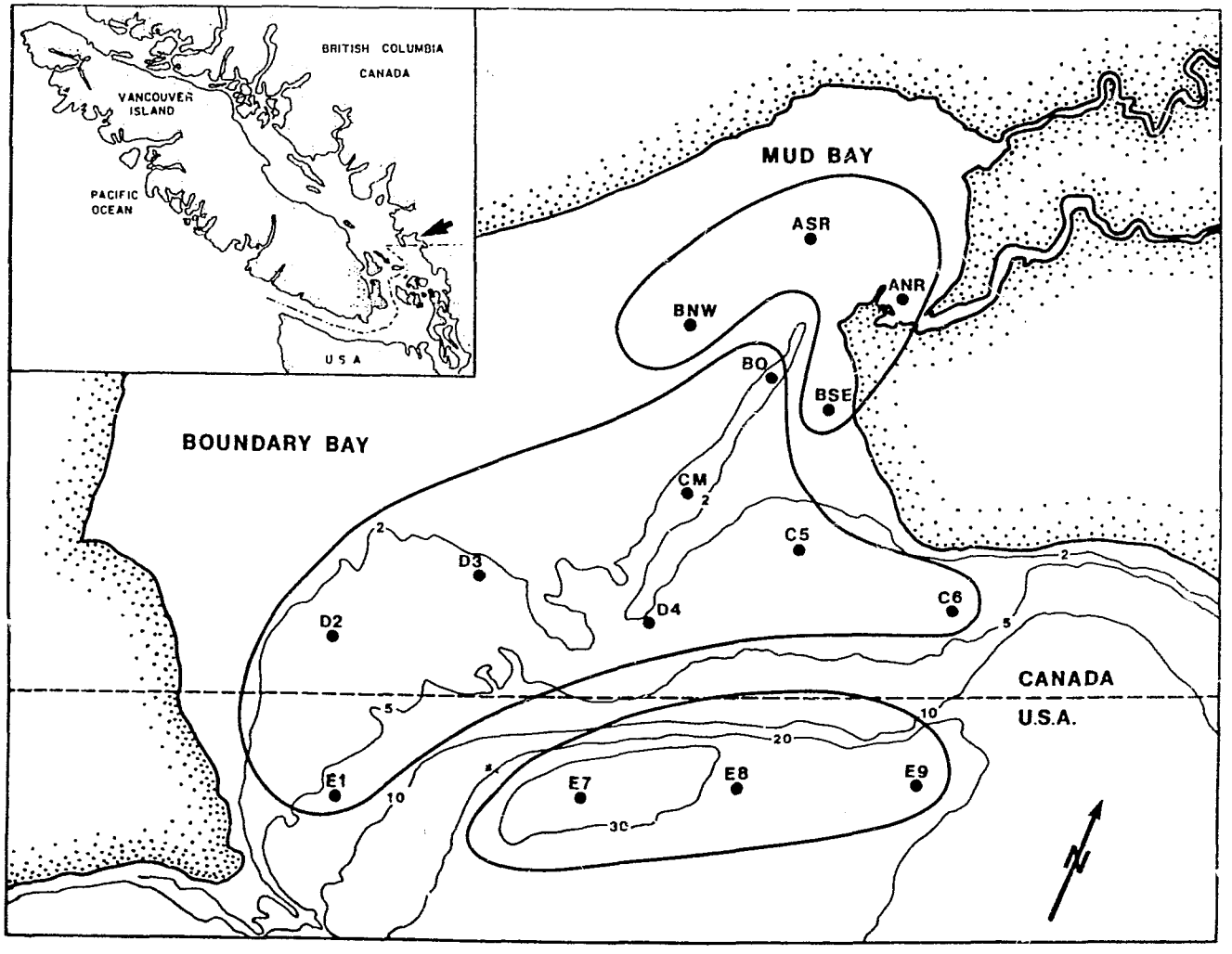

Figure 29. Station maps showing significant groupings for biomass-weighted sigtree analysis for Boundary Bay. Groups numbers match those illustrated in Fig. 28.

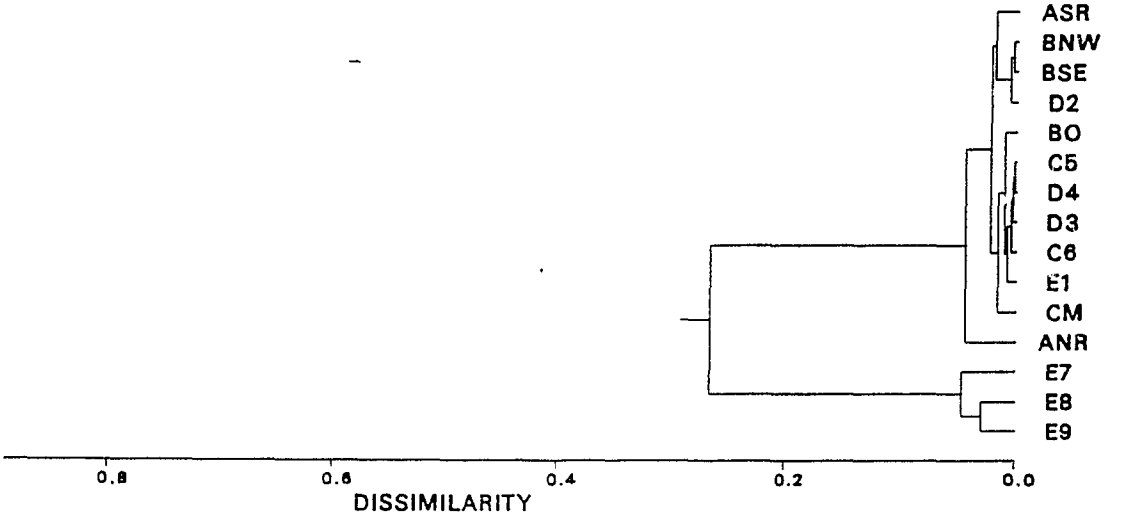

Figure 30. Environmental cluster dendrogram for Boundary Bay. Variables include depth, percent silt/clay, percent sand and geographic location.

hypothesis that the environmental dendrogram was different from either faunal dendrogram could not be rejected at any linkage level at $p \leq 2\%$ for either analysis (Appendices 3p,3q). Therefore, the Comtrel results suggest that there was no relationship between the environmental cluster pattern and the two faunal patterns.

C. DISCUSSION

The use of a small screen size (0.5mm) in this study resulted in high mean abundance values per station compared to the Hecate Strait, Alice Arm and Shelf surveys, whereas biomass and total taxa values were comparable to other studies. It might therefore be concluded that much of the fauna collected in Boundary Bay was quite small.

The shallow, sandy, intertidal and high subtidal stations were dominated by crustaceans, whereas the deep, silty subtidal stations were co-dominated by polychaetes and crustaceans. This pattern fits that described by Oliver *et al.* (1980) for shallow subtidal sandflats in California. In that study, the shallow areas (6-14m) were dominated by crustaceans, whereas the deeper areas (14-30m) were dominated by polychaetes. The authors concluded that the sediments in the shallow stations were commonly disrupted by wave activity and occupied by small, mobile, deposit-feeding crustaceans, with few tubicolous or burrowing animals. Tube development by burrowers is considerably reduced by the presence of marsh grass as well (Eckman 1983). The deeper stations had less disturbed sediments with more tube dwelling or burrowing species (Oliver *et al.* op. cit.), suggesting that a gradient of dominance change occurs with depth and changing substrate type. In Boundary Bay, the deeper stations may represent a transitional area between the two extremes described by Oliver *et al.* (op.cit.). This gradient pattern is similar to that found on a larger scale moving offshore over the pacific northwest continental shelf (Jumars and Banse 1989). The zonation between the two areas was most clearly accentuated by the high abundance of the ophiuroid *Dendraster excentricus* in the shallow, sandy stations, which were almost completely absent in the deeper silty stations. The

deep stations were in turn dominated in abundance and biomass by another species of ophiuroid, *Amphiodia urtica*.

Aside from the significance of the three groups in the biomass-weighted analysis versus only two in the raw abundance analysis, the two faunal cluster patterns were very similar. This suggests that the pattern of small faunal distribution was not particularly different from that of large fauna. Both the raw abundance and biomass-weighted abundance sigtree analyses in Boundary Bay resulted in a clear separation of the shallow, sandy stations from the deeper, silty stations. Considering the shift from polychaete to mixed polychaete/crustacean dominance in these two areas, this result is not surprising. However, only the biomass-weighted analysis resulted in a significant distinction between the four stations nearest to the estuarine influence (Mud Bay area) and closest to shore, from the remaining high subtidal sandy stations. According to Swinbanks and Murray (1981), and field notes from this study, at least three of the four shallow stations (excluding BSE) were in eel-grass beds. Station BSE bordered this zone and a zone of shell debris which used to be an oyster lease. All four stations were above chart datum, suggesting some tidal exposure (however, the depth of station ANR suggests that it was in a deep tidal channel which may have constant submergence or else experience changing depth). The splitting of the shallow, sandy stations into two groups suggests that the large fauna (particularly bivalves) may be distributed more discretely than small fauna, due to zonation of flora, tidal exposure and wave action (Oliver *et al.* 1980). Kellerhals and Murray (1969) and Swinbanks and Murray (1981) characterized the floral and faunal zones of the Boundary Bay intertidal area. They indicated that salinity does not vary appreciably over the exposed tidal flats, but that mean exposure is the main factor affecting intertidal zonation patterns. Lie (1968) examined the shallow, sandy communities of several stations in Puget Sound. He found many dominant species in common with those found in the current study (see also Burd *et al.* 1987).

The biomass was overwhelmingly dominated by bivalves in all stations. Therefore, changes in patterns of bivalve dominance would have the greatest effect on faunal distribution patterns in the biomass-weighted

analysis. For example, Swinbanks and Murray (1981) indicate that the burrowing bivalve *Mya arenaria* does not occur in the eel-grass zone. This species was common in BSE, but not the other three near-shore stations (Burd *et al.* 1987). The ubiquitous bivalve *Psephidia lordi* (the highest biomass contributor in the sandy stations) was also rare in the four near-shore stations, but common in the remaining sandy stations. This bivalve was found in abundance in all benthic survey areas discussed in this thesis.

The lack of significant linkages in the Comtrel comparison of faunal versus environmental dendrograms, despite the obvious similarity in patterns, points out the limitations of this method as a comparative tool when used in this simplistic manner. The faunal composition is obviously depth and substrate related to some extent, but the third factor (distance between stations) would not correspond to the along-shore zonation of faunal composition. As well, the environmental pattern does not take into account zonation of the various types of eelgrass (see Swinbanks and Murray 1981).

CHAPTER 8. FJORD SURVEY

A. INTRODUCTION

The fjord stations were surveyed originally to examine the smilarity or dissimilarity in faunal composition in different fjords along the mainland B.C. coast. These stations were included in the thesis because they are located north and south of the Alice Arm/Hastings Arm stations, in a similar habitat, but with no mining influence. As such, it was worthwhile to examine what "normal" fjord benthic faunal distributions were like, to see if the faunal distribution in Alice Arm was similar.

The stations included in this chapter were sampled in October of 1987. The survey consisted of a widespread collection of stations sampled in several B.C. fjords, from north of Alice Arm (see Chapter 3) south to 52^{o} latitude (Fig. 31). The stations were not located in areas affected by major anthropogenic factors. Station names (Fig. 31) were retained from the original survey, and were named as follows: F1203 where F1=Fjord survey cruise 1; and 203 = station 20-3. The first group of stations included 5a, 5b, 5c and 5d in Burke Channel, and stations 9 and 10 in Dean Channel (Fig. 31). The second geographic group included stations 13, 14-1, 14-3, 14-5, and station 15 in Douglas Channel. The final group of stations was located in Portland Canal, just north of Alice Arm and included stations 18, 20-1,20-3 and 20-5.

Station locations, depths and sediment types are given in Appendix 1. The fjord stations were the deepest sampled in the entire set of surveys (222 to 570 m), and were located in reasonably well-flushed basins, although stations 5A and 5C had sediments which smelled of hydrogen sulfide, suggesting oxygen deficiency. All of the stations in the fjord survey were located at depths ranging from 222m to 570m. Stations 5a, 14-1 and 14-3 had 50-75% sand, whereas the rest consisted of 75-100% silt (Appendix 1).

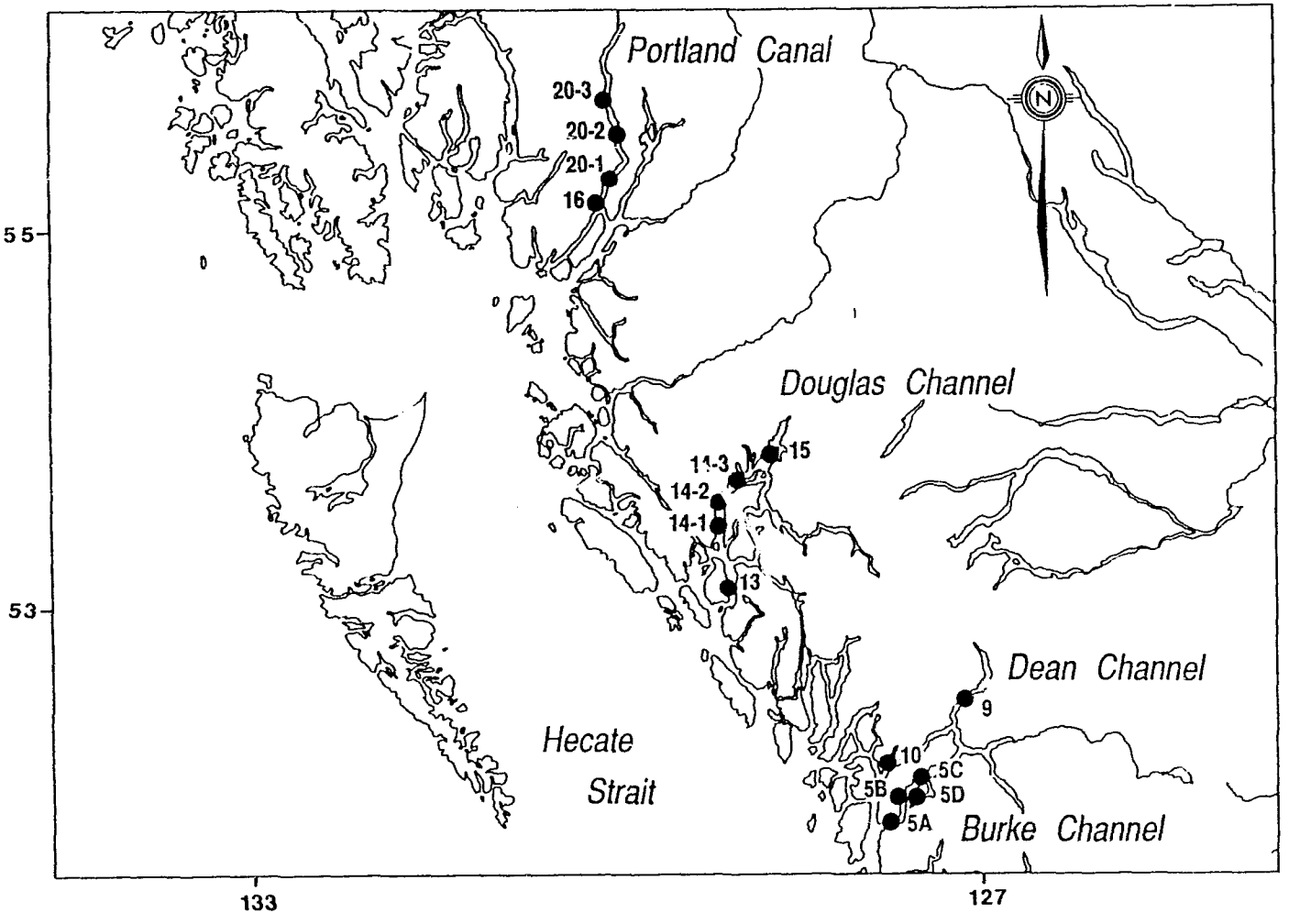

Figure 31. Station locations for the Fjord survey. The different geographic areas (Portland Canal, Douglas Channel and Dean Channel) are indicated with stations numbers.

B. RESULTS

1. Summary Statistics

The values for estimated biomass, mean abundance and total taxa per station are given in Table 13. Several stations (5b,5d) had very few animals, and values for station 10 were relatively low. The low faunal numbers in stations 5b and 5d may have been related to sampling problems during the initial cruise. Apparently there was some washout in the grabs upon retrieval. Faunal values were relatively high for stations 14-1,14-3,18 and 15. Biomass and abundance values were relatively high in the outermost stations of all three fjord areas (5A,14-1,18). Overall, abundances were low compared to the other survey areas (Chapters 3-7). Biomass values and number of taxa were comparable to most other surveys.

Polychaetes were the dominant taxon in the fjord stations, followed by echinoderms, crustaceans and bivalves (Table 14). In total, molluscs (bivalvia, aplacophora, scaphoda and gastropoda) represented the second most abundant phylum. Abundance dominants included the polychaetes *Maldane glebifex*, *Spiophanes berkeleyorum*, *Lumbrineris zonata*, *L. luti*, *Galathowenia oculata*, *Anobothrus gracilis*, *Levinsenia gracilis* and *Glyphanostomum pallescens*, the amphipod *Haploops tubicola*, the echinoderms *Ophiura leptoctenia* and *Brisaster latifrons* and the bivalve *Cadulus tolmiei*.

Biomass was dominated by echinoderms, including *Chiridota albatrossi*, *Molpadia intermedia*, *Ctenodiscus crispatus* and *Ophiura leptoctenia*. Other biomass dominants were the bivalves *Yoldia martyria*, *Cadulus tomiei* and *Macoma moesta*, the polychaetes *Nephtys punctata*, *Maldane glebifex*, *Pista brevibranchiata*, *Goniada annulata*, *Ampharete finmarchica*, *Scionella japonica*, *Spiophanes berkeleyorum* and the gastropod *Plicifusus kroyeri*.

Table 13. Mean biomass (wet weight in g/ $0.1m^2$), mean abundance (numbers per $0.1m^2$) and total taxa for all grabs in each fjord station. Values were based on two replicates per station.

	Mean Biomass $g/0.1m^2$	Mean Abundance $No/0.1m^2$	Total Taxa
F15A	3.33	43	33
F15B	0.05	5	9
F15C	1.79	24	18
F15D	0.13	2	4
F19	1.86	41	16
F110	1.08	13	14
F113	2.75	26	23
F1141	3.11	151	69
F1143	3.67	70	49
F1145	2.17	37	33
F115	1.97	39	31
F118	5.47	401	62
F1201	2.60	22	14
F1203	3.31	19	19
F1205	4.90	192	39

Table 14. Total abundance (numbers/ m^2) for major taxonomic groups in the fjord stations. Poly/Biv = ratio of polychaetes to bivalves.

	Abundance No/m^2
Polychaeta	496
Echinodermata	67
Crustacea	75
Bivalvia	59
Aplacophora	10
Scaphopoda	4
Gastropoda	10
Poly/Biv	8.4

2. Multivariate Statistical Analyses

Because abundance values for most fjord stations were low, and a large screen size (1mm) was used for sampling, a significance of 5% was used for testing statistical hypotheses. Therefore, the power of the test was probably low (see Chapter 2 section F),but a higher significance level would have introduced increased type I error. No Significant linkages at 7.5% were found.

Three significant groups and three singleton stations were identified in the Sigtree analysis of abundance (Fig. 32). The largest group consisted of a mixture of stations from all the fjords sampled. The second group consisted of two of the Portland canal stations, and the third group contained the two impoverished stations in Burke Channel (5B,5D), the latter of which was significantly distinct but not significantly homogeneous.

In the biomass-weighted abundance analysis, all but two of the stations formed one significant and homogeneous group at $p \leq 5\%$ (Fig. 33). The two stations which were significantly homogeneous and distinct from all others included the impoverished stations 5b and 5d.

The Comtre2 analysis tested the null hypothesis at each linkage level that the two faunal dendrograms were the same. The hypothesis could not be rejected at any linkage level (Appendix 3r), suggesting that the two dendrograms were not different.

3. Environmental Analysis

The environmental dendrogram (Fig. 34) showed that most stations were similar in terms of depth and substrate type. The mixed sand/silt stations (5a, 14-1, 14-3) clustered separately from the silty stations. Station 13, which was outside Douglas Channel, was dissimilar in terms of depth (550m) to all the other stations, and had a sediment composition midway between the two groups mentioned above.

There were no significant linkages in the Comtrel comparison between the raw abundance dendrogram and the environmental dendrogram (Appendix

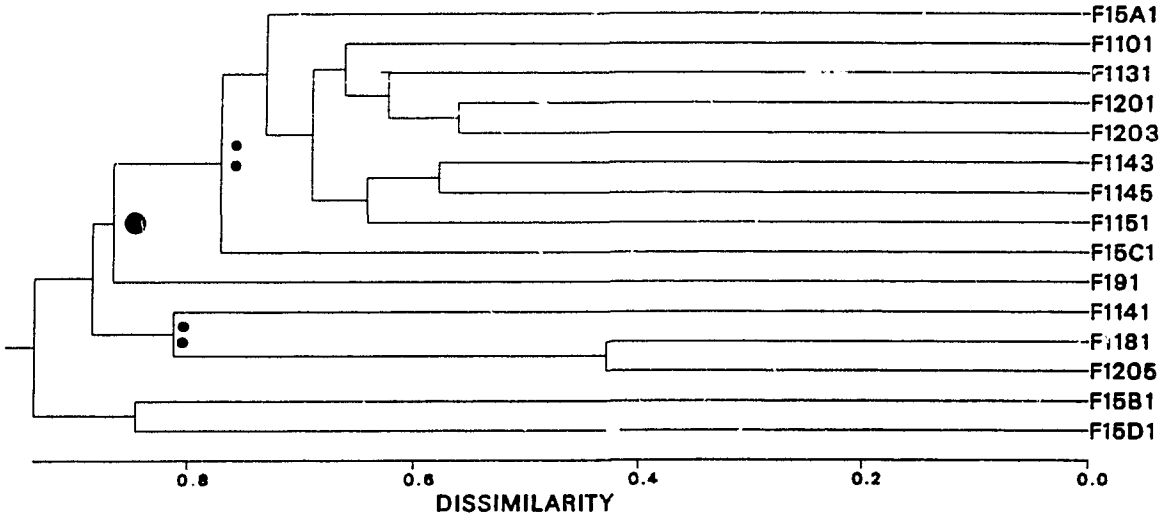

Figure 32. Cluster dendrogram for raw abundance data from the fjords survey. Significances at the 1% level are indicated by one large dot, and at the the 5% level by two small dots.

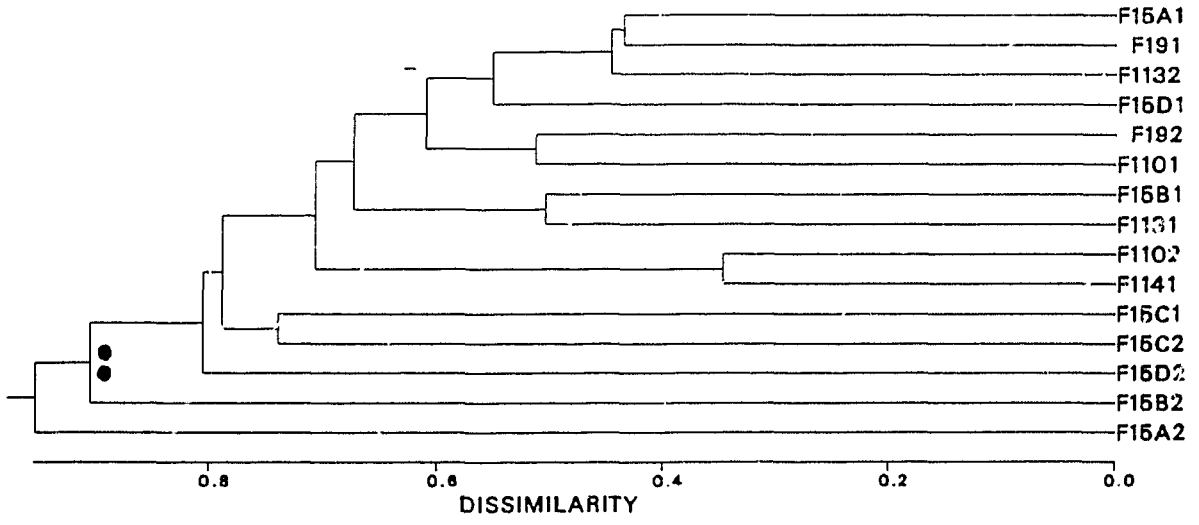

Figure 33. Cluster dendrogram for biomass weighted abundance data from the fjords survey. Significances at the 5% level are indicated by two small dots.

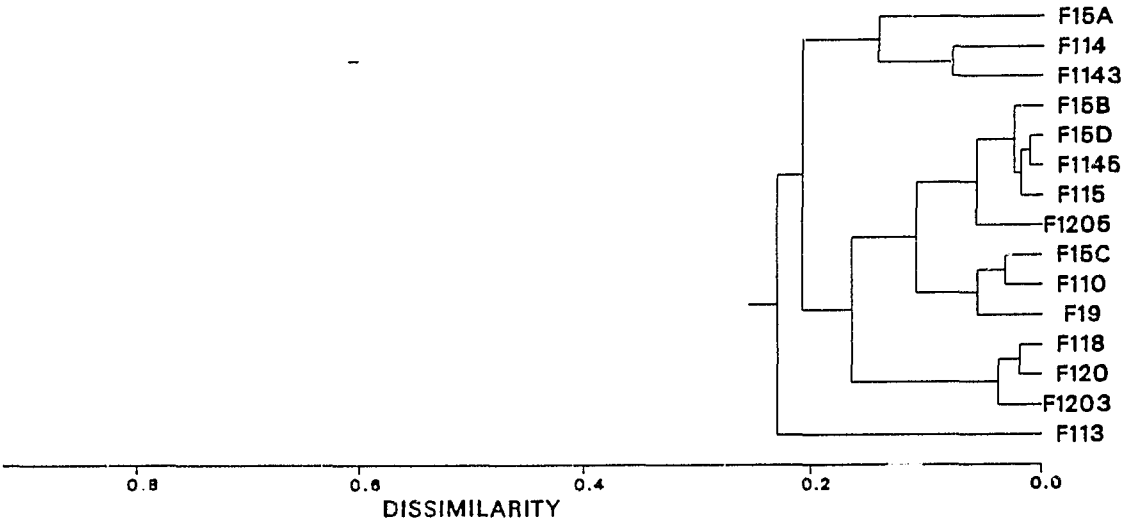

Figure 34. Environmental cluster dendrogram for the fjords survey. Variables include depth, percent silt/clay, percent sand and geographic location.

3s). Therefore the hypothesis that the two dendrograms were different could not be rejected at any linkage. There was one significant linkage (out of 14) between the environmental dendrogram and the biomass-weighted dendrogram (Appendix 3t). The similarities between the biomass-weighted and environmental dendrogram were not striking, except in the pairing of some stations.

C. DISCUSSION

Stations from the three main fjord areas were not distinct from each other in terms of the composition of large and small fauna. The similarity in faunal composition is somewhat surprising considering the distance between sampling areas. There were often greater differences in community composition within fjords than between widely spaced fjords. Although unmeasured, the rates of sedimentation, hydrographic and nutrient conditions of each fjord might be expected to be unique and variable based on the unique history of each runoff system, so that one might hypothesize that each fjord would be characterized by its own community structure. The results of this survey suggest instead that there may be some uniformity in conditions within all coastal fjords in B.C., manifested in commonality of benthic faunal structure. There may also be a suite of ubiquitous species tolerant of a wide range of conditions (particularly in terms of sedimentation), with widely dispersed larval forms, which form the basic component of all B.C. fjord benthic assemblages. This latter possibility is not unreasonable, since all of the fjords sampled are well flushed and subject to exchange with outside waters.

The biomass-weighted dendrogram was more closely related than the abundance pattern to the environmental dendrogram. However, this relationship was not striking (1 out of 14 linkages significant). Therefore it can be concluded that the environmental parameters measured did not effectively characterize the macrofaunal composition of the fjords sampled. It is not surprising that the composition of benthic fauna was not strongly related to the environmental

factors, since the results of the Alice Arm survey suggested that submarine turbidity currents (c.f. Borhnold 1983, Prior *et al.* 1984) and depositional characteristics can have a much stronger influence on fjord benthos than depth or sediment type.

CHAPTER 9. COMPARISON OF ALL SURVEY AREAS

A. INTRODUCTION

Because of the obvious problems involved in comparing studies which use different sampling methods, there have been no similar attempts to quantitatively compare benthic faunal patterns on a large scale. In this chapter I will discuss the relative merits of the multivariate inferential analyses for a faunal study based over such a broad geographic area. The discussion will include the potential effects of the different sampling methods, the information value, consensus and differences in results for analyses of abundance versus biomass-weighted data and how these relate to the summary statistics. Finally, the usefulness of the multivariate analyses (Sigtree, Comtre1, Comtre2) will be discussed in relation to the combined dataset for all surveys.

This chapter will also include a general comparison of the faunal composition of the different survey areas described in chapters 3 to 8. Oceanographic studies of the B.C. coastline provide information for speculating on the dispersal patterns of fauna among the survey areas. Comparisons of faunal patterns over all the survey areas will also be related to station patterns based on environmental variables. Conclusions and hypotheses generated from these comparisons will be discussed in relation to north/south or onshore/offshore gradients in the distribution of benthic species composition of both large and small fauna.

B. RESULTS

In this chapter, all of the data from survey areas described in Chapters 3 to 8 were combined into two large faunal databases, one for raw abundance data (ABUNBASE), the other for biomass-weighted abundance data (BIOBASE). As well, the environmental data common to all surveys (depth, sediment type, geographic location) were combined into one environmental database (ENVIROBASE). These databases represent a mixture of all the survey stations, as well as temporal data for the stations

from Hecate Strait, Alice Arm, Shelf, and Vancouver Harbour. The faunal databases contained a total of 500 replicates at 191 stations, with 690 species.

The entire list of station locations, depths and sediment types is included in Appendix 1. The data were collected from a range of habitat types from low intertidal (Boundary Bay), through shallow subtidal (Vancouver Harbour), deep coastal fjords (Alice Arm, fjords), shallow to deep marine straits (Hecate Strait), and finally, inner continental shelf (Shelf). Substrate types ranged from very fine silts to very coarse sand and gravel or shell debris. Habitat types were summarized for each survey area in Chapters 3 to 8 and will be examined in this chapter.

1. Summary Statistics

Mean biomass, mean abundance and number of species overall for each survey area have been combined in Table 15. These values were based on results from Tables 2, 4, 6, 8, 11 and 13. For ranges in values the reader is refered back to the original tables. The highest mean biomass values occured in the data from the two Vancouver Harbour surveys, followed by Alice Arm (1986) and Boundary Bay, and the lowest values were found in the first two Alice Arm surveys. Generally, mean biomass values for all areas fell within a range of about 20 to 60 g/m^2. Mean abundance values were highest for Vancouver Harbour and Boundary Bay and lowest for the Alice Arm/Hastings Arm and the remaining fjord stations. Abundance values fluctuated from about 50 to about 1700 animals per m^2. The taxa numbers were highest in the shelf surveys, and lowest in Alice Arm and fjords. Like biomass, taxa numbers varied by about a factor of 4 for different areas.

Total abundance per square meter for major taxonomic groups was summarized for all the survey areas as mean abundances per square meter (Table 16), along with polychaete to bivalve ratio. Percent of total abundance for each taxon were calculated (Table 17) to examine the relative contribution of taxa in different areas regardless of overall abundance, which varied considerably from one survey area to another. The ENVIROBASE group (see below) is also listed for

Table 15. Mean biomass (wet weight in g/0.1 m^2), mean abundance (number/0.1 m^2) and mean total taxa per station for all survey areas in the study. Values were averaged for all stations from Tables 2, 4, 6, 8, 11 and 13.

		Mean Biomass g/0.1m^2	Mean Abundance No/0.1m^2	Total Taxa
Alice/Hastings Arm	1982	2.01	109	22
Alice/Hastings Arm	1983	1.72	52	19
Alice/Hastings Arm	1986	4.35	110	36
Alice/Hastings Arm	1989	2.98	45	26
Hecate Strait	Cruise 1	2.73	190	59
Hecate Strait	Cruise 2	2.49	245	61
Hecate Strait	Cruise 3	1.78	208	59
Shelf	Cruise 1	3.10	237	86
Shelf	Cruise 2	3.01	228	84
Vancouver/Port Moody	1987	6.15	1664	41
Vancouver/Port Moody	1989	4.50	735	39
Boundary Bay	1986	3.21	1001	47
B.C. fjords	1988	2.55	72	29

Table 16. Summary of total abundance (numbers/ m^2) for major taxa for the different survey areas, from Tables 3, 5, 7, 9, 12 and 14. Poly/Biv = ratio of polychaetes to bivalves. Poly=polychaetes; Biv=bivalves; Gastro=gastropods; Echino=echinoderms; Crust=crustaceans. Poly/Biv= ratio of polychaetes to bivalves.

Survey Area	time	Poly	Biv	Gastro	Echino	Crust	Sediment	Poly/Biv
Alice Arm	1982	[illegible]	466	7	28	23	Silty	0.76
Hastings Arm	1982	1183	308	30	23	9	Silty	3.84
Alice Arm	1983	82	280	5	43	26	Silty	0.29
Hastings Arm	1983	83	600	12	18	22	Silty	0.14
Alice Arm	1986	495	533	6	82	80	Silty	0.93
Hastings Arm	1986	76	413	23	27	27	Silty	0.18
Alice Arm	1989	206	147	38	91	11	Silty	1.40
Hastings Arm	1989	76	47	2	20	12	Silty	1.62
Hecate 1	Area A	817	621	27	35	95	Silty	1.32
Hecate 2	Area A	1713	818	69	73	207	Silty	2.09
Hecate 3	Area A	1388	301	25	19	39	Silty	4.61
Hecate 1	Area B	727	1711	17	45	91	Sand/gravel	0.42
Hecate 2	Area B	2103	1431	17	73	93	Sand/gravel	1.47
Hecate 3	Area B	940	2105	23	145	59	Sand/gravel	0.45
Hecate 1	Area C	790	351	42	10	103	Silty sand	2.25
Hecate 2	Area C	1181	573	53	47	85	Silty sand	2.06
Hecate 3	Area C	1317	327	23	27	85	Silty sand	4.03
Hecate 2	Area D	440	0	33	3	81	Sandy	N/A
Hecate 3	Area D	419	311	51	15	173	Sandy	1.35
Shelf 1	A1-C1	1326	120	8	20	148	Silty	10.36
Shelf 1	C4-D4	1507	313	5	38	350	Sandy	4.74
Shelf 2	A1-C1	1582	185	13	33	190	Silty	8.26
Shelf 2	C4-D4	1052	333	5	18	83	Sandy	3.08
Vancouver Hbr	1987	11917	8367	1936	22	1364	Sandy silt	1.42
Port Moody Arm	1987	2966	988	149	0	290	Silty	3.00
Vancouver Hbr	1989	5156	2534	359	3	1010	Sandy silt	2.03
Port Moody Arm	1989	3068	1562	227	4	1906	Silty	1.96
Boundary Bay	ANR-E1	1814	3396	349	38	5624	Coarse sand	0.53
Boundary Bay	E7-E9	1277	470	140	600	1203	Sandy silt	2.72
B.C. fjords	All	496	59	10	67	75	Silty	8.41

Table 17. Summary of relative abundances (percent) for major taxa for all survey areas, recalculated from Table 16. Poly=polychaetes; Biv=bivalves; Gastro=gastropods; Echino=echinoderms; Crust=crustaceans. Poly/Biv= ratio of polychaetes to bivalves.

Survey Area	time	Poly	Biv	Gastro	Echino	Crust	ENVIROBASE Group (Fig. 37)
Alice Arm	1982	40.4%	53.0%	0.8%	3.2%	2.6%	5
Hastings Arm	1982	76.2%	19.8%	1.9%	1.5%	0.6%	5
Alice Arm	1983	18.8%	64.2%	1.1%	9.9%	6.0%	5
Hastings Arm	1983	11.3%	81.6%	1.6%	2.4%	3.0%	5
Alice Arm	1986	41.4%	44.6%	0.5%	6.9%	6.7%	5
Hastings Arm	1986	13.4%	73.0%	4.1%	4.8%	4.8%	5
Alice Arm	1989	41.8%	29.8%	7.7%	18.5%	2.2%	5
Hastings Arm	1989	48.4%	29.9%	1.3%	12.7%	7.6%	5
Hecate 1	Area A	51.2%	38.9%	1.7%	2.2%	6.0%	4
Hecate 2	Area A	59.5%	28.4%	2.4%	2.5%	7.2%	4
Hecate 3	Area A	78.3%	17.0%	1.4%	1.1%	2.2%	4
Hecate 1	Area B	28.1%	66.0%	0.7%	1.7%	3.5%	3
Hecate 2	Area B	56.6%	38.5%	0.5%	2.0%	2.5%	3
Hecate 3	Area B	28.7%	64.3%	0.7%	4.4%	1.8%	3
Hecate 1	Area C	61.0%	27.1%	3.2%	0.8%	7.9%	4
Hecate 2	Area C	60.9%	29.6%	2.7%	2.4%	4.4%	4
Hecate 3	Area C	74.0%	18.4%	1.3%	1.5%	4.8%	4
Hecate 2	Area D	79.0%	0.0%	5.9%	0.5%	14.5%	4
Hecate 3	Area D	43.2%	32.1%	5.3%	1.5%	17.9%	4
Shelf 1	A1-C1	81.8%	7.4%	0.5%	1.2%	9.1%	7,6
Shelf 1	C4-D4	68.1%	14.1%	0.2%	1.7%	15.8%	4
Shelf 2	A1-C1	79.0%	9.2%	0.6%	1.6%	9.5%	7
Shelf 2	C4-D4	70.6%	22.3%	0.3%	1.2%	5.6%	4
Vancouver Hbr	1987	50.5%	35.4%	8.2%	0.1%	5.8%	1,2
Port Moody Arm	1987	67.5%	22.5%	3.4%	0.0%	6.6%	1
Vancouver Hbr	1989	56.9%	28.0%	4.0%	0.0%	11.1%	1,2
Port Moody Arm	1989	45.3%	23.1%	3.4%	0.1%	28.2%	1
Boundary Bay	ANR-E1	16.2%	30.3%	3.1%	0.3%	50.1%	3
Boundary Bay	E7-E9	34.6%	12.7%	3.8%	16.3%	32.6%	2
B.C. fjords	All	70.2%	8.3%	1.4%	9.5%	10.6%	5.6

each area in Table 17.

Abundance of polychaetes per square meter varied by several orders of magnitude. In Vancouver Harbour (cruise 1), polychaete numbers were an order of magnitude higher than in any other survey. Because of the very small screen size (0.3mm) used in Vancouver Harbour, many of the polychaetes were small. The lowest polychaete abundance values occurred in several of the Alice Arm surveys (not related to screen size, see chapter 3). Relative to other taxa, polychaetes tended to be less abundant in sandy areas (Boundary Bay, Hecate area B and D, Shelf C4-D3) than in silty ones.

Bivalves were abundant in most areas, particularly in sandy substrates. Relative abundance was low in the fjords (Table 17), and in the silty stations of the Shelf survey. Bivalve abundances were highest in the mixed sand/silt Vancouver Harbour stations in 1987. Bivalves dominated the fauna in Alice Arm from 1982 to 1986, in Hastings Arm in 1983 and 1986 and in the shallow, sandy Boundary Bay stations. Bivalves were completely lacking in Hecate Strait area D (an area with low biomass) during cruise 2, This probably ocurred because of a mistake in the original processing of samples (see Chapter 4).

Relative to other taxa, gastropods were most common in the shallow survey areas (Vancouver Harbour, Boundary Bay), and considerably less common in the deep areas. In particular, gastropods were very low in abundance in the shelf surveys, and in the deepest stations sampled (B.C. fjords). In Alice Arm, gastropods were rare from 1982 to 1986 and common in 1989.

Crustaceans were the most common taxa after polychaetes and bivalves. Although crustaceans were lowest in abundance in the deep near-shore survey areas (fjord, Alice Arm) and moderately abundant in Hecate Strait and shelf stations, there was very little difference in abundance of crustaceans relative to other taxa in the aformentioned areas (Table 17). However, crustaceans were very common or dominant in the shallow, nearshore areas (Vancouver Harbour, Boundary Bay), and were the dominant taxa in the shallow, sandy Boundary Bay stations.

Echinoderms were low in abundance in most areas. The ophiuroid *Amphiodia urtica* was very abundant in the subtidal, silty Boundary Bay

stations. Echinoderms were also high in abundance relative to other taxa in Alice Arm in 1983 and 1989 (Table 17), in Hastings Arm in 1989 and in the Fjords survey. Relative echinoderm abundance was low in area D in Hecate Strait, in Vancouver Harbour and Port Moody Arm and in the shallow, sandy stations of Boundary Bay. Echinoderms were absent in Port Moody Arm during the first cruise (actually 3 specimens of unidentified *Amphiodia* were present - see Burd and Brinkhurst 1990b).

Abundance and biomass dominants were described in the individual chapters (3-8). The presence or absence of all species in each survey area was listed in Appendix 4. Species which occurred in all survey areas were the bivalves *Psephidia lordi*, *Nucula tenuis* and *Axinopsida serricata*, the crustacean *Heterophoxus oculatus*, the echinoderm *Molpadia intermedia*, and the polychaetes *Lacesta lopezi*, *Galathowenia oculata*, *Levinsenia gracilis*, *Prionospio steenstrupi*, *Sternaspis scutata*, and *Lumbrineris luci*. Many of the aforementioned species were abundance or biomass dominants in the various study areas. Most of these were small species, except for *M. intermedia*. A second group of species ocurred in almost all survey areas. These were the bivalve *Mya arenaria*, the gastropod *Mitrella gausapata*, and the polychaetes *Cossura longocirrata*, *Leitoscoloplos pugettensis*, *Glycinde armigera* and *Pholoe minuta*. Because almost 700 taxa were identified in this set of surveys, it was not feasible to qualitatively describe trends in patterns of individual species in this thesis. Similarity in species composition is therefore best handled by the use of a multivariate inferential comparison (such as Sigtree - see below).

2. Statistical Analyses

It was difficult to decide upon a significance level in the following statistical analyses, since the databases contained a mixture of abundances, replicate numbers, grab sizes and screen sizes for the stations. In chapters 3-8, probabilities for rejection of hypotheses ranging from 1% to 7.5% were used. For the comparison of all survey areas in this chapter, 1% was most conservative in terms of type 1 error and the escalating error resulting from multiple tests, but problematical in

terms of power for some of the survey areas (Alice Arm, fjords and shelf in particular). Therefore, a probability of 1% was considered significant for all linkages, and probabilities of 2% were discussed for Sigtree analyses when they occurred within the Alice Arm, fjords, and shelf survey station groups. Because the multiple comparisons problem was greater with Comtre than Sigtree (for discussion see Chapter 2 section F), a significance level of 1% was used for rejection of the hypotheses in Comtre.

a. Sigtree analysis of abundance data

The cluster pattern and significant linkages for the raw abundance data (ABUNBASE) are shown in Fig. 35. The patterns within areas were very similar to those described for the individual survey areas (Chapters 3-8), except for instances where certain stations or groups were mixed with stations from other survey areas.

Vancouver Harbour and Port Moody Arm stations (Chapter 6) were intermixed to some degree, forming 5 significantly ($p \leq 1\%$) distinct, (but not necessarily homogeneous) groups (groups 1-5, Fig. 35). This set of stations formed a coherent subset of the overall dendrogram, with all but the three defaunated stations (see below) more similar to each other than to the other survey areas. Two significantly distinct and homogeneous ($p \leq 1\%$) groups (6,7) of the Boundary Bay shallow, sandy stations was linked most closely with the overall Vancouver Harbour/Port Moody set of stations. Three of the sandy Boundary Bay stations were missing from this group (see groups 9 and 10).

All but the four most seriously defaunated Alice Arm stations from 1982 formed a significantly distinct (but non-homogeneous) group at the 1% level (groups 8-11). Within this group, the 1983 and 1986 E stations grouped with the remaining three shallow, sandy Boundary Bay stations. Two of these Boundary Bay stations formed a significantly distinct group at 2% (group 9) as well as a significantly distinct and homogeneous group of the E stations from Alice Arm in 1982 to 1986, plus a Boundary Bay sandy station (group 10). Most of the fjord stations clustered together

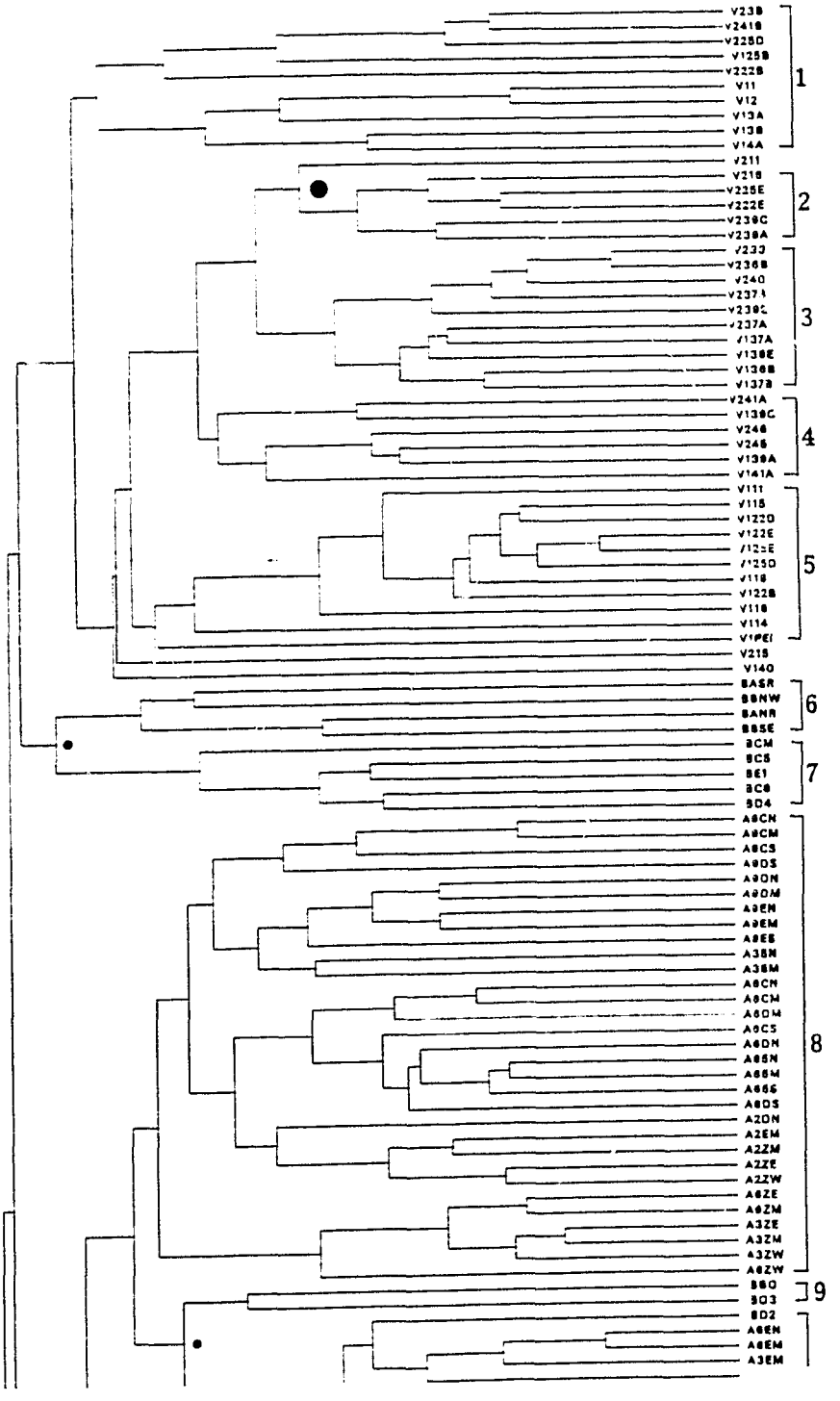

Figure 35. Cluster dendrogram for abundance data from ABUNBASE. Significances at the 1% level are indicated by the single large dot and at the 2% level in Alice Arm, fjords and Shelf by the small dot.

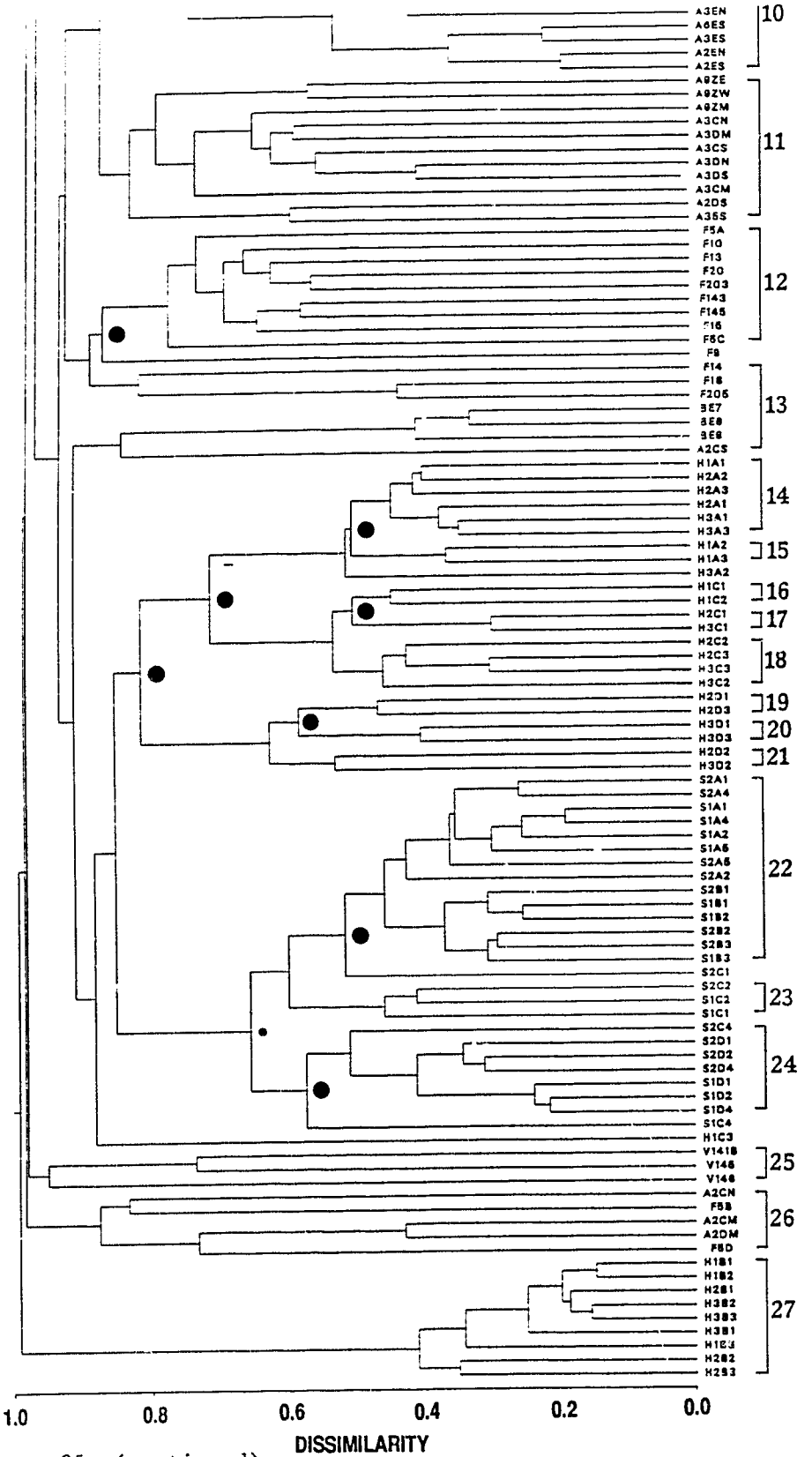

Figure 35. (continued)

as a significantly distinct and homogeneous group ($p \leq 1\%$, group 12) with one significantly distinct station and one group of three significant but non-homogeneous stations (group 13). The two impoverished fjord stations (5B,5D) were not grouped with the rest of the fjord stations. The fjord stations were most similar to, but significantly distinct from the Alice Arm groups.

The Hecate stations from areas A, C and D formed a coherent unit, with two significantly distinct groups of A stations (groups 15,16), three groups of C stations (17-19) and three groups of D stations (20-22). This group was most similar to the Shelf stations. Station H1C3, which was impoverished in abundance and biomass (chapter 4), was significantly distinct from the other Hecate Strait and shelf stations.

The subtidal Boundary Bay stations formed a significantly distinct but non-homogeneous group along with an impoverished 1982 station (2CS) from Alice Arm. The shelf stations formed a coherent unit, with the silty A and B stations significantly distinct ($p \leq 1\%$) from the silty C1 and C2 stations. The sandy shelf stations (C4-D3) formed three distinct groups at $p \leq 1\%$ (each C4 station as a singleton, and the D stations as a group). The Boundary Bay subtidal group (plus A2CS-group 14 above) was most similar to the Hecate Strait and Shelf stations.

Two significant but non-homogeneous groups of low abundance stations were evident (Fig. 35), with the three defaunated Vancouver Harbour (1987) stations (see Chapter 6) forming one group (group 26), and the Alice Arm (2CN, 2CM, 2DM) and fjord (5B,5D) impoverished stations forming the second group (group 27). Therefore, the Alice Arm and fjord stations displayed some similarity in the pattern of faunal impoverishment.

The final group was distinctly dissimilar to all other groups, and included the shallow, coarse substrate stations from Hecate area B (group 28). The species composition of these stations was significantly distinct but not homogeneous ($p=4.4\%$) despite the low dissimilarities between stations within the group.

b. Sigtree analysis of biomass-weighted abundance data

The cluster pattern of biomass-weighted data (BIOBASE) is shown in Fig. 36. As in ABUNBASE, the first unit of stations included several significant Vancouver harbour and Port Moody Arm station groups (groups 1-7). The Port Moody Arm stations clustered separately from the Vancouver Harbour stations in 4 significant and homogeneous ($p \leq 1\%$) groups. Station V216 was the only Vancouver Harbour station mixed with the Port Moody Stations. Station V216 was also grouped with the silty stations from Port Moody Arm in the environmental analysis (group 1, Fig. 36). The Vancouver Harbour stations were split into several groups and single stations. The Boundary Bay subtidal silty stations all formed one distinct (but not homogeneous) group (8) and clustered with the Vancouver Harbour stations. Station V11 (Vancouver Harbour) was distinct and joined group containing the remaining Vancouver/Port Moody and silty Boundary Bay stations.

The Hecate A and C stations each formed distinct and homogeneous groups (groups 9,10, $p \leq 1\%$), and were most similar to each other. The Shelf stations formed one significantly distinct but non-homogeneous group, including both the sandy and the silty stations (group 11). The Shelf A and B stations almost formed a significantly distinct group from all of the C and D stations ($p = 2.8\%$) as in ABUNBASE (see Chapter 4). The shelf group was most similar to the Hecate A and C groups. The low biomass and abundance station, C3 from Hecate cruise 1, joined the larger Hecate/Shelf grouping (as in ABUNBASE).

The next set of stations in the dendrogram included all of the Alice Arm and Hastings Arm stations (group 12), except the impoverished stations (group 17). All the Fjord stations except F5D were intermixed with the Alice Arm stations, with most of the fjord stations similar to each other.

Group 13 (Fig. 36) was a distinct and homogeneous group of all the sandy, intertidal (A3R-E1) and high, subtidal Boundary Bay stations (E7-E9). This was in contrast with the results from Chapter 7, in which these stations formed two distinct groups (probability of two groups = 4.4% in BIOBASE). The aforementioned Boundary Bay group was most similar to,

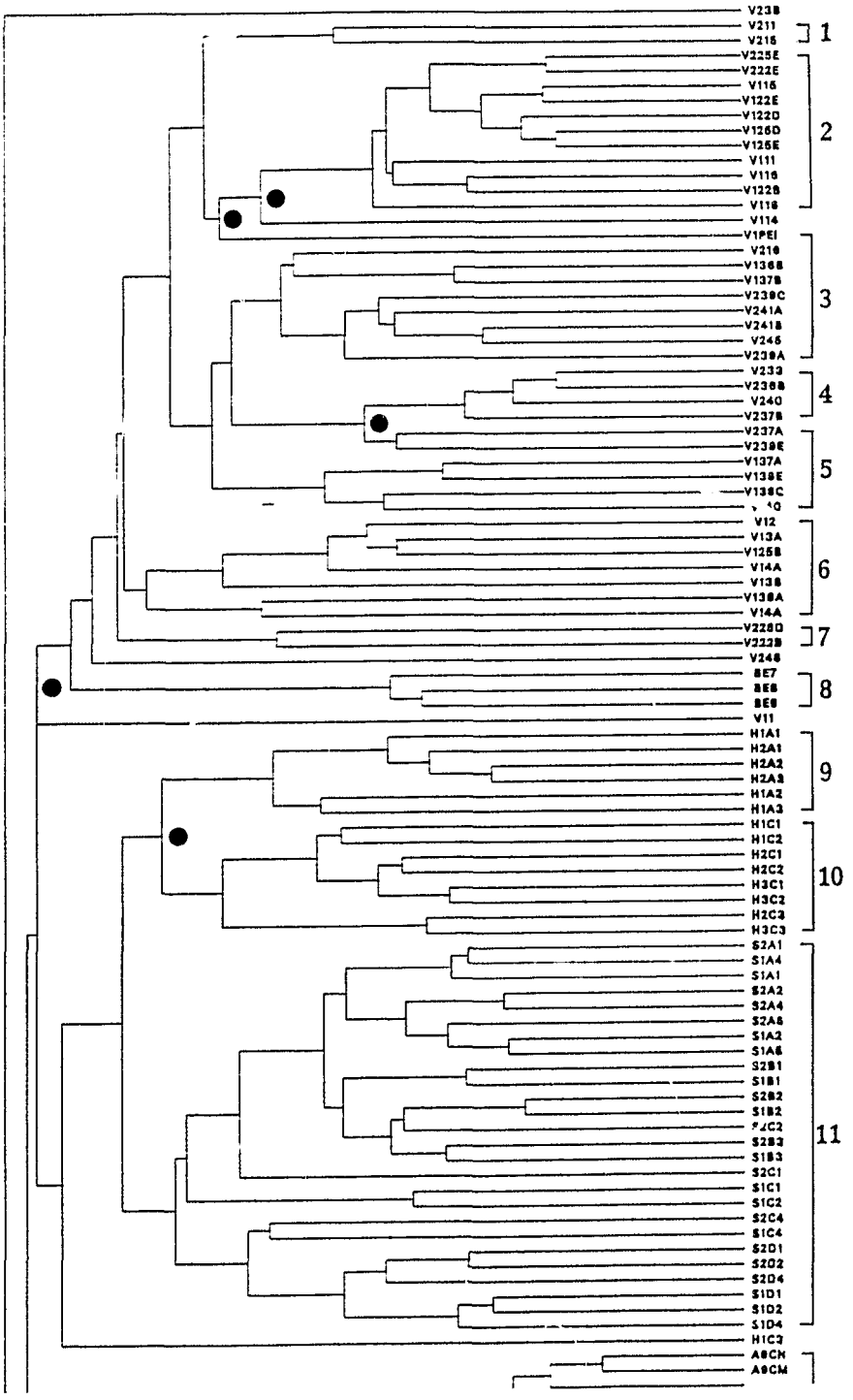

Figure 36. Cluster dendrogram for biomass weighted abundance data from BIOBASE. Significances at the 1% level are indicated by the single large dot.

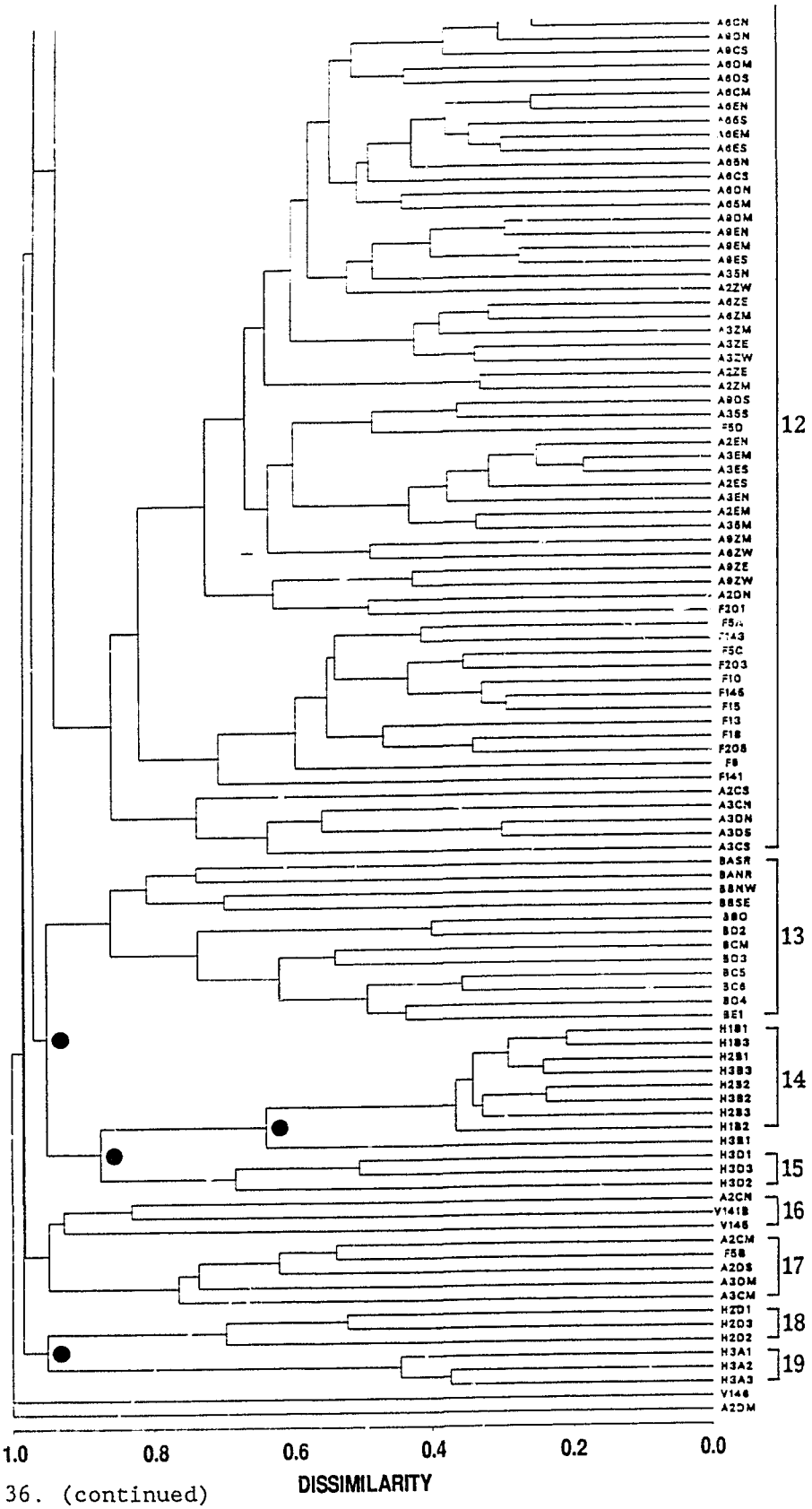

Figure 36. (continued)

but distinct from the Hecate B stations (group 14). As well, the Hecate B stations were clustered with, but distinct from the Hecate D stations from cruise 3 (group 15), as noted in Chapter 4.

Groups 16 and 17 in BIOBASE were distinct but non-homogeneous groups of defaunate stations, similar to groupings in ABUNBASE. There was no clear distinction in BIOBASE between the Vancouver Harbour, fjord and Alice Arm defaunated stations. The remaining impoverished Alice Arm station (A2DM) and one Port Moody Arm station (V146) were singletons dissimilar to all other stations. One final isolated set of stations included the area D stations from the second Hecate Strait survey (group 18) and the area A stations from the third Hecate Strait cruise (group 19). These formed two distinct and homogeneous groups, and shared a similar defaunation pattern in the large fauna.

c. Comtre2 Comparison of ABUNBASE and BIOBASE

The hypothesis that the two faunal dendrograms were the same could not be rejected at any linkage level below a probability of 21% (Appendix 3u). In fact, most of the probabilities on the linkages were 90% or higher, suggesting that there was no significant difference between the abundance and biomass-weighted patterns.

d) Cluster analysis of environmental data

Figure 37 depicts the habitat differences among groups, based on ENVIROBASE. Because the environmental data was not replicated at each station in some surveys, it was not possible to run a Sigtree analysis on this data. Therefore, the resulting groups in the cluster analysis of environmental factors have been arbitrarily sorted into seven convenient descriptive units as illustrated in the dendrogram (Fig. 38):

1) Group 1 encompassed all of the shallow subtidal, silty stations in Vancouver Harbour and Port Moody Arm, in the southern portion of B.C.

2) Group 2 represented the shallow subtidal mixed sand/silt stations, also located in southern B.C. This included most of the remaining

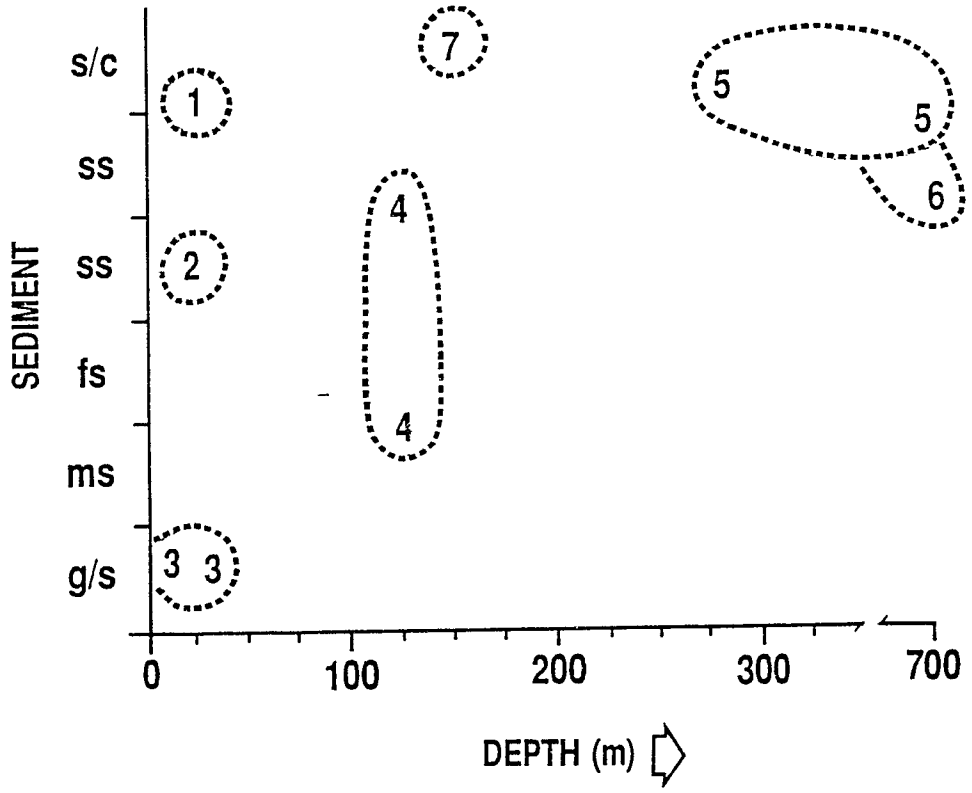

Figure 37. Graphical depiction of the relationship between the station groups illustrated in Fig. 38, based on depth and sediment type. G/S = gravel/coarse sand, MS = medium sand, FS=fine sand, ss =silty sand or sandy silt, S/C = silt/clay. Numbers refer to arbitrarily selected groups shown in Fig. 38.

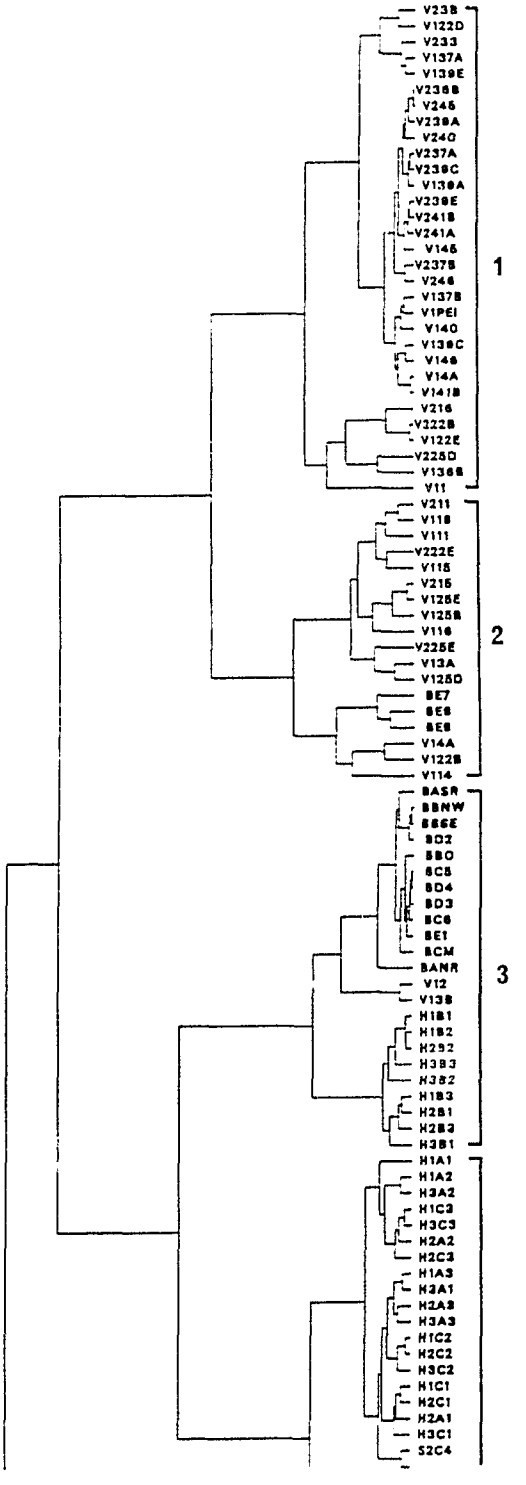

Figure 38. Environmental cluster dendrogram for the overall set of surveys. Variables include depth, percent silt/clay, percent sand and geographic location.

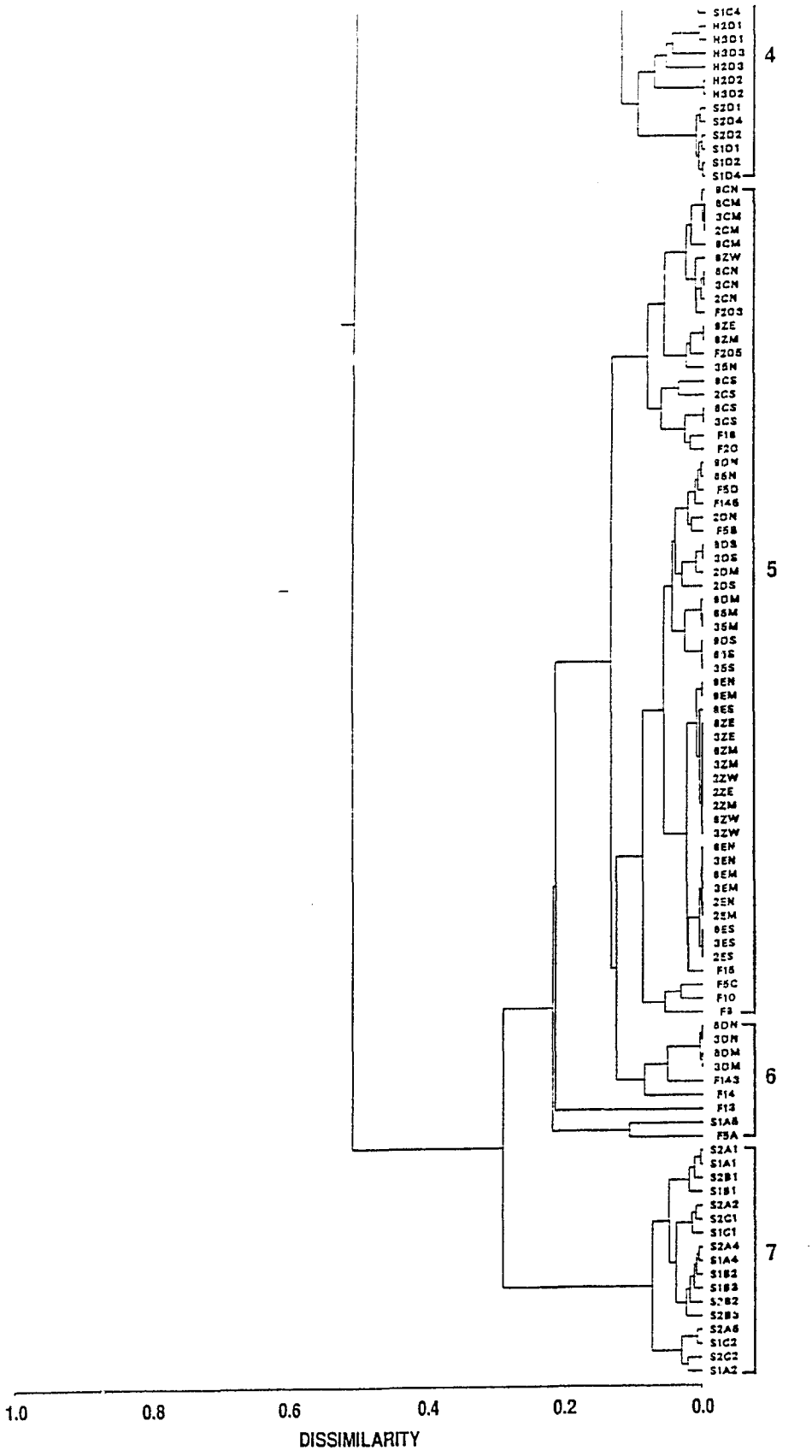

Figure 38. (continued)

Vancouver Harbour stations and the three deepest subtidal stations sampled in Boundary Bay (E7-E9).

3) Group 3 included the intertidal and shallow subtidal, coarse sand/gravel stations from Boundary Bay, two sandy Vancouver Harbour stations and all of the B area stations from Hecate Strait. This grouping is interesting because the stations span the entire B.C. coastline, and include intertidal and shallow shelf-type habitats. The common factor in all stations was that they had high bottom current, gravel and course sand substrates.

4) Group 4 consisted of all the moderately deep, offshore sandy-silt to fine sand stations, including the remaining Hecate Strait (areas A,C,D) and sandy shelf (C4,D1-D3) stations. This mixture also included stations from a broad geographic range of the coast.

5) Group 5 included a large number of deep nearshore, silty stations, encompassing most of the Alice Arm/Hastings Arm and fjord stations.

6) Group 6 was a small set of Alice Arm and fjord stations which were more sandy (Appendix 1) than the rest and attached to group 5. This group was quite similar to group 5.

7) The final group (7) included the silty stations (A,B,C1,C2) from the continental Shelf survey.

e. Comparison of Faunal and Environmental Patterns

The results of the Comtrel comparisons of ABUNBASE and BIOBASE with the environmental dendrogram (ENVIROBASE-Figs 37,38) are shown in Appendices 3v and 3w. The comparison of ENVIROBASE with ABUNBASE had 26 rejections at the 1% level, whereas the comparison with BIOBASE had 23 rejections at the 1% level.

Both ABUNBASE and BIOBASE had features in common with ENVIROBASE. All three analyses provided coherent groupings of stations within a given area. However, in several cases, stations from a given survey area did not group together in any of the three dendrograms.

The Boundary Bay shallow sandy stations were considerably different from the silty subtidal stations in all three cluster dendrograms. In the environmental pattern, the Boundary Bay shallow, sandy stations were

more similar to the shallow, coarse sediment Hecate Area B stations. This pattern also occurred in BIOBASE but not in ABUNBASE, where the stations were most similar to the Vancouver/Port Moody group. Similarly, the subtidal silty Boundary Bay stations were most similar to Vancouver Harbour/Port Moody Arm in both ENVIROBASE and BIOBASE, but not in ABUNBASE, where they were most similar to the Hecate Strait and Shelf stations.

The Shelf silty stations formed a distinct group in ENVIROBASE, and were linked most closely with the shelf sandy stations and the Hecate A and C stations in both ABUNBASE and BIOBASE. The Hecate A and C stations were nearest neighbors in the three dendrograms, although stations from each area were grouped with each other in ENVIROBASE and formed a total of six significantly distinct areas in ABUNBASE. In BIOBASE, Hecate Areas A and C each formed a significantly distinct and homogeneous group. In ENVIROBASE the sandy Shelf stations linked most closely with the area D stations from Hecate Strait. In both ABUNBASE and BIOBASE, the sandy shelf stations were most similar to the silty shelf stations. However, in ABUNBASE, the D stations from Hecate Strait were part of the Hecate A,C group which was most closely linked with all of the shelf stations. In BIOBASE, the Hecate D stations were totally dissimilar to the shelf sandy stations, and grouped instead with the Hecate B and sandy Boundary Bay stations. ENVIROBASE and BIOBASE therefore disagreed with ABUNBASE as to the distinct and total dissimilarity between the Hecate area B group and any other station groups.

In ENVIROBASE the Alice Arm and fjord stations were mixed together. This occurred in BIOBASE, although the fjord stations mostly grouped together. In ABUNBASE, the fjord stations were significantly distinct from the Alice Arm stations with the following exception. In both ABUNBASE and BIOBASE there was an overlap between these two survey areas in the impoverished stations (F5B, A2CN, A2CM, A2DM). Station F5D was not distinct as an impoverished station in BIOBASE, but was distinct in ABUNBASE.

The severely impoverished stations identified in ABUNBASE and BIOBASE (see preceding paragraph) from Alice Arm, Vancouver Harbour or fjords, or the moderately impoverished stations such as Hecate H1C3 were not

distinct in ENVIROBASE. Furthermore, ENVIROBASE and ABUNBASE did not distinguish the stations impoverished in terms of estimated biomass in Hecate Strait (cruise 2 area D, cruise 3 area A, H1B3), in Alice Arm in 1982 and 1983 (A2DM, A2DS, A3DM, A3CM), all of which were readily distinguishable in BIOBASE and in Table 15.

C. DISCUSSION

1. Summary Statistics

Mean biomass values for areas or stations cannot be considered realistic sample measures since these numbers were compiled by converting abundance data to estimated biomass by multiplying abundances by the mean wet weight of each species. However, for relative comparison of different areas in the study, the method of determination of estimated mean biomass per station was at least consistent. In situations where there were gross differences among stations or areas, the mean biomass values provided valuable discriminatory information. However, it was surprising how similar the mean biomass values were among areas, since different sampling methods were used in various surveys and biomass measurements tend to be notoriously variable (Crisp 1984). It may be that sampling differences had little effect on biomass measurements.

Biomass values for open shelf stations off Washington averaged 1.92 g ash-free dry weight/ m^2 (Lie 1969), which are comparable to biomasses measures in the gulf of Alaska shelf (Shevtsov 1964). Ellis (1969) measured dry weights (not ash free) in the Strait of Georgia and found values of 17 to 60 g/ m^2, with two Burrard Inlet (Vancouver Harbour) stations averaging about 14g/m^2. Wet weight calculations can be converted to ash-free dry weights (AFDW) using published factors (Thorson 1957, Ellis 1969, Lie 1969). The AFDW conversions average (roughly) about 10% of wet weight. Using this rough factor, mean estimated AFDW values for the surveys in this study ranged from 1.7 to 6.1 g/ m^2 (from Table 15). These values were therefore similar to previously published values for coastal waters of the Pacific northwest.

The sampling program in this study was never designed to determine the effects of sampling parameters on numerical abundance, biomass and taxa number. Therefore it is only possible to speculate on the relative effects of different sampling procedures on these values. Based on grab size, screen sizes and general handling of taxa and identifications, the summary statistics from Alice Arm, Hecate Strait and other fjords should be comparable. Abundance and numbers of taxa were lower generally in Alice Arm and fjords than in Hecate Strait, whereas biomass values were similar in all areas. Because of the variety of screen sizes and grab sizes used, it is difficult to compare summary statistics from Vancouver Harbour, Boundary Bay and the shelf areas. Not surprisingly, the surveys using small screen sizes (other than Shelf) such as Boundary Bay and Vancouver Harbour, had much higher abundance values than surveys that used larger seive sizes. In the shelf surveys, which utilized a 0.25mm screen for about 50% of each grab sample, the loss of meiofauna was considerable, but there were also many taxa that were never identified to species or identified in only one of the two surveys (such as ostracods and aplacophora, Brinkhurst 1987). Therefore, abundance values were reduced due to the elimination of unidentified taxa in the shelf stations. Biomass values were less influenced than abundance by the screen size differences, since the additional abundances were contributed mainly by very small taxa. The small grab size used in Boundary Bay and Vancouver Harbour ($0.05m^2$) probably resulted in the collection of fewer rare taxa per station than for the other surveys. Conversely, in the shelf survey, in which the largest grab ($0.25m^2$ grab compared to $0.1m^2$ used for Hecate Strait, fjords and Alice Arm) was used, there was an increase in the number of taxa with respect to all other surveys, despite considerable losses due to the elimination of unidentified taxa. The grab size may have affected taxa number, whereas the screen size probably affected abundance. It is uncertain what effect either of these two factors had on estimated biomass.

Despite the sampling problems, some generalizations can be made which span the datasets. There was no indication that there were differences in mean abundance and mean biomass among stations within a given geographic area because of different sediment types. This is not

surprising, since coarse substrate areas often have high suspended organic particle loads, supporting a high biomass of suspension feeders, with few deposit feeders (for review see Pearson and Rosenberg (1987).

The higher estimated biomass values observed in the southern near-shore sampling areas (Vancouver Harbour, Boundary Bay) may be related partially to sampling methods, although little biomass would have been contributed by small species captured only on a small mesh screen. Alternatively, the high biomass values may be due to high productivity related to organic input from large estuarine outflows (such as the Fraser River). Productivity in Vancouver Harbour may also be affected by organic input (sewage). In the Baltic Sea, progressive eutrophication due to organic pollution has been proven to produce a long-term general increase in benthic faunal biomass (Cederwall and Elmgren 1980), although in areas of restricted water circulation this eutrophication can lead to faunal declines (c.f. Josefson and Rosenberg 1988, Rosenberg and Loo 1988). The shelf area surveyed is thought to be a productive fisheries ground, partially because of coastal upwelling, and the estuarine influence from Juan de Fuca Strait (Crawford and Dewey 1989, see Chapter 5). Estimated biomass values from the Shelf were similar to Boundary Bay and higher than Alice Arm, Hecate Strait or fjords despite the elimination of unidentified fauna. Estimated biomass values for Hecate Strait, Alice Arm and the fjords were appreciably lower than for the southern sampling areas, though the data are not consistent enough to interpret this result. Furthermore, Pearson and Rosenberg (1987) suggest in their review that there is no firm evidence to support the contention that there are basic latitudinal gradients in biomass, abundance or diversity of benthic organisms.

Some general trends in number of taxa were evident. As expected, polychaetes were commonest in silty areas, whereas bivalves were more common (but not necessarily dominant) in sandy areas. Polychaete abundance was low and bivalve abundance was high in Alice Arm in 1982 and 1983 and in Hastings Arm in 1983 despite the silty substrates. In Chapter 3 I postulated that this shift in the polychaete to bivalve ratio was related to high sedimentation rates from the deposition and shifting of mine tailings in Alice Arm and high silt loads from natural run-off in

Hastings Arm. High sedimentation may in fact set up conditions of high energy, which in some ways mimic the high suspended sediment load which can be characteristic of sandy habitats, favouring bivalves over polychaetes. Because the polychaete to bivalve ratio was so different in Alice Arm compared to the other B.C. fjords, it was not surprising that the two survey areas were dissimilar in terms of small (mostly polychaetes) species composition (Fig. 35). In contrast, with respect to larger fauna, Alice Arm/Hastings Arm and the fjords surveys had similar species compositions (Fig. 36). The complete absence of bivalves in Hecate area 2D (chapter 4) due to a sample processing error resulted in an unreliable ratio of polychaetes to bivalves.

Echinoderms were low in abundance in Vancouver Harbour/Port Moody Arm, but not in Boundary Bay. Because the same grab size was used in both sets of surveys, differences were obviously not related to sample size. There is no immediately obvious reason for the low concentration of echinoderms in Vancouver Harbour, although pollution could have some effect. In contrast, gastropods were much commoner in the aforementioned shallow areas than in the remaining surveys, and rarest offshore on the continental shelf. Since most gastropods are herbivorous (Barnes 1980), they require the presence of light for their food resource. The abundance of gastropods in the shallow areas and of the herbivorous *Olivella baetica* in Hecate area B are therefore not surprising. Crustaceans were also commonest in the intertidal to high subtidal (Boundary Bay) and in Vancouver Harbour, but were also relatively common in all remaining areas except Alice Arm and Hastings Arm.

The distribution of those species found in all survey area (Appendix 4) could be examined in greater detail, but is beyond the scope of this study. It is possible that the distribution of some of these species could provide important information on larval dispersal by prevailing currents. Certainly, the ubiquitous distribution of a number of often abundant species suggests considerable coastal transport of larval forms. Some of these species might be considered important primary colonizers, particularly in disturbed areas such as Alice Arm where seven of the eleven ubiquitous species were found. One of two ubiquitous bivalve species (*Psephidia lordi* and *Nucula tenuis*) dominated the fauna in Alice

Arm/Hastings Arm in all survey years. *Psephidia lordi* is not, however, a colonizing species, since it broods its young and therefore must "walk" to any new location (R. Reid, U. Victoria, pers. comm.).

2. Multivariate Statistical Analyses

The cluster analysis of ABUNBASE was heavily weighted in favour of the abundant small fauna, whereas the analysis of BIOBASE was weighted in favour of the largest fauna (see chapter 1, section 1A). Thus the comparison of the two faunal Sigtree analyses should show the distribution patterns in two different size components of the benthic assemblages.

As discussed in Chapter 2, section F, the significance testing of such a large set of stations as in ABUNBASE and BIOBASE is a problem because of the multiple tests issue. A total of 190 linkages were tested each for ABUNBASE and BIOBASE. So many tests produce an overall significance in the two faunal analyses which is very unsastisfactory, despite the fact that the problem is considerably reduced in Sigtree because each significant linkage automatically makes any higher, dependent linkages significant (see Chapter 2, section E1). However, the probability assigned to each linkage by Sigtree is independently determined (Nemec and Brinkhurst 1988a). Therefore, if we ignore the problem of overall significance, Sigtree does provide an excellent indication of the within group versus between group sample variance at each linkage level, and illustrates the significance levels that can be expected in surveys with different grab sizes, replicate numbers and screen sizes.

The probability vallues generated by Comtre1 and Comtre2 are more problematical. In both analyses, each linkage test is truly independent of the previous ones, so that the total number of linkages is directly related to the overall significance. The error therefore increases in direct proportion to the number of linkages being tested, making the multiple tests problem truly serious. Significant linkages at 1% were enumerated, but the usefulness of Comtre1 in particular at this scale, is questionable. There was little difference between the Comtre1 analyses

for the two types of faunal dendrograms, suggesting that both ABUNBASE and BIOBASE were related to some extent to the environmental dendrogram. Sixteen to eighteen percent of linkages were significant in in the two Comtrel analyses.

a. ABUNBASE versus BIOBASE

The results of Sigtree analyses of ABUNBASE and BIOBASE illustrate obvious differences in distribution patterns of large and small animals. Despite this, the Comtre2 comparison of ABUNBASE and BIOBASE did not produce any significant linkages. Thus it appears that Comtre2 lacked sufficient discrimination to distinguish the two cluster patterns.

The smaller number of significant groups in BIOBASE versus ABUNBASE suggests that emphasizing the large species evened out or blurred some faunal distinctions, such as the distinction between the sandy versus silt stations on the shelf off Vancouver Island. It is most likely the lesser number of significant linkages in BIOBASE was caused by the increased variability among replicates. Increased variability of this type was unavoidable because of the dominance of the rare, variable large taxa in the analysis caused by biomass-weighting of species. An exception was the result from Vancouver Harbour (Chapter 6), where there were more significant linkages at 1% in the biomass-weighted analysis than in the raw abundance analysis. In Hecate Strait, the large number of replicates should have reduced station variance, so that the fewer significant linkages in the biomass-weighted analysis produced a more sensible station pattern, and may have reflected the fact that the effect size tested was more appropriate than in the abundance analyses.

b. Comparison of faunal and environmental patterns

Although the Comtrel results showed a slightly stronger correlation of the environmental pattern with ABUNBASE than with BIOBASE, the multiple tests problem and the very minor differences between the two Comtrel tests (Appendices 3v,3w) make this result meaningless. The most striking difference between ABUNBASE and BIOBASE was the disposition of

the stations from the shallowest survey, Boundary Bay. Results of both analyses showed that the fauna of shallow, sandy stations in Boundary Bay was distinctly different from that of the deeper, silty stations. In terms of environmental factors, the shallow, sandy Boundary Bay stations were most similar to the shallow, sandy stations in Hecate area B (Group 3 in ENVIROBASE). The deep, silty Boundary stations were very similar environmentally to the majority of the Vancouver Harbour stations (group 2 in ENVIROBASE). Therefore, the relationship of Boundary Bay stations to stations in other survey areas was the same in BIOBASE and ENVIROBASE, whereas ABUNBASE placed the deep, silty stations from Boundary Bay (Fig. 35, group 14) with the Hecate A,C,D and Shelf stations, and the shallow Boundary stations split between the Vancouver Harbour and Alice Arm groups (Fig. 35, groups 6,7,9,10). The distribution of large fauna from Boundary Bay was therefore better explained by the environmental conditions measured, than that of the small fauna.

The upwelling of the Juan de Fuca current and subsequent flow past the nearshore shelf region off the southwest coast of Vancouver Island in spring and summer was discussed in Chapter 5. As well, Thomson *et al.* (1989) discuss a "broad biomass conduit" for larvae and eggs of commercial species in the winter months, which is formed by currents moving along the entire shelf off Vancouver Island from the entrance of Juan de Fuca Strait to Queen Charlotte Sound, and in the reverse direction in summer. Jumars and Banse (1989) speculate that favourable recruitment conditions in the shelf benthos of the Pacific northwest may be caused by winter storm disturbance. The widespread use of storms as a mechanism for invertebrate larval dispersal is undocumented, however.

The prevailing current flow around the north end of Vancouver Island has not been documented. Summer upwelling and currents may well carry the larvae of many Boundary Bay and shelf species around Vancouver Island up to Queen Charlotte Sound and subsequently into Hecate Strait, producing some similarity in species composition among the Boundary Bay, Shelf and Hecate Strait survey areas (see Figs. 35, 36).

The similarity in distribution of small fauna in ABUNBASE between the shallow sandy Boundary Bay and the Vancouver Harbour stations may be based on proximity. It should be noted that several Vancouver Harbour

stations grouped with the shallow, sandy stations of Boundary Bay in ENVIROBASE (group 3, Figs. 37,38). The grouping of three of the shallow Boundary Bay stations with Alice Arm/Hastings Arm may be attributable largely to the abundance of the small bivalve *Psephidia lordi* in both areas, which does not disperse with the currents, but spreads along the bottom (R. Reid, University of Victoria, pers. comm.).

The bivalves *Tellina nuculoides* and *Tellina carpenteri* occurred in variable abundance in both Boundary Bay and Hecate Strait area B. *T. carpenteri* occurs on shallow shellgrounds and sand, whereas *T. nuculoides* is common in deeper areas characterized by the same substrate types (R. Reid, University of Victoria, pers. comm.). The similarity between the shallow Boundary Bay and the area B stations from Hecate Strait in BIOBASE implies a broad geographic distribution of the larger fauna from both areas, but does not imply the same type of transport of species along the outer coastal shelf as indicated in ABUNBASE, since there was no similarity in species composition of the large organisms from any of the Boundary Bay stations, and the shelf stations off Vancouver Island. The prevailing current flow between the mainland and Vancouver Island suggests considerable transport of water occurs between southern B.C. through Johnstone Strait and into Hecate Strait in summer and in the reverse direction in winter (Thomson 1977, Thomson *et al.* 1989). This circulation pattern may have an effect on the exchange of larval forms of the benthic fauna between Hecate Strait and Boundary Bay.

Jumars and Banse (1989) make the interesting suggestion that "community structure and sediment type may correlate well in part because larvae of given species and sediments of given grain sizes have similar settling velocities rather than the grain size of the bed determining the larval choice." This theory is outlined by Hannan (1984) and suggested by Eckman (1983), and implies that the largest larvae will always settle fastest, in larger grain size areas (sandy to gravelly) than small larvae (silty areas). Therefore the distribution pattern of macrobenthic larvae may be partially determined by the size of the larvae.

The other survey area in which there was considerable discrepancy between BIOBASE and ABUNBASE was Hecate Strait. In ABUNBASE the Hecate B stations formed the most distinctive group in the entire dataset (Fig.

35, group 28). Some overlap in faunal composition of area B with the other Hecate stations was expected based on proximity and somewhat similar habitat (Fig. 37). There was virtually no overlap in composition of the small fauna (Fig. 35), but considerable overlap in areas B and D (cruise 3 only) in terms of the larger fauna (Fig. 36). Hecate Area B was actually quite unique because it was dominated by two species (*Tellina nuculoides* and *Spiophanes bombyx*), whereas fauna at the other areas of Hecate Strait was not dominated by a few species. Such dominance suggests that a strongly physically controlled environment exists in area B of Hecate Strait, which produces conditions unsuitable for many of the species common in surrounding areas. The combined results of ABUNBASE and BIOBASE suggest that Hecate Strait area B had fauna characteristic of high subtidal habitats with course substrates, as well as a complement of small fauna unique from all other areas of Hecate Strait or the rest of the coast. Area D of Hecate Strait was characterized by small organisms similar to other Hecate Strait areas (A and C), and larger species in common with course substrate beach fauna.

There was also more overlap among large relative to small fauna between Alice Arm/Hastings Arm and the other fjord stations. The overlap in large fauna is supported by the fact that the relative abundance of polychaetes and bivalves (Tables 16,17) was quite different between the Alice Arm/Hastings Arm and other fjord stations. The results imply that unique sediment conditions probably exist in Alice Arm and Hastings Arm, which seem to affect the small fauna (particularly polychaetes) most profoundly. In Chapter 3, I speculated that high sedimentation played a major role in faunal composition of both Alice Arm and Hastings Arm in several years. If this is so, the large fauna would be expected to tolerate high sediment loads better than small fauna due to more efficient escapement following burial (Reid and Baumann 1984). Thus, the large fauna in Alice Arm is more typical of B.C. fjords than the small fauna.

The dendrograms from ABUNBASE and BIOBASE showed the greatest dissimilarity to the dendrogram based on ENVIROBASE among the stations with reduced abundance and biomass. As well, the results of the Sigtree analyses from ABUNBASE and BIOBASE differed with respect to the groupings

of impoverished stations, depending on whether the stations were low in abundance or biomass. Faunal impoverishment was expected to show up as declines of both abundance and biomass. Such faunal impoverishment was observed in samples from Alice Arm (stations A2CM, A2CN, A2DM), Port Moody Arm (stations V141B, V145, V146) and one fjord station (station F5B), and was therefore evident in the resulting station patterns of both ABUNBASE and BIOBASE. However, samples from Hecate Strait exhibited a more subtle and interesting form of faunal reduction, which was a decline in estimated biomass with little if any decline in abundance (stations H3B1, and all samples from areas H2D and H3A). ABUNBASE did not provide any hint of the unusual defaunation patterns at stations with depleted biomass, whereas BIOBASE and the summary statistics did.

CHAPTER 10: SUMMARY AND CONCLUSIONS

The purpose of this thesis was to compare benthic faunal composition and environmental factors from the British Columbia coast, on a broader geographic and temporal scale than has been attempted previously in this area. The data management and analytical approach were specifically designed to test the hypothesis that the distribution patterns of large and small macrofauna were different in various habitat conditions. In this final section of the thesis, I will comment on the effects of sampling methods on results, and draw conclusions on the data management and analytical approach used in this study. The comparison of faunal characteristics and patterns was covered in detail in chapter 9, but will also be summarized in this chapter.

Environmental problems often require the use of inadequately or variably sampled data. Even where sampling procedures are adequate and consistent, ecological data tend to be patchy and variable. Much research has focused on developing methods and approaches for processing complex ecological data (Burd *et al.* 1990), but there has been less emphasis on data management than on statistical methods or models. The analytical methods used must obviously be robust, readily interpretable and flexible enough for a broad range of applications. However, without reasonable management and transformation of the data such methods provide limited information.

A. SAMPLING METHODS

Results from the independent surveys (chapters 3 to 8) and the comparison of all areas combined (Chapter 9) suggest that problems and variations in faunal values may occur because of the use of different sampling methods. Unfortunately, the sampling procedures used in this study were not designed to determine sampling efficiency, though this has been done in other studies (for review see Holme and McIntyre 1984, Rees 1984, Reish 1959). Some researchers have also examined the efficiency of sample devices for determining the spatial aggregation of fauna (Downing 1979, for review see Burd *et al.* 1990). As yet, there is no satisfactory

study relating relative size of individuals and biomass to retention properties of screens, particularly for soft-bodied, easily fragmented infaunal species. The following discussion on sampling devices is therefore speculative.

Three sampling variables affected the results of individual surveys and an overall comparison of survey areas. These included grab size, screen size and number of replicates per station. The hypothesized effects of these variables on the power of the inferential tests were discussed throughout the thesis. Screen size apparently had an effect on sample abundance. The smaller the screen, the higher the faunal abundance. The effect of screen size on estimated biomass for stations was not clear. Theoretically, the inclusion of more animals should increase estimated biomass, but if these new additions are all very small, the overall difference might be negligable. The grab size seemed to affect only number of taxa. In larger grabs, more taxa were found, and more rare species were incorporated into the analyses. Larger grabs therefore would have had little effect on raw abundance data, which virtually ignore the very rare species, but could potentially have had a profound effect on the results of biomass-weighted analyses, in which large, rare animals could contribute substantially to the analysis. Therefore, sampler size can theoretically affect estimated biomass. The use of 5 replicates per station instead of 2 or 3 does not directly affect abundance or biomass, but should improve the chances of capturing less abundant fauna. Therefore, the direct effect of replicate number is similar to that of sampler size.

There is a danger in using benthic infaunal data processed with small screens. If abundance is too high, particularly with a small grab size, then biologically meaningless rejections of a null hypothesis can occur. This problem is one of "effect size" and is difficult to predict prior to sampling in a given area. In effect, the researcher may find valid differences, but on a spatial scale smaller than is of concern for the purposes of the study. In this case, the probability of acceptance for a null hypothesis must be adjusted to a lower level to compensate for the high power of the test. On the other hand, if abundance is high but the sampler size is too small to effectively capture the less abundant fauna,

and only 2 replicates per station are sampled, there may be considerable variability between replicates and a stringent probability for acceptance of a hypothesis may seriously reduce statistical power. For analyses with a high number of significance tests (i.e. ABUNBASE and BIOBASE), high abundance and low probabilities for accepting the null hypothesis in turn reduce the multiple comparisons problem.

It is difficult to say if sample area, or grab size, would affect the power of the test. The use of more replicates per station is very similar to that of increased sampler size. Since replicate number has been shown to have profound effects on the power of Sigtree (A. Nemec, unpublished report), theoretically, a larger grab should improve inferential power as well. A larger sampler should result in lower variance within stations, (for discussion see Chapter 2 section D3), thus improving the power of the test. Therefore, for a situation in which abundance is high due to the use of a small screen size, but with few replicates per station, a larger sampler should provide more realistic results. Thus the fact that the within-sample variability was higher in Vancouver Harbour (grab size of 0.05 m^2) than in Hecate Strait (grab size of 0.1 m^2), resulting in fewer significant linkages in the Vancouver Harbour analysis even though organisms were ten times more abundant than in Hecate Strait, probably was partially related to the smaller sampler used in the former area, as well as the greater number of replicates in the Hecate Strait survey.

Based on the results of this study, I conclude that the mid-sized sampler ($0.1m^2$) with 5 replicates provides the most reliable results. Logistic concerns must also be addressed, for example, the largest sampler used in this study ($0.25m^2$ Smith-McIntyre grab) is not easily handled, particularly in rough seas or aboard small boats. Samples obtained using a 1mm screen, and 5 replicate grabs of 0.1 m^2, yielded results with adequate power for Sigtree at a probability of acceptance of 1% (i.e. Hecate Strait - Nemec unpublished report to IOS). However, for analyses with many stations, the overall significance of Sigtree is reduced at a probability of acceptance of 1%. As well, the inclusion of impoverished or low abundance stations in the survey will adversely affect power. Therefore, a conservative approach would include a screen

size of 0.5mm and 5 replicates per station with a $0.1m^2$ sampler, as recommended for representative macrofaunal sampling (Holme and McIntyre 1984)). Not only would this be manageable in terms of power and effect size for significance tests (see chapter 1, section C2d), it would ensure a reasonable confidence that sample density had been accurately measured (Downing 1979). If the cost of processing samples is a major consideration, then fewer stations may have to be sampled. In the end, there is little point in sampling many stations if the results from all of them underrepresent faunal density and number of taxa.

In near-shore areas where use of a grab with area 0.1 m^2 is not practical, the use of a smaller sampler may be unavoidable. In this case, 5 replicates is still recommended, but a smaller screen size is not, since screens with a seive size less than 0.5 mm collect considerable meiofauna, which functionally respond to environmental conditions in a completely different manner from macrofauna (Schwinghamer 1981, 1983). In this case, a smaller number of significance tests (linkages) with a higher probability of acceptance is recommended.

Eliminating the meiofauna either by increasing screen size or by removal of species (nematodes, copepods, foraminifera), caused inevitable loss of pattern discrimination. However, eliminating the meiofauna from the analyses helped to remove discrepencies between surveys sampled with different methods. The pattern of macrofaunal abundance provides real and useful ecological information, as long as it is interpreted strictly as a specific size component of the community. Additionally, my study indicated that there were different distribution patterns even within the macrofauna, which may be separated and examined independently (i.e. large versus small fauna).

B. DATA MANAGEMENT

The data management approach used herein has opened up a perspective on community analysis that could readily be expanded. Separating the community into component parts by size and analysing them separately has proven to have interpretive advantages. The technique used herein was arbitrary, and other approaches could be tried, such as examining

separately patterns in different taxonomic groups, in different trophic groups, feeding guilds, etc.

Biomass methods could provide an added dimension of knowledge to the mainly abundance-based benthic studies of the past (Burd *et al.* 1990). For example, using data similar in form to that collected for this study, Edgar (1990) empirically tested a model for estimating secondary productivity of benthic macrobenthic from biomass data. The biomass-weighting method used in this thesis could be applied in a similar way.

Station patterns based on biomass-weighted abundances were believable, and often clearer than those based on numerical abundance alone (i.e. Hecate Strait). Despite this, I do not advocate replacing numerical abundance data with biomass-weighted data. I conclude that the combination of both approaches was more valuable than either the abundance or biomass-weighted approaches alone. I further conclude that the use of either method alone may often be inadequate to characterize macrofaunal distribution patterns.

C. PERFORMANCE OF ANALYTICAL METHODS

The multivariate analytical approach has proven useful with difficult and broadly based data. Despite the eliminations of unidentified and meiofaunal taxa necessary to combine the data into a consistent database, the results of the Sigtree analyses on numerical data indicate that within given survey areas, results were consistent with preliminary results based on the original unedited datasets (Burd *et al.* 1987, Brinkhurst 1987, Burd and Brinkhurst 1987, Brinkhurst *et al.* 1987, Burd and Brinkhurst 1990a,b, Kathman *et al.* 1983, 1984). Sigtree provided important discrimination of the station groupings in cluster analyses. The Comtre methods provided a means of inferential non-linear comparisons of two dendrograms. Thus the methods are meant to be complementary.

Sigtree simulates and resamples the dataset using all of the abundance (or biomass-weighted abundance) information in the original faunal datamatrix, whereas the Comtre methods utilize only the station patterns in the cluster dendrogram. In this manner, Sigtree is essentially a randomization or "bootstrap" method. Therefore Sigtree is

a within versus between sample variance test. Because Sigtree does not test the fit of data to a preconceived distribution model (as parametric methods do), the method is only as reliable as the data. Sigtree is limited to comparison of datasets with consistent scales (i.e. faunal abundance only), an infinite number of sample units can be compared at a detailed level, as long as the datasets are partially symmetrical (i.e. same species list). Using Sigtree, the objective comparison of biomass-weighted data with numerical data emphasized subtle yet important differences in the behaviour of large versus small fauna.

I found cluster analysis of environmental data visually most useful for comparison with cluster patterns of faunal data. Comtrel can be used to compare two such dendrograms even though they are formed from completely different types of data. Comtrel tests the null hypothesis that 2 dendrograms are different at any given linkage level. However, those dendrograms must consist of identical sample units (stations), and only 2 dendrograms can be compared simultaneously. The major limitation inherent in this method is that it ignores the specific combination of elements which went into both cluster patterns and compares only the final patterns. Therefore, it does not take within and between sample variance into consideration. Each cluster pattern is produced by a hierarchical, agglomerative averaging process which has been shown to suffer from considerable information loss relative to the original data matrix used (see Gordon 1987). Furthermore, Comtrel is not a simulation method, and lacks the advantage of Sigtree by making no assumptions about the underlying distribution of the dataset.

In all survey areas, the faunal pattern based on biomass-weighted data was as closely or more closely related to the environmental pattern than the pattern based on numerical data, using both Comtrel and visual comparisons. Therefore, the large fauna often showed distribution patterns predicted by environmental factors, whereas the smaller fauna did not. This was particularly evident in the biomass-weighted Comtrel comparison with sediment chemistry factors in Vancouver Harbour/Port Moody Arm (chapter 6).

I conclude from this study that the use of Comtrel is only viable for studies with a limited number of stations, for which environmental

factors with strong effects can be identified, or when adequate environmental detail is available. For comparisons of dendrograms with many stations, Comtre1 suffers from escalating error (multiple comparisons problem). As well, the results of the Comtre1 comparison often did not make sense (Shelf surveys) or did not provide sufficient detail for discrimination of faunal patterns (e.g. Boundary Bay). In several comparisons, Comtre1 showed no significant linkages when the two patterns being compared were obviously in basic agreement. In some cases, this may have been because an insufficient number of environmental factors could effectively be incorporated to distinguish stations (e.g. Alice Arm). The circumstance for which Comtre 1 was most useful was in the comparison of complex sediment chemistry data for Vancouver Harbour/Port Moody Arm with faunal distributions. The results presented for Vancouver Harbour (Chapter 6) indicate that some, or all of the factors describing sediment chemistry were very important in effecting the distribution of fauna, particularly the large fauna. By an elimination and substitution process, the most effective combination of environmental factors could be derived with very little difficulty using Comtre1.

The results of this study suggest that Comtre2 was of limited value. Comtre2 is a bootstrap method which requires absolute symmetry of the matrices (i.e. same species, same stations) and is thus limited to the comparison of two identical dendrograms. Like Comtre1, Comtre2 does not utilize the species information in the inferential process, but bootstraps only the resulting cluster patterns based on the agglomerative averaging process. In all cases except Alice Arm (chapter 3), the numerical abundance and biomass-weighted dendrograms were not significantly different at any linkage. This was obviously not true in some cases (Vancouver Harbour, fjords, Hecate Strait), suggesting that the level of discrimination of this method was insufficient for the task.

I conclude that only Sigtree provided the level of detail and discrimination required for faunal analyses, and that Comtre1 had limited value in the assessment of the relationship between faunal data and complex environmental data. The Sigtree analyses illustrated a strong consistency in distribution patterns of small and large fauna and the

vital differences, such as the discrimination between stations impoverished in biomass and those impoverished in numerical abundance.

C. COMPARISON OF INFAUNAL ASSEMBLAGES IN B.C.

The comparison of a widely dispersed and environmentally varied set of survey areas in a quantitative manner is one which has not been attempted on this scale for benthic infaunal marine assemblages, at least in the Pacific northwest. On a qualitative scale, there have been global theories proposed (Thorson 1957, 1966). Generally, insights into factors influencing distributions of fauna can only be gained by in-depth comparison of a wide variety of habitat types or by reviews of studies from a given habitat type (such as continental shelves in the Pacific northwest, e.g. Jumars and Banse 1989). For many years, researchers have been reluctant to attempt broad-scale quantitative comparisons because of variations in sampling equipment, season, temporal scale, habitat conditions (often unmeasured) and taxonomic difficulties.

The fact that most stations within a given survey area remained grouped with the others from that area in the overall ABUNBASE and BIOBASE analyses, suggests a strong spatial conservativism in faunal composition. Some notable exceptions to this spatial coherence are described in Chapter 9, which provided insights into the similarities in faunal structure found in certain habitat types regardless of the geographic dispersion of stations, or the use of different sampling techniques. In particular, the distinct nature and similarity among impoverished stations regardless of their geographic location, is emphasized in the Sigtree analyses. As well, the differential distribution of large and small fauna was most noticeable in the distinction between stations with low estimated biomass and those with low mean abundance, the overlap in faunal composition of Alice Arm and fjords only in the large fauna, and the distinct separation of Boundary Bay stations based on distribution patterns for large and small fauna.

It is increasingly obvious, as outlined by Nichols (1985), that profound changes in benthic community composition occur at different temporal scales even in undisturbed habitats. Because of this, it is

important to examine species composition over very long periods of time to develop a "feel" for the periodicity and quality of temporal species patterns.

I have shown that infaunal assemblages in British Columbia tend to be spatially conservative, but show definite environmentally related similarities over a great geographic distance. Schwinghamer (1981) and Warwick (1984) have already suggested that the meiofauna display functional responses to environmental conditions different to those of the macrofauna. In this study, the relationship between faunal distribution and environment varied between large and small components of the macrofauna. The results of this work, and that of Schwinghamer (1981) and Warwick (1984) suggest that the detailed examination of community structure on the basis of animal size as well as numerical abundance may enhance pattern analysis in multispecies assemblages.

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APPENDICES

Appendix 1. Station names, locations, depth, sediment characters. The first letter designates the survey area (V=Van. Hor, A=Alice Arm/H=Hastings Arm, H=Hecate Strait, B=Boundary Bay, S=Shelf, F=fjords). The second number represents the cruise (1,2,3 or 2,3,6,9 for years) when applicable (i.e. not for Boundary Bay or Fjords). The next one or two characters represent station names, and the last number always represents replicate number (1 to 5).

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
Vancouver Harbour: October 1987 (2 replicates per station)						
V111	123°07.45	49°18.72	12.0	5.0	78.4	16.6
V112	123°04.82	49°18.25	12.0	5.0	78.4	16.6
V121	123°07.27	49°18.65	16.0	64.5	35.5	0.0
V122	123°07.27	49°18.65	16.0	64.5	35.5	0.0
V13A1	123°06.62	49°18.73	13.0	2.4	80.0	17.6
V13A2	123°06.62	49°18.73	13.0	2.4	80.0	17.6
V13B1	123°06.67	49°18.48	15.0	26.5	74.4	0.0
V13B2	123°06.67	49°18.48	15.0	26.5	74.4	0.0
V14A1	123°06.48	49°18.50	23.0	43.7	56.3	0.0
V14A2	123°06.48	49°18.50	23.0	43.7	56.3	0.0
V1111	123°04.82	49°18.72	30.0	12.3	73.2	14.5
V1112	123°04.82	49°18.25	30.0	12.3	73.2	14.5
V1141	123°05.85	49°18.10	30.0	55.3	44.7	0.0
V1142	123°05.85	49°18.10	30.0	55.3	44.7	0.0
V1151	123°05.00	49°18.10	40.0	49.9	47.9	2.2
V1152	123°05.00	49°18.10	40.0	49.9	47.9	2.2
V1161	123°03.88	49°17.60	24.0	46.5	50.0	3.5
V1162	123°03.88	49°17.60	24.0	46.5	50.0	3.5
V1191	123°06.30	49°17.52	22.0	26.6	67.8	5.5
V1192	123°06.30	49°17.52	22.0	26.6	67.8	5.5
V1221	123°05.09	49°17.20	14.0	77.8	22.2	0.0
V1222	123°05.09	49°17.20	14.0	77.8	22.2	0.0
V1223	123°05.10	49°17.37	35.0	73.4	26.6	0.0
V1224	123°05.10	49°17.37	35.0	73.4	26.6	0.0
V1225	123°04.62	49°17.55	35.0	62.5	36.5	2.0
V1226	123°04.62	49°17.55	35.0	62.5	36.5	2.0
V1251	123°04.63	49°17.35	22.0	62.5	36.5	1.0
V1252	123°04.63	49°17.35	22.0	62.5	36.5	1.0
V1253	123°04.62	49°17.46	37.0	57.1	39.7	3.2
V1254	123°04.62	49°17.46	37.0	57.1	39.7	3.2
V1255	123°04.62	49°17.55	35.0	90.2	9.8	0.0
V1256	123°04.62	49°17.55	35.0	90.2	9.8	0.0
V1361	122°53.80	49°17.60	18.0	85.2	14.3	0.5
V1362	122°53.80	49°17.60	18.0	85.2	14.3	0.5
V1371	122°53.38	49°17.82	17.0	89.2	9.6	1.2
V1372	122°53.38	49°17.82	17.0	89.2	9.6	1.2
V1373	122°53.40	49°17.71	18.0	96.0	4.0	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
V1374	122°53.40	49°17.71	18.0	96.0	4.0	0.0
V1391	122°53.05	49°17.95	14.0	92.7	6.5	0.8
V1392	122°53.05	49°17.95	14.0	92.7	6.5	0.8
V1393	122°53.05	49°17.77	15.0	84.2	14.6	1.2
V1394	122°53.05	49°17.77	15.0	84.2	14.6	1.2
V1395	122°53.06	49°17.60	15.0	86.1	10.2	3.7
V1396	122°53.06	49°17.60	15.0	86.1	10.2	3.7
V1401	122°52.87	49°17.98	11.0	91.2	8.8	0.0
V1402	122°52.87	49°17.98	11.0	91.2	8.8	0.0
V1411	122°52.73	49°17.98	10.0	91.4	8.6	0.0
V1412	122°52.73	49°17.98	10.0	91.4	8.6	0.0
V1413	122°52.48	49°18.03	9.0	94.8	5.2	0.0
V1414	122°52.48	49°18.03	9.0	94.8	5.2	0.0
V1451	122°51.86	49°17.42	16.0	92.2	7.8	0.0
V1452	122°51.86	49°17.42	16.0	92.2	7.8	0.0
V1461	122°51.74	49°17.37	14.0	90.3	9.7	0.0
V1462	122°51.74	49°17.37	14.0	90.3	9.7	0.0
V1PE1	123°13.97	49°19.78	67.0	80.0	18.0	2.0
V1PE2	123°13.97	49°19.78	67.0	80.0	18.0	2.0
Vancouver Harbour: 1989 (3 replicates per station)						
V211	123°07.50	49°18.70	13.0	80.2	17.9	1.9
V212	123°07.50	49°18.70	13.0	80.2	17.9	1.9
V213	123°07.50	49°18.70	13.0	80.2	17.9	1.9
V2111	123°05.00	49°18.30	26.0	50.5	48.6	0.9
V2112	123°05.00	49°18.30	26.0	50.5	48.6	0.9
V2113	123°05.00	49°18.30	26.0	50.5	48.6	0.9
V2151	123°05.00	49°18.10	36.0	57.3	41.7	1.0
V2152	123°05.00	49°18.10	36.0	57.3	41.7	1.0
V2153	123°05.00	49°18.10	36.0	57.3	41.7	1.0
V2161	123°03.90	49°17.60	25.0	70.4	28.5	1.1
V2162	123°03.90	49°17.60	25.0	70.4	28.5	1.1
V2163	123°03.90	49°17.60	25.0	70.4	28.5	1.1
V2256	123°05.10	49°17.20	14.0	52.5	38.2	9.3
V2257	123°05.10	49°17.20	14.0	52.5	38.2	9.3
V2258	123°05.10	49°17.20	14.0	52.5	38.2	9.3
V2253	123°05.10	49°17.50	40.0	83.3	16.6	0.1
V2254	123°05.10	49°17.50	40.0	83.3	16.6	0.1
V2255	123°05.10	49°17.50	40.0	83.3	16.6	0.1
V2226	123°04.60	49°17.30	20.0	53.7	46.3	0.0
V2227	123°04.60	49°17.30	20.0	53.7	46.3	0.0
V2228	123°04.60	49°17.30	20.0	53.7	46.3	0.0
V2221	123°04.60	49°17.50	35.0	72.2	27.3	0.5
V2222	123°04.60	49°17.50	35.0	72.2	27.3	0.5
V2223	123°04.60	49°17.50	35.0	72.2	27.3	0.5
V291	122°54.70	49°17.50	19.0	84.1	11.2	4.7
V292	122°54.70	49°17.50	19.0	84.1	11.2	4.7
V293	122°54.70	49°17.50	19.0	84.1	11.2	4.7

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
V2361	122°53.80	49°17.60	14.0	95.3	4.7	0.0
V2362	122°53.80	49°17.60	14.0	95.3	4.7	0.0
V2363	122°53.80	49°17.60	14.0	95.3	4.7	0.0
V2374	122°53.40	49°17.80	16.0	98.3	1.6	0.1
V2375	122°53.40	49°17.80	16.0	98.3	1.6	0.1
V2376	122°53.40	49°17.80	16.0	98.3	1.6	0.1
V2371	122°53.30	49°17.70	18.0	94.4	5.3	0.3
V2372	122°53.30	49°17.70	18.0	94.4	5.3	0.3
V2373	122°53.30	49°17.70	18.0	94.4	5.3	0.3
V2394	122°53.10	49°17.00	11.0	96.1	3.3	0.6
V2395	122°53.10	49°17.00	11.0	96.1	3.3	0.6
V2396	122°53.10	49°17.00	11.0	96.1	3.3	0.6
V2397	122°53.10	49°17.80	15.0	96.6	3.3	0.1
V2398	122°53.10	49°17.80	15.0	96.6	3.3	0.1
V2399	122°53.10	49°17.80	15.0	96.6	3.3	0.1
V2401	122°53.10	49°17.10	17.0	95.1	4.9	0.0
V2402	122°53.10	49°17.10	17.0	95.1	4.9	0.0
V2403	122°53.10	49°17.10	17.0	95.1	4.9	0.0
V2391	122°52.90	49°18.00	12.0	95.0	4.0	1.0
V2392	122°52.90	49°18.00	12.0	95.0	4.0	1.0
V2393	122°52.90	49°18.00	12.0	95.0	4.0	1.0
V2411	122°52.70	49°18.00	10.0	95.5	4.2	0.3
V2412	122°52.70	49°18.00	10.0	95.5	4.2	0.3
V2413	122°52.70	49°18.00	10.0	95.5	4.2	0.3
V2414	122°52.40	49°18.00	10.0	97.0	2.9	0.1
V2415	122°52.40	49°18.00	10.0	97.0	2.9	0.1
V2416	122°52.40	49°18.00	10.0	97.0	2.9	0.1
V2461	122°51.90	49°17.40	13.0	98.9	1.1	0.0
V2462	122°51.90	49°17.40	13.0	98.9	1.1	0.0
V2463	122°51.90	49°17.40	13.0	98.9	1.1	0.0
V2451	122°51.80	49°17.30	14.0	95.0	5.0	0.0
V2452	122°51.80	49°17.30	14.0	95.0	5.0	0.0
V2453	122°51.80	49°17.30	14.0	95.0	5.0	0.0
Boundary Bay: November 1985 (2 replicates per station)						
BASR1	122°53.30	49°04.12	2.0	3.0	97.0	0.0
BASR2	122°53.30	49°04.12	2.0	3.0	97.0	0.0
BANR1	122°52.18	49°03.42	5.0	7.0	93.0	0.0
BANR2	122°52.18	49°03.42	5.0	7.0	93.0	0.0
BBNW1	122°54.20	49°03.36	1.5	0.3	99.7	0.0
BBNW2	122°54.20	49°03.36	1.5	0.3	99.7	0.0
BBO1	122°53.48	49°03.18	9.0	0.2	99.8	0.0
BBO2	122°53.48	49°03.18	9.0	0.2	99.8	0.0
BBSE1	122°53.12	49°02.54	1.0	0.1	99.9	0.0
BBSE2	122°53.12	49°02.54	1.0	0.1	99.9	0.0
BCM1	122°55.30	49°01.36	11.0	1.0	99.0	0.0
BCM2	122°55.30	49°01.36	11.0	1.0	99.0	0.0
BC51	122°53.30	49°01.30	6.0	0.6	99.4	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
BC52	122°53.30	49°01.30	6.0	0.6	99.4	0.0
BC61	122°51.54	49°01.00	7.0	0.4	99.6	0.0
BC62	122°51.54	49°01.00	7.0	0.4	99.6	0.0
BD21	123°00.00	49°00.24	2.5	0.1	99.9	0.0
BD22	123°00.00	49°00.24	2.5	0.1	99.9	0.0
BD31	122°58.00	49°01.24	5.5	0.2	99.8	0.0
BD32	122°58.00	49°01.24	5.5	0.2	99.8	0.0
BD41	122°55.36	49°01.00	6.0	0.4	99.6	0.0
BD42	122°55.36	49°01.00	6.0	0.4	99.6	0.0
BE11	123°00.06	48°59.18	7.0	0.8	99.2	0.0
BE12	123°00.06	48°59.18	7.0	0.8	99.2	0.0
BE71	122°56.42	48°59.24	38.0	33.0	67.0	0.0
BE72	122°56.42	48°59.24	38.0	33.0	67.0	0.0
BE81	122°54.24	48°59.24	37.0	40.0	60.0	0.0
BE82	122°54.24	48°59.24	37.0	40.0	60.0	0.0
BE91	122°52.12	48°59.24	27.0	39.0	61.0	0.0
BE92	122°52.12	48°59.24	27.0	39.0	61.0	0.0
Alice Arm: October 1982 (2 replicates per station)						
A2CN1	129°31.70	55°26.67	262.0	92.4	7.5	0.0
A2CN2	129°31.70	55°26.67	262.0	97.8	2.1	0.0
A2CM1	129°31.88	55°26.50	274.0	98.5	1.5	0.0
A2CM2	129°31.88	55°26.50	279.0	90.7	9.2	0.0
A2CS1	129°31.74	55°26.50	235.0	84.9	14.2	0.9
A2CS2	129°31.74	55°26.50	214.0	67.6	32.2	0.8
A2DN1	129°33.60	55°26.80	349.0	84.5	15.2	0.2
A2DN2	129°33.60	55°26.80	349.0	94.5	5.4	0.0
A2DM1	129°33.59	55°26.74	347.0	81.3	18.6	0.0
A2DM2	129°33.59	55°26.74	347.0	77.3	22.2	0.4
A2DS1	129°33.50	55°26.70	343.0	67.5	32.4	0.0
A2DS2	129°33.50	55°26.70	343.0	65.4	34.5	0.0
A2EN1	129°37.00	55°27.20	376.0	98.0	2.0	0.0
A2EN2	129°37.00	55°27.20	376.0	97.5	2.5	0.0
A2EM1	129°37.00	55°27.10	376.0	97.5	2.4	0.0
A2ES1	129°37.00	55°27.00	371.0	96.7	3.3	0.0
A2ES2	129°37.00	55°27.00	373.0	97.9	2.0	0.0
H2ZE1	129°45.60	55°29.30	395.0	99.4	0.6	0.0
H2ZE2	129°45.60	55°29.30	395.0	99.6	0.3	0.0
H2ZM1	129°45.80	55°29.30	395.0	99.0	0.8	0.3
H2ZM2	129°45.80	55°29.30	395.0	99.7	0.3	0.0
H2ZW1	129°45.95	55°29.20	395.0	99.3	0.7	0.0
H2ZW2	129°45.95	55°29.20	395.0	99.2	0.7	0.0
Alice Arm: October 1983 (2 replicates per station)						
A3CN1	129°31.70	55°26.67	262.0	95.6	4.4	0.0
A3CN2	129°31.70	55°26.67	262.0	98.3	1.7	0.0
A3CM1	129°31.88	55°26.50	274.0	96.4	3.6	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
A3CM2	129°31.88	55°26.50	279.0	93.2	6.9	0.0
A3CS1	129°31.74	55°26.50	235.0	84.5	15.5	0.0
A3CS2	129°31.74	55°26.50	214.0	96.4	3.6	0.0
A3DN1	129°33.60	55°26.80	349.0	25.9	74.1	0.0
A3DN2	129°33.60	55°26.80	349.0	68.4	31.6	0.0
A3DM1	129°33.59	55°26.74	347.0	47.5	52.5	0.0
A3DM2	129°33.59	55°26.74	347.0	48.2	51.8	0.0
A3DS1	129°33.50	55°26.70	343.0	88.3	11.7	0.0
A3DS2	129°33.50	55°26.70	343.0	77.3	22.7	0.0
A35N1	129°35.27	55°27.10	327.0	87.0	13.0	0.0
A35N2	129°35.27	55°27.10	327.0	94.4	5.6	0.0
A35M1	129°35.38	55°27.08	370.0	77.2	22.8	0.0
A35M2	129°35.38	55°27.08	371.0	82.4	17.6	0.0
A35S1	129°35.38	55°27.03	370.0	56.3	43.7	0.0
A35S2	129°35.38	55°27.03	370.0	75.8	24.2	0.0
A3EN1	129°37.00	55°27.20	376.0	98.1	1.9	0.0
A3EN2	129°37.00	55°27.20	376.0	98.5	1.5	0.0
A3EM1	129°37.00	55°27.10	376.0	98.5	1.5	0.0
A3EM2	129°37.[illegible]	55°27.10	376.0	98.3	1.7	0.0
A3ES1	129°37.00	55°27.00	371.0	97.9	2.1	0.0
A3ES2	129°37.00	55°27.00	373.0	97.1	2.9	0.0
H3ZE1	129°45.60	55°29.30	395.0	99.7	0.4	0.0
H3ZE2	129°45.60	55°29.30	395.0	98.7	1.3	0.0
H3ZM1	129°45.80	55°29.30	395.0	98.8	1.2	0.0
H3ZM2	129°45.80	55°29.30	395.0	99.7	0.3	0.0
H3ZW1	129°45.95	55°29.20	395.0	99.8	0.2	0.0
H3ZW2	129°45.95	55°29.20	395.0	99.8	0.2	0.0
Alice Arm: October 1986 (2 replicates per station)						
A6CN1	129°31.70	55°26.67	262.0	95.6	4.4	0.0
A6CN2	129°31.70	55°26.67	262.0	98.3	1.7	0.0
A6CM1	129°31.88	55°26.50	274.0	96.4	3.6	0.0
A6CM2	129°31.88	55°26.50	279.0	93.2	6.9	0.0
A6CS1	129°31.74	55°26.50	235.0	84.5	15.5	0.0
A6CS2	129°31.74	55°26.50	214.0	96.4	3.6	0.0
A6DN1	129°33.60	55°26.80	349.0	25.9	74.1	0.0
A6DN2	129°33.60	55°26.80	349.0	68.4	31.6	0.0
A6DM1	129°33.59	55°26.74	347.0	47.5	52.5	0.0
A6DM2	129°33.59	55°26.74	347.0	48.2	51.8	0.0
A6DS1	129°33.50	55°26.70	343.0	88.3	11.7	0.0
A6DS2	129°33.50	55°26.70	343.0	77.3	22.7	0.0
A65N1	129°35.45	55°27.17	369.0	87.0	13.0	0.0
A65N2	129°35.45	55°27.17	360.0	94.4	5.6	0.0
A65M1	129°35.38	55°27.08	370.0	77.2	22.8	0.0
A65M2	129°35.38	55°27.08	371.0	82.4	17.6	0.0
A65S1	129°35.38	55°27.03	370.0	56.3	43.7	0.0
A65S2	129°35.38	55°27.03	370.0	75.8	24.2	0.0
A6EN1	129°37.00	55°27.20	376.0	98.1	1.9	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
A6EN2	129°37.00	55°27.20	376.0	98.5	1.5	0.0
A6EM1	129°37.00	55°27.10	376.0	98.5	1.5	0.0
A6EM2	129°37.00	55°27.10	376.0	98.3	1.7	0.0
A6ES1	129°37.00	55°27.00	371.0	97.9	2.1	0.0
A6ES2	129°37.00	55°27.00	373.0	97.1	2.9	0.0
H6ZE1	129°45.60	55°29.30	395.0	99.7	0.4	0.0
H6ZE2	129°45.60	55°29.30	395.0	98.7	1.3	0.0
H6ZM1	129°45.80	55°29.30	395.0	98.8	1.2	0.0
H6ZM2	129°45.80	55°29.30	395.0	99.7	0.3	0.0
H6ZW1	129°45.95	55°29.20	395.0	99.8	0.2	0.0
H6ZW2	129°45.95	55°29.20	395.0	99.8	0.2	0.0
Alice Arm: October 1989 (2 replicates per station)						
A9CN1	129°31.70	55°26.67	280.0	92.4	7.5	0.0
A9CN2	129°31.70	55°26.67	278.0	97.8	2.1	0.0
A9CM1	129°31.88	55°26.50	294.0	98.5	1.5	0.0
A9CM2	129°31.88	55°26.50	296.0	90.7	9.2	0.0
A9CS1	129°31.74	55°26.50	240.0	84.9	14.2	0.9
A9CS2	129°31.74	55°26.50	271.0	67.6	32.2	0.8
	129°33.60	55°26.80	365.0	84.5	15.2	0.2
	129°33.60	55°26.80	362.0	94.5	5.4	0.0
	129°33.59	55°26.74	370.0	81.3	18.6	0.0
	129°33.59	55°26.74	374.0	77.3	22.2	0.4
A9ES1	129°33.50	55°26.70	371.0	67.5	32.4	0.0
A9ES2	129°33.50	55°26.70	369.0	65.4	34.5	0.0
A9EN1	129°37.00	55°27.20	403.0	98.0	2.0	0.0
A9EN2	129°37.00	55°27.20	400.0	97.5	2.5	0.0
A9EM1	129°37.00	55°27.10	402.0	97.4	2.6	0.0
A9EM2	129°37.00	55°27.10	401.0	97.5	2.4	0.0
A9ES1	129°37.00	55°27.00	394.0	96.7	3.3	0.0
A9ES2	129°37.00	55°27.00	395.0	97.9	2.0	0.0
H9ZE1	129°45.40	55°29.30	267.0	99.4	0.6	0.0
H9ZE2	129°45.40	55°29.30	267.0	99.6	0.3	0.0
H9ZM1	129°45.60	55°29.30	321.0	99.0	0.8	0.3
H9ZM2	129°45.60	55°29.30	322.0	99.7	0.3	0.0
H9ZW1	129°45.90	55°29.20	322.0	99.3	0.7	0.0
H9ZW2	129°45.90	55°29.20	321.0	99.2	0.7	0.0
Hecate Strait: June 1985 (5 replicates per station)						
H1A11	131°24.60	54°18.60	130.0	27.5	72.8	0.0
H1A12	131°24.60	54°18.60	130.0	28.2	71.8	0.0
H1A13	131°24.60	54°18.60	130.0	27.0	73.0	0.0
H1A14	131°24.60	54°18.60	130.0	30.1	69.9	0.0
H1A15	131°24.60	54°18.60	130.0	29.4	70.6	0.0
H1A21	131°20.00	54°19.30	135.0	54.9	45.5	0.0
H1A22	131°20.30	54°20.70	166.0	66.2	33.1	0.8
H1A23	131°31.00	54°18.50	157.0	22.9	77.8	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
H1A24	131°30.50	54°17.50	129.0	15.5	84.3	0.2
H1A25	131°25.50	54°18.80	140.0	29.9	70.2	0.0
H1A31	131°27.80	54°18.20	140.0	17.2	82.8	0.0
H1A32	131°27.80	54°18.20	140.0	25.9	74.1	0.0
H1A33	131°27.80	54°18.20	140.0	23.9	76.1	0.0
H1A34	131°27.80	54°18.20	140.0	21.0	79.0	0.0
H1A35	131°27.80	54°18.20	140.0	22.3	77.7	0.0
H1B11	131°17.20	53°32.50	28.0	1.2	98.2	0.6
H1B12	131°17.20	53°32.50	28.0	13.9	74.8	11.3
H1B13	131°17.20	53°32.50	28.0	1.7	85.5	12.9
H1B14	131°17.20	53°32.50	28.0	2.3	96.5	1.3
H1B15	131°17.20	53°32.50	28.0	1.0	85.7	13.3
H1B21	131°19.50	53°32.80	26.0	0.4	95.3	3.2
H1B22	131°13.80	53°33.00	29.0	0.7	96.2	2.4
H1B23	131°13.80	53°30.00	26.0	1.1	54.5	44.3
H1B24	131°19.80	53°33.00	29.0	2.2	94.8	3.0
H1B25	131°17.00	53°31.20	31.0	1.2	96.3	1.5
H1B71	131°18.00	53°32.00	29.0	1.9	87.9	10.2
H1B72	131°18.00	53°32.00	29.0	2.0	89.5	8.5
H1B73	131°18.00	53°32.00	29.0	1.3	95.5	3.2
H1B74	131°18.00	53°32.00	29.0	2.7	93.8	3.5
H1B75	131°18.00	53°32.00	29.0	1.6	97.3	1.1
H1C11	130°48.40	53°11.50	128.0	11.1	88.6	0.3
H1C12	130°48.40	53°11.50	128.0	7.5	91.9	0.6
H1C13	130°48.40	53°11.50	128.0	22.0	78.0	0.0
H1C14	130°48.40	53°11.50	128.0	9.2	90.6	0.1
H1C15	130°48.40	53°11.50	128.0	10.4	89.3	0.3
H1C21	130°50.20	53°12.70	128.0	8.8	87.6	3.9
H1C22	130°45.30	53°12.60	159.0	41.9	58.7	1.0
H1C23	130°45.50	53°09.60	146.0	23.9	76.2	1.0
H1C24	130°50.60	53°09.40	121.0	13.3	54.6	2.0
H1C25	130°47.70	53°11.00	128.0	7.1	92.5	0.2
H1C71	130°45.60	53°11.40	148.0	25.8	74.2	0.0
H1C72	130°45.60	53°11.40	148.0	26.0	74.0	0.0
H1C73	130°45.60	53°11.40	148.0	25.0	75.0	0.0
H1C74	130°45.60	53°11.40	148.0	25.0	75.0	0.0
H1C75	130°45.60	53°11.40	148.0	25.0	75.0	0.0
Hecate Strait: October 1985 (5 replicates per station)						
H2A11	131°24.60	54°18.60	130.0	11.7	88.3	0.0
H2A12	131°24.60	54°18.60	130.0	9.8	90.2	0.0
H2A13	131°24.60	54°18.60	130.0	21.1	78.9	0.0
H2A14	131°24.60	54°18.60	130.0	15.9	84.1	0.0
H2A15	131°24.60	54°18.60	130.0	17.1	82.9	0.0
H2A21	131°20.00	54°19.30	124.0	31.6	68.1	0.2
H2A22	131°20.30	54°20.70	166.0	57.7	42.1	3.0
H2A23	131°31.00	54°18.50	150.0	11.3	88.5	0.0
H2A24	131°30.50	54°17.50	129.0	11.6	87.7	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
H2A25	131°25.50	54°18.80	144.0	24.8	75.0	0.0
H2A31	131°27.80	54°18.20	146.0	13.7	86.1	0.1
H2A32	131°27.80	54°18.20	146.0	16.0	84.0	0.0
H2A33	131°27.80	54°18.20	146.0	20.0	80.1	0.0
H2A34	131°27.80	54°18.20	146.0	20.8	79.2	0.0
H2A35	131°27.80	54°18.20	146.0	18.1	81.9	0.0
H2B11	131°17.20	53°32.50	29.0	1.2	98.4	0.4
H2B12	131°17.20	53°32.50	29.0	1.3	97.6	1.1
H2B13	131°17.20	53°32.50	29.0	1.8	97.2	1.0
H2B14	131°17.20	53°32.50	29.0	1.3	96.0	2.7
H2B15	131°17.20	53°32.50	29.0	1.7	97.6	0.7
H2B21	131°19.50	53°32.80	26.0	2.6	93.1	4.3
H2B22	131°13.80	53°33.00	28.0	1.5	92.9	6.1
H2B23	131°13.80	53°30.00	29.0	1.9	71.7	26.9
H2B24	131°19.80	53°33.00	29.0	3.9	95.6	1.0
H2B25	131°17.00	53°31.20	29.0	4.8	78.1	20.8
H2B71	131°18.00	53°32.00	25.0	1.0	95.6	3.4
H2B72	131°18.00	53°32.00	25.0	2.0	97.3	0.7
H2B73	131°18.00	53°32.00	25.0	1.1	93.4	5.5
H2B74	131°18.00	53°32.00	25.0	1.0	97.0	2.1
H2B75	131°18.00	53°32.00	25.0	1.1	96.3	2.6
H2C11	130°48.40	53°11.50	135.0	9.7	90.2	0.1
H2C12	130°48.40	53°11.50	135.0	8.9	90.7	0.0
H2C13	130°48.40	53°11.50	135.0	8.4	90.5	1.1
H2C14	130°48.40	53°11.50	135.0	14.6	85.4	0.0
H2C15	130°48.40	53°11.50	135.0	17.0	82.9	0.1
H2C21	130°50.20	53°12.70	126.0	9.3	84.7	5.8
H2C22	130°45.30	53°12.60	157.0	40.3	58.8	0.6
H2C23	130°45.50	53°09.60	153.0	22.2	77.0	8.0
H2C24	130°50.60	53°09.40	117.0	7.4	70.6	21.9
H2C25	130°47.70	53°11.00	128.0	9.0	90.3	0.5
H2C71	130°45.60	53°11.40	146.0	26.7	73.4	0.0
H2C72	130°45.60	53°11.40	146.0	19.1	54.4	26.5
H2C73	130°45.60	53°11.40	146.0	23.3	76.4	0.3
H2C74	130°45.60	53°11.40	146.0	20.3	67.0	12.7
H2C75	130°45.60	53°11.40	146.0	18.4	72.5	9.1
H2D11	130°53.00	53°06.30	97.0	7.6	92.4	0.0
H2D12	130°53.00	53°06.30	97.0	2.0	98.1	0.0
H2D13	130°53.00	53°06.30	97.0	5.3	94.8	0.0
H2D14	130°53.00	53°06.30	97.0	5.7	94.3	0.0
H2D15	130°53.00	53°06.30	97.0	7.6	92.4	0.0
H2D21	130°57.00	53°08.00	70.0	2.4	97.3	0.0
H2D22	130°51.80	53°07.80	106.0	1.7	3.8	93.7
H2D23	130°51.80	53°04.80	77.0	5.9	60.5	33.4
H2D24	130°56.60	53°04.80	55.0	3.6	96.3	9.0
H2D25	130°54.80	53°06.40	87.0	5.4	88.8	0.7
H2D71	130°55.50	53°06.30	82.0	8.8	91.2	0.0
H2D72	130°55.50	53°06.30	82.0	26.5	73.5	0.0
H2D73	130°55.50	53°06.30	82.0	12.1	87.9	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
H2D74	130°55.50	53°06.30	82.0	12.2	87.8	0.0
H2D75	130°55.50	53°06.30	82.0	9.9	90.0	0.0
Hecate Strait: January 1986 (5 replicates per station)						
H3A11	131°24.60	54°18.60	139.0	20.7	79.1	0.0
H3A12	131°24.60	54°18.60	139.0	17.2	82.7	0.0
H3A13	131°24.60	54°18.60	139.0	20.1	79.9	0.0
H3A14	131°24.60	54°18.60	139.0	19.4	80.6	0.0
H3A15	131°24.60	54°18.60	139.0	18.1	81.9	0.0
H3A21	131°20.00	54°19.30	139.0	47.5	52.4	5.0
H3A22	131°20.30	54°20.70	166.0	72.6	27.9	4.0
H3A23	131°31.00	54°18.50	152.0	11.4	86.8	9.0
H3A24	131°30.50	54°17.50	135.0	13.1	86.8	8.0
H3A25	131°25.50	54°18.80	146.0	27.2	72.5	8.0
H3A31	131°27.80	54°18.20	142.0	23.0	75.8	0.0
H3A32	131°27.80	54°18.20	142.0	12.1	87.9	0.0
H3A33	131°27.80	54°18.20	142.0	13.4	86.6	0.0
H3A34	131°27.80	54°18.20	142.0	13.0	87.0	0.0
H3A35	131°27.80	54°18.20	142.0	8.9	91.0	0.0
H3B11	131°17.20	53°32.50	36.0	0.9	96.7	2.3
H3B12	131°17.20	53°32.50	36.0	2.7	93.2	4.1
H3B13	131°17.20	53°32.50	36.0	1.9	88.7	9.3
H3B14	131°17.20	53°32.50	36.0	2.6	94.4	3.0
H3B15	131°17.20	53°32.50	36.0	0.8	89.4	9.8
H3B21	131°19.50	53°32.80	18.0	3.7	95.3	0.8
H3B32	131°13.80	53°33.00	29.0	0.8	95.8	3.3
H3B43	131°13.80	53°30.00	29.0	0.8	84.5	14.6
H3B54	131°19.80	53°33.00	29.0	1.0	28.4	70.4
H3B65	131°17.00	53°31.20	27.0	0.9	96.5	2.5
H3B71	131°18.00	53°32.00	27.0	1.0	91.8	7.2
H3B72	131°18.00	53°32.00	27.0	1.2	97.1	1.7
H3B73	131°18.00	53°32.00	27.0	12.7	85.2	2.1
H3B74	131°18.00	53°32.00	27.0	13.5	82.1	4.4
H3B75	131°18.00	53°32.00	27.0	18.4	79.2	2.3
H3C11	130°48.40	53°11.50	130.0	10.7	86.7	2.6
H3C12	130°48.40	53°11.50	130.0	8.8	46.5	44.8
H3C13	130°48.40	53°11.50	130.0	12.3	87.4	0.2
H3C14	130°48.40	53°11.50	130.0	9.8	89.0	1.1
H3C15	130°48.40	53°11.50	130.0	13.5	86.1	0.5
H3C21	130°50.20	53°12.70	125.0	4.0	95.7	0.3
H3C22	130°45.30	53°12.60	154.0	16.5	21.2	62.3
H3C23	130°45.50	53°09.60	147.0	24.6	75.4	0.0
H3C24	130°50.60	53°09.40	128.0	11.3	70.9	17.8
H3C25	130°47.70	53°11.00	128.0	8.2	91.5	0.3
H3C71	130°45.60	53°11.40	148.0	28.7	71.3	0.0
H3C72	130°45.60	53°11.40	148.0	31.5	68.4	0.0
H3C73	130°45.60	53°11.40	148.0	24.5	75.5	0.0
H3C74	130°45.60	53°11.40	148.0	24.5	75.5	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
H3C75	130°45.60	53°11.40	148.0	32.4	67.6	0.0
H3D11	130°53.00	53°06.30	95.0	3.7	96.3	0.0
H3D12	130°53.00	53°06.30	95.0	5.0	95.0	0.0
H3D13	130°53.00	53°06.30	95.0	2.2	97.8	0.0
H3D14	130°53.00	53°06.30	95.0	6.1	93.9	0.0
H3D15	130°53.00	53°06.30	95.0	3.0	97.0	0.0
H3D21	130°57.00	53°08.00	69.0	2.2	97.0	0.8
H3D22	130°51.80	53°07.80	108.0	2.0	4.0	94.0
H3D23	130°51.80	53°04.80	79.0	4.7	50.0	45.4
H3D24	130°56.60	53°04.80	55.0	4.3	95.7	0.0
H3D25	130°54.80	53°06.40	84.0	2.4	97.6	0.0
H3D71	130°55.50	53°06.30	75.0	2.4	97.6	0.0
H3D72	130°55.50	53°06.30	75.0	2.7	97.3	0.0
H3D73	130°55.50	53°06.30	75.0	2.3	97.7	0.0
H3D74	130°55.50	53°06.30	75.0	2.2	97.8	0.0
H3D75	130°55.50	53°06.30	75.0	2.3	97.7	0.1
Shelf: April 1981 (2 replicates per station)						
S1A11	125°29.00	48°47.00	107.0	97.9	2.1	0.0
S1A12	125°29.00	48°47.00	107.0	97.8	2.2	0.0
S1A21	125°33.09	48°45.03	145.0	98.1	1.9	0.0
S1A22	125°33.09	48°45.03	145.0	99.4	0.6	0.0
S1A41	125°29.04	48°44.02	123.0	98.6	1.4	0.0
S1A42	125°29.04	48°44.02	123.0	98.0	2.0	0.0
S1A51	125°32.01	48°41.00	175.0	97.6	2.4	0.0
S1A52	125°32.01	48°41.00	175.0	97.4	2.6	0.0
S1B11	125°16.05	48°38.03	106.0	95.6	4.4	0.0
S1B12	125°16.05	48°38.03	106.0	94.2	5.8	0.0
S1B21	125°16.06	48°35.05	119.0	93.7	6.3	0.0
S1B22	125°16.06	48°35.05	119.0	96.8	3.2	0.0
S1B31	125°24.04	48°35.05	133.0	99.7	0.3	0.0
S1B32	125°24.04	48°35.05	133.0	98.5	1.5	0.0
S1C11	125°19.03	48°30.08	142.0	97.3	2.7	0.0
S1C12	125°19.03	48°30.08	142.0	98.0	2.0	0.0
S1C21	125°22.00	48°26.01	163.0	99.5	0.5	0.0
S1C22	125°22.00	48°26.01	163.0	99.6	0.4	0.0
S1C41	125°35.08	48°23.08	133.0	18.9	81.1	0.0
S1C42	125°35.08	48°23.08	133.0	18.9	81.1	0.0
S1D11	126°00.08	48°37.00	111.0	7.3	92.7	0.0
S1D12	126°00.08	48°37.00	111.0	9.7	90.3	0.0
S1D21	126°05.00	48°43.01	114.0	7.9	92.1	0.0
S1D22	126°05.00	48°43.01	114.0	8.2	91.8	0.0
S1D41	126°02.08	48°40.09	111.0	6.4	93.6	0.0
S1D42	126°02.08	48°40.09	111.0	6.5	93.5	0.0
Shelf: September 1981 (2 replicates per station)						
S2A11	125°29.00	48°47.00	107.0	97.0	3.0	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
S2A12	125°29.00	48°47.00	107.0	97.4	2.6	0.0
S2A21	125°33.09	48°45.03	151.0	99.0	1.0	0.0
S2A22	125°33.09	48°45.03	151.0	99.3	0.7	0.0
S2A41	125°29.04	48°44.02	122.0	97.7	2.3	0.0
S2A42	125°29.04	48°44.02	122.0	96.9	3.1	0.0
S2A51	125°32.01	48°41.00	197.0	76.1	23.9	0.0
S2A52	125°32.01	48°41.00	197.0	53.2	46.8	0.0
S2B11	125°16.05	48°38.03	109.0	93.5	6.5	0.0
S2B12	125°16.05	48°38.03	109.0	92.0	8.0	0.0
S2B21	125°16.06	48°35.05	120.0	99.1	1.0	0.0
S2B22	125°16.06	48°35.05	120.0	98.3	1.7	0.0
S2B31	125°24.04	48°35.05	127.0	98.9	1.0	0.0
S2B32	125°24.04	48°35.05	127.0	98.3	1.7	0.0
S2C11	125°19.03	48°30.08	142.0	95.9	4.1	0.0
S2C12	125°19.03	48°30.08	142.0	92.6	7.4	0.0
S2C21	125°22.00	48°26.01	173.0	98.8	1.2	0.0
S2C22	125°22.00	48°26.01	173.0	98.7	1.3	0.0
S2C41	125°35.08	48°23.08	133.0	15.6	84.4	0.0
S2C42	125°35.08	48°23.08	133.0	15.6	84.4	0.0
S2D11	126°00.08	48°37.00	115.0	8.5	91.5	0.0
S2D12	126°00.08	48°37.00	115.0	6.3	93.7	0.0
S2D21	126°05.00	48°43.01	118.0	6.6	95.0	0.0
S2D22	126°05.00	48°43.01	118.0	7.6	92.4	0.0
S2D41	126°02.08	48°40.09	118.0	8.7	91.3	0.0
S2D42	126°02.08	48°40.09	118.0	6.3	93.7	0.0
Other fjords: October 1987 (2 replicates per station)						
F5A1	127°40.50	51°59.50	241.0	49.6	50.4	0.0
F5A2	127°40.50	51°59.50	241.0	43.5	56.0	0.5
F5B1	127°38.50	52°05.00	343.0	92.5	7.5	0.0
F5B2	127°38.50	52°05.00	343.0	92.1	7.9	0.0
F5C1	127°33.00	52°09.00	433.0	91.9	8.1	0.0
F5C2	127°33.00	52°09.00	433.0	75.9	24.1	0.0
F5D1	127°27.50	52°05.70	363.0	90.0	9.8	0.2
F5D2	127°27.50	52°05.70	363.0	91.5	7.8	0.7
F91	127°01.80	52°38.10	494.0	97.9	2.1	0.0
F92	127°01.80	52°38.10	494.0	97.9	2.1	0.0
F101	127°46.20	52°15.80	445.0	97.4	2.6	0.0
F102	127°46.20	52°15.80	445.0	96.5	3.5	0.0
F131	129°07.90	53°10.50	570.0	77.8	22.2	0.0
F132	129°07.90	53°10.50	570.0	66.3	33.7	0.0
F141	129°12.00	53°34.00	301.0	22.5	74.4	3.1
F142	129°12.00	53°34.00	301.0	29.0	67.9	3.1
F143	129°09.00	53°39.00	370.0	26.3	59.6	14.1
F144	129°09.00	53°39.00	370.0	26.5	66.0	7.5
F145	129°02.90	53°43.70	360.0	94.7	5.3	0.0
F146	129°02.90	53°43.70	360.0	92.6	7.4	0.0
F151	128°50.00	53°48.50	357.0	99.4	0.6	0.0

Appendix 1. (continued)

STATION	LONGITUDE	LATITUDE	DEPTH	%SILT	%SAND	%GRAVEL
F152	128°50.00	53°48.50	357.0	98.7	1.3	0.0
F181	130°10.70	55°04.40	222.0	99.3	0.7	0.0
F182	130°10.70	55°04.40	222.0	99.1	0.9	0.0
F201	130°02.00	55°25.00	233.0	97.0	3.0	0.0
F202	130°02.00	55°25.00	233.0	97.3	2.7	0.0
F203	129°59.50	55°19.00	256.0	98.5	1.5	0.0
F204	129°59.50	55°19.00	256.0	98.0	2.0	0.0
F205	130°07.50	55°10.00	310.0	96.3	3.7	0.0
F206	130°07.50	55°10.00	310.0	96.2	3.8	0.0

Appendix 2. Complete species list for ABUNBASE and BIOBASE. Species are listed in alphabetical order by Genus and taxa. Mean wet weight per individual measured for each species is included. Values of zero indicate weights less than 0.01 mg or eliminated taxa (i.e. copepods). An * indicates that the mean weight was estimate from congeneric species because no specimens could be obtained.

NO.	PHYLUM	CLASS	ORDER	FAMILY	GENUS, SPECIES	Mean Wt. (mg)
1000	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Pontogenei	Accedomoera vagor	1.92
1001	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Acesta catharinae	0.66
1002	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Acesta lopezi	0.33
1003	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Acesta neosuecica	1.41
1004	PYCNOGONID	N/A	PEGMATA	Ammotheida	Achelia alaskensis	0.00
1005	PYCNOGONID	N/A	PEGMATA	Ammotheida	Achelia nudiuscula	0.01
1006	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanida	Acila castrensis	54.80
1007	CRUSTACEA	COPEPODA	HARPACTICO	Cletodidae	Acrenhydrosoma perplexum	0.00
1008	MOLLUSCA	GASTROPODA	NEOGASTROP	Cancellari	Admete gracillor	1.00
1009	MOLLUSCA	BIVALVIA	VENEROIDA	Thyasirida	Adontorhina cyclia	1.60
1010	MOLLUSCA	BIVALVIA	VENEROIDA	Thyasirida	Adontorhina ferruginosa	5.89
1011	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Aglaophamus malmgreni	8.30
1012	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Aglaophamus rubella anops	2.00
1013	CRUSTACEA	OSTRACODA	HALOCYPRIDA	Halocyprid	Alacia alata minor	0.10
1014	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Allia nolani	0.10*
1015	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Allia quadrilobata	1.51
1016	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Allia ramosa	0.20*
1017	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Hyalidae	Allorchestes angusta	1.00
1018	MOLLUSCA	GASTROPODA	MESOGASTRO	Rissoidae	Alvania compacta	0.65
1019	MOLLUSCA	GASTROPODA	MESOGASTRO	Rissoidae	Alvania rosana	0.40
1020	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Amage anops	0.10
1021	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Ampelisca agassizi	2.36
1022	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Ampelisca brevisimulata	0.33
1023	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Ampelisca careyi	4.95
1024	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Ampelisca cristata	0.65
1025	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Ampelisca hancocki	0.50
1026	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Ampelisca lobata	1.50
1027	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Ampelisca pugetica	0.10
1028	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Ampelisca unsocalae	1.60
1029	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Ampharete acutifrons	50.12
1030	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Ampharete finmarchica	51.00
1031	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Ampharete labrops	2.49
1032	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Amphicteis glabra	255.40
1033	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Amphicteis mucronata	180.40
1034	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Amphicteis scaphobranchiata	230.45
1035	ANNELIDA	POLYCHAETA	TEREBELLID	Pectinarii	Amphictene moorei	8.33
1036	ECHINODERM	OPHIUROIDE	OPHIURIDA	Amphiurida	Amphiodia periercta	3.06
1037	ECHINODERM	OPHIUROIDE	OPHIURIDA	Amphiurida	Amphiodia urtica	428.00
1038	ECHINODERM	OPHIUROIDE	OPHIURIDA	Amphiurida	Amphiopholus pugetana	9.00
1039	ECHINODERM	OPHIUROIDE	OPHIURIDA	Amphiurida	Amphiopholus squamata	9.00

Appendix 2. (continued)

1040	ECHINODERM	OPHIUROIDE	OPHIURIDA	Amphiurida	Amphioplus macraspis	20.00
1041	ECHINODERM	OPHIUROIDE	OPHIURIDA	Amphiurida	Amphioplus strongyloplax	24.00
1042	MOLLUSCA	GASTROPODA	NEOGASTROPO	Collumbelli	Amphissa bicolor	25.50
1043	MOLLUSCA	GASTROPODA	NEOGASTROP	Columbelli	Amphissa columbiana	223.30
1044	MOLLUSCA	GASTROPODA	NEOGASTROP	Columbelli	Amphissa versicolor	3.40
1045	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Anaitides citrina	0.00
1046	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Anaitides groenlandica	42.35
1047	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Anaitides hartmani	0.43*
1048	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Anaitides mucosa	0.47
1049	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Anaitides williamsi	7.00
1050	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Ancistrosyllis groenlandica	3.00
1051	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Anobothrus gracilis	3.15
1052	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Lysianassi	Anonyx lilljeborgi	0.00
1053	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Antinoella sarsi	3.51
1054	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Aoridae	Aoroides columbiae	0.28
1055	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Aoridae	Aoroides inermis	0.48
1056	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Aoridae	Aoroides intermedius	0.43
1057	ANNELIDA	POLYCHAETA	SPIONIDA	Apistobran	Apistobranchus ornatus	0.00*
1058	ANNELIDA	POLYCHAETA	SPIONIDA	Apistobran	Apistobranchus tullbergi	2.20
1059	CRUSTACEA	CRUSTACEA	TANAIDACEA	Leptognathi	Araphura brevimana	0.05
1060	CRUSTACEA	MYSIDACEA	MYSIDACEA	Mysidae	Archaeomysis grebnitzkii	10.00
1061	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Arcteobia spinelytris	14.19
1062	CRUSTACEA	DECAPODA	CARIDEA	Crangonida	Argis alaskensis	1119.30
1063	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Argissidae	Argissa hamatipes	7.00
1064	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Aricidea cerruti	3.00
1065	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Aricidea minuta	0.75
1066	ANNELIDA	POLYCHAETA	OPHELIIDA	Opheliidae	Armandia brevis	0.66
1067	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Artacama coniferi	523.50
1068	ANNELIDA	POLYCHAETA	TEREBELLID	Trichobran	Artacamella hancocki	3.00
1069	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Asabellides lineata	0.00
1070	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Asabellides sibirica	0.30
1071	ANNELIDA	POLYCHAETA	OPHELIIDA	Scalibregm	Asclerocheilus beringianus	4.10
1072	MOLLUSCA	BIVALVIA	VENEROIDA	Astartidae	Astarte esquimalti	1.20
1073	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Asychis disparidentata	84.40
1074	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Asychis similis	283.90
1075	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Atylidae	Atylus collingi	0.50
1076	MOLLUSCA	BIVALVIA	VENEROIDA	Thyasirida	Axinopsida serricata	6.70
1077	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Axiothella rubrocincta	0.70
1078	CRUSTACEA	CIRRIPEDIA	THORACICA	Balanidae	Balanus crenatus	157.05
1079	ANNELIDA	POLYCHAETA	CAPITELLIDA	Capitellid	Barentolla americana	5.25
1080	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Oedoceroti	Bathymedon nepos	0.40
1081	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Oedoceroti	Bathymedon pumilis	0.58*
1082	MOLLUSCA	GASTROPODA	MESOGASTRO	Cerithiida	Bittium attenuatum	31.40
1083	MOLLUSCA	GASTROPODA	MESOGASTRO	Cerithiida	Bittium munitum	27.00
1084	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Boccardia pugettensis	11.00
1085	ANNELIDA	POLYCHAETA	FLABELLIGE	Flabellige	Brada sachalina	57.70
1086	ANNELIDA	POLYCHAETA	FLABELLIGE	Flabellige	Brada villosa	44.43
1087	CRUSTACEA	COPEPODA	HARPACTICO	Ectinosoma	Bradya typica	0.00
1088	ECHINODERM	ECHINOIDEA	SPATANGOID	Schizaster	Brisaster latifrons	2638.90

Appendix 2. (continued)

1089	MOLLUSCA	GASTROPODA	NEOGASTROP	Buccinidae	Buccinum glaciale	18.10
1090	CRUSTACEA	COPEPODA	HARPACTICO	Diosaccida	Bulbamphiascus imus	0.00
1091	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Byblis gaimardi	31.80
1092	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Byblis millsi	4.70
1093	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Byblis mulleni	7.00
1094	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Byblis pearcyi	5.00
1095	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Byblis veleronis	7.00
1096	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Byglides macrolepida	0.60*
1097	MOLLUSCA	SCAPHOPODA	GADILIDA	Cadulidae	Cadulus aberrans	31.80
1098	MOLLUSCA	SCAPHOPODA	GADILIDA	Cadulidae	Cadulus hepburni	25.00
1099	MOLLUSCA	SCAPHOPODA	GADILIDA	Cadulidae	Cadulus tolmiei	27.91
1100	MOLLUSCA	GASTROPODA	MESOGASTRO	Caecidae	Caecum crebricinctum	4.60
1101	MOLLUSCA	GASTROPODA	MESOGASTRO	Calyptraei	Calyptraea fastigata	27.20
1102	CRUSTACEA	CUMACEA	CUMACEA	Nannastaci	Campylaspis canaliculata	0.10
1103	CRUSTACEA	CUMACEA	CUMACEA	Nannastaci	Campylaspis rubicunda	0.10
1104	CRUSTACEA	CUMACEA	CUMACEA	Nannastaci	Campylaspis rubromaculata	0.05*
1105	CRUSTACEA	DECAPODA	BRACHYURA	Cancridae	Cancer gracilis	1456.80
1106	CRUSTACEA	DECAPODA	BRACHYURA	Cancridae	Cancer magister	141.60
1107	CRUSTACEA	DECAPODA	BRACHYURA	Cancridae	Cancer productus	41.50
1108	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Capitella capitata	0.20
1109	CRUSTACEA	AMPHIPODA	CAPPRELLID	Caprellida	Caprella irregularis	0.45
1110	CRUSTACEA	AMPHIPODA	CAPPRELLID	Caprellida	Caprella laeviuscula	0.08
1111	MOLLUSCA	BIVALVIA	SEPTIBRANC	Cuspidarii	Cardiomya californica	4.90
1112	MOLLUSCA	BIVALVIA	SEPTIBRANC	Cuspidarii	Cardiomya oldroydi	1.00
1113	MOLLUSCA	BIVALVIA	SEPTIBRANC	Cuspidarii	Cardiomya pectinata	0.30
1114	MOLLUSCA	BIVALVIA	SEPTIBRANC	Cuspidarii	Cardiomya planetica	85.67
1115	MOLLUSCA	BIVALVIA	SEPTIBRANC	Cuspidarii	Cardiomya pseustes	349.10
1116	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Caulleriella bioculata	0.35
1117	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Caulleriella hamata	0.35
1118	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulida	Caulleriella oculata	0.35
1119	CRUSTACEA	COPEPODA	HARPACTICO	Cerviniida	Cervinia synartha	0.00
1120	APLACOPHORA	CAUDOFOVEAT	CHAETODERM	Chaetoderm	Chaetoderma A	67.30
1121	MOLLUSCA	APLACOPHOR	CHAETODERM	Chaetoderm	Chaetoderma argenteum	20.00
1122	MOLLUSCA	APLACOPHORA	CHAETODERMA	Chaetoderma	Chaetoderma attenuatum	13.79
1123	APLACOPHORA	CAUDOFOVEAT	CHAETODERM	Chaetoderm	Chaetoderma B	11.28
1124	MOLLUSCA	APLACOPHORA	CHAETODERMA	Chaetoderma	Chaetoderma robustum	0.00
1125	MOLLUSCA	APLACOPHORA	CHAETODERMA	Chaetoderma	Chaetoderma whitlachi	1.00
1126	POLYPLACOP	LORICATA	NEOLORICATA	Chaetopleur	Chaetopleura gemma	6.25
1127	ANNELIDA	POLYCHAETA	SPIONIDA	Chaetopter	Chaetopterus variopedatus	6.00
1128	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Chaetozone A	0.15
1129	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Chaetozone acuta	3.00
1130	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Chaetozone B	0.05
1131	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Chaetozone setosa	2.26
1132	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Chaetozone spinosa	0.37
1133	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nereidae	Cheilonereis cyclurus	106.50
1134	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Cheirimedia zotea	0.31
1135	TUNICATA	ASCIDIACEA	APLOUSOBRA	Corellidae	Chelyosoma columbianum	227.20
1136	ECHINODERM	HOLOTHUROI	APODIDA	Chiridotid	Chiridota albatrossi	267.07
1137	ECHINODERM	HOLOTHUROI	APODIDA	Chiridotid	Chiridota nanaimensis	0.00

Appendix 2. (continued)

1138	MOLLUSCA	BIVALVIA	OSTREOIDA	Pectiniida	Chlamys hastata	2.30
1139	MOLLUSCA	BIVALVIA	OSTREOIDA	Pectiniida	Chlamys rubida	2.00
1140	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Chone duneri	0.35
1141	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Chone ecaudata	7.80
1142	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Chone magna	32.90
1143	MOLLUSCA	BIVALVIA	VENEROIDA	Cardiidae	Ciliatocardium ciliatum	121.95
1144	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Cirratulus cirratus	1.88
1145	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Cirrophorus branchiatus	0.85
1146	ANNELIDA	POLYCHAETA	TEREBELLID	Pectinarii	Cistenides granulata	64.00
1147	CRUSTACEA	OSTRACODA	PODOCOPIDA	Trachylebe	Cletocythe noblissimus	0.00
1148	MOLLUSCA	BIVALVIA	VENEROIDA	Cardiidae	Clinocardium nuttalli	4.10
1149	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Clymenura columbiana	10.17
1150	MOLLUSCA	GASTROPODA	NEOGASTROP	Neptunidae	Colus halli	0.00
1151	MOLLUSCA	BIVALVIA	VENEROIDA	Veneridae	Compsomyax subdiaphana	111.80
1152	MOLLUSCA	BIVALVIA	VENEROIDA	Cooperelli	Cooperella subdiaphana	1.43
1153	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Corophiida	Corophium ascherusicum	0.30
1154	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Corophiida	Corophium insidiosum	0.05
1155	ANNELIDA	POLYCHAETA	COSSURIDA	Cossuridae	Cossura longocirrata	0.06
1156	ANNELIDA	POLYCHAETA	COSSURIDA	Cossuridae	Cossura modica	0.13
1157	ANNELIDA	POLYCHAETA	COSSURIDA	Cossuridae	Cossura soyeri	0.10
1158	CRUSTACEA	DECAPODA	CARIDEA	Crangonida	Crangon alaskensis	16.25
1159	CRUSTACEA	DECAPODA	CARIDEA	Crangonida	Crangon alba	3.40
1160	CRUSTACEA	DECAPODA	CARIDEA	Crangonida	Crangon stylirostris	0.00
1161	MOLLUSCA	BIVALVIA	MYTILLOIDA	Mytilidae	Crenella decussata	8.60
1162	MOLLUSCA	BIVALVIA	MYTILLOIDA	Mytilidae	Crenella seminuda	0.00*
1163	MOLLUSCA	GASTROPODA	MESOGASTRO	Calyptraei	Crepidula adunca	11.30
1164	MOLLUSCA	GASTROPODA	MESOGASTRO	Calyptraei	Crepipatella lingulata	23.00
1165	ANNELIDA	POLYCHAETA	SABELLIDA	Serpulidae	Crucigera irregularis	36.30
1166	ANNELIDA	POLYCHAETA	SABELLIDA	Serpulidae	Crucigera zygophora	30.00
1167	MOLLUSCA	GASTROPODA	NEOGASTROP	Turridae	Cryptogemma adrastia	0.00
1168	ECHINODERM	ASTEROIDEA	PAXILLOSID	Goniopecti	Ctenodiscus crispatus	4461.30
1169	CRUSTACEA	CUMACEA	CUMACEA	Nannastaci	Cummella vulgaris	0.05
1170	MOLLUSCA	BIVALVIA	SEPTIBRANC	Cuspidarii	Cuspidaria apodema	41.10
1171	MOLLUSCA	BIVALVIA	VENEROIDA	Carditidae	Cyclocardia ventricosa	51.79
1172	MOLLUSCA	GASTROPODA	CEPHALASPI	Cylichnida	Cylichna alba	14.33
1173	MOLLUSCA	GASTROPODA	CEPHALASPI	Cylichnida	Cylichna attonsa	16.64
1174	MOLLUSCA	GASTROPODA	CEPHALASPI	Cylichnida	Cylichnella culc[illegible]lla	72.00
1175	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Lysianassi	Cyphocaris challengerii	12.35
1176	MOLLUSCA	BIVALVIA	MYTILLOIDA	Mytilidae	Dacrydium vitreum	5.00
1177	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Decamastus gracilis	1.75
1178	MOLLUSCA	BIVALVIA	OSTREOIDA	Pectiniida	Delectopecten vancouverensis	58.35
1179	MOLLUSCA	BIVALVIA	OSTREOIDA	Pectiniida	Delectopecten vitreus	1.15
1180	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Demonax media	0.00
1181	ECHINODERM	ECHINOIDEA	CLYPEASTER	Dendraster	Dendraster excentricus	22.50
1182	MOLLUSCA	SCAPHOPODA	DENTALIIDA	Dentaliida	Dentalium agassizii	7.40
1183	MOLLUSCA	SCAPHOPODA	DENTALIIDA	Dentaliida	Dentalium pretiosum	33.93
1184	CRUSTACEA	AMPHIPODA	CAPPRELLID	Aeginellid	Deutella californica	0.03
1185	CRUSTACEA	AMPHIPODA	CAPPRELLID	Aeginellid	Diasterope pilosa	0.50
1186	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylis alaskensis	2.30

Appendix 2. (continued)

1187	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylis aspera	10.00
1188	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylis bidentata	5.00
1189	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylis dalli	5.00
1190	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylis hirsuta	5.00
1191	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylis parasinulosa	14.20
1192	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylis pellucida	0.95
1193	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylis spinulosa	4.00
1194	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylis umatellensis	8.90
1195	CRUSTACEA	CUMACEA	CUMACEA	Diastylidae	Diastylopsis dawsoni	0.40*
1196	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Diastylopsis tenuis	0.40
1197	ANNELIDA	POLYCHAETA	EUNICIDA	Onuphidae	Diopatra ornata	12.30
1198	MOLLUSCA	BIVALVIA	VENLROIDA	Ungulinida	Diplodonta orbella	1.10
1199	CRUSTACEA	MYSIDACEA	MYSIDACEA	Mysidae	Disacanthomysis dybowskii	38.50
1200	ANNELIDA	POLYCHAETA	EUNICIDA	Dorvilleid	Dorvillea pseudorubrovittata	16.18
1201	ANNELIDA	POLYCHAETA	EUNICIDA	Dorvilleid	Dorvillea rudolphi	2.39
1202	ANNELIDA	POLYCHAETA	EUNICIDA	Arabellida	Drilonereis falcataminor	3.30
1203	ANNELIDA	POLYCHAETA	EUNICIDA	Arabellida	Drilonereis longa	0.20
1204	ANNELIDA	POLYCHAETA	EUNICIDA	Arabellida	Drilonerles falcata	3.30
1205	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Dulichiida	Dulichia rhabdoplastis	0.83
1206	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Dulichiida	Dyopedos monacanthus	0.40
1207	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Dulichiida	Dyopedos normani	4.00
1208	CNIDARIA	ANTHOZOA	ACTINIARIA	Edwardsiid	Edwardsia sipunculoides	0.00
1209	NEMERTEA	ANOPLA	HETERONEME	Emplectone	Emplectonema gracile	0.05*
1210	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Ericthonius hunteri	9.30
1211	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Eteone longa	5.92
1212	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Etionides coineauidifficilis	1.70
1213	CRUSTACEA	DECAPODA	CARIDEA	Hippolytid	Eualus avinus	170.00
1214	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Euchone analis	0.80
1215	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Euchone arenae	0.83
1216	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Euchone hancocki	0.10
1217	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Euchone incolor	1.41
1218	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Euclymene geralis	2.05
1219	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Euclymene zonalis	5.50
1220	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Eudistylia catharinae	0.00
1221	CRUSTACEA	CUMACEA	CUMACEA	Leuconidae	Eudorella emarginata	5.20
1222	CRUSTACEA	CUMACEA	CUMACEA	Leuconidae	Eudorella pacifica	1.64
1223	CRUSTACEA	CUMACEA	CUMACEA	Leuconidae	Eudorellopsis biplicata	1.00
1224	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Eulalia bilineata	0.05
1225	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Eulalia levicornuta	0.05
1226	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Eulalia sanguinea	0.90*
1227	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Eulalia viridis	4.54
1228	CRUSTACEA	EUPHAUSIAC	EUPHAUSIAC	Euphausiid	Euphausia pacifica	32.70
1229	CRUSTACEA	OSTRACODA	MYODOCOPOI	Philomedid	Euphilomedes carcharodonta	1.30
1230	CRUSTACEA	OSTRACODA	MYODOCOPOI	Philomedid	Euphilomedes producta	8.80
1231	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Eusyllis assimilis	2.00
1232	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Eusyllis blomstrandi	2.30
1233	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Exogone lourei	0.03
1234	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Exogone molesta	0.10
1235	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Exogone naidina	0.65

Appendix 2. (continued)

1236	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syliidae	Exogone verugera	0.05
1237	ANNELIDA	POLYCHAETA	FLABELLIGE	Flabellige	Flabelligera affinis	69.90
1238	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Phoxocepha	Foxiphalus cognatus	0.50
1239	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Phoxocepha	Foxiphalus obtusidens	15.45
1240	ANNELIDA	POLYCHAETA	OWENIIDA	Oweniidae	Galathowenia oculata	2.03
1241	MOLLUSCA	BIVALVIA	VENEROIDA	Psammobiid	Gari californica	0.00
1242	MOLLUSCA	GASTROPODA	CEPHALASPI	Gastropter	Gastropteron pacificum	7.40
1243	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Gattyana ciliata	137.70
1244	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Gattyana cirrosa	3.40
1245	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Gattyana treadwelli	18.20
1246	ANNELIDA	POLYCHAETA	PHYLLODOCI	Glyceridae	Glycera americana	319.80
1247	ANNELIDA	POLYCHAETA	PHYLLODOCI	Glyceridae	Glycera capitata	49.89
1248	ANNELIDA	POLYCHAETA	PHYLLODOCI	Glyceridae	Glycera oxycephala	150.00
1249	ANNELIDA	POLYCHAETA	PHYLLODOCI	Goniadidae	Glycinde armigera	72.35
1250	ANNELIDA	POLYCHAETA	PHYLLODOCI	Goniadidae	Glycinde picta	8.60
1251	MOLLUSCA	BIVALVIA	ARCOIDA	Glycymerid	Glycymeris subobsoleta	11.00
1252	ANNELIDA	POLYCHAETA	TEREBELLIDA	Arabellidae	Glyphanostomum pallescens	2.10
1253	CRUSTACEA	ISOPODA	ISOPODA	Gnathiidae	Gnathia trilobata	0.10
1254	CRUSTACEA	ISOPODA	ISOPODA	Sphaeromat	Gnorimosphaeroma oregonensis	2.67
1255	SIPUNCULA	N/A	SIPUNCULID	Golfingiid	Golfingia margaritacea	30.20
1256	SIPUNCULA	N/A	SIPUNCULID	Golfingiid	Golfingia vulgaris	22.40
1257	ANNELIDA	POLYCHAETA	PHYLLODOCI	Goniadidae	Goniada annulata	95.06
1258	ANNELIDA	POLYCHAETA	PHYLLODOCI	Goniadidae	Goniada brunnea	175.40
1259	ANNELIDA	POLYCHAETA	PHYLLODOCI	Goniadidae	Goniada maculata	100.00
1260	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Dexaminida	Guernea reduncans	0.10
1261	CRUSTACEA	ISOPODA	ISOPODA	Anthuridae	Haliophasma geminata	0.00
1262	MOLLUSCA	GASTROPODA	CEPHALASPI	Atyidae	Haminoea vesicula	3.70
1263	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ampeliscid	Haploops tubicola	0.87
1264	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Harmothoe imbricata	11.80
1265	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Harmothoe lunulata	6.40
1266	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Phoxocepha	Harpiniopsis fulgaris	0.20
1267	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Phoxocepha	Harpiniopsis fulgens	0.05
1268	ECHINODERM	HOLOTHUROI	APODIDA	Phyllophor	Havelockia benti	0.00
1269	ANNELIDA	POLYCHAETA	PHYLLODOCI	Glyceridae	Hemipodus borealis	2.00
1270	ECHINODERM	ASTEROIDEA	SPINULOSID	Echinaster	Henricia sanguinolenta	1.00
1271	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Heteromastus abiseta	0.00
1272	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Heteromastus filiformis	7.40
1273	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Heteromastus filobranchus	6.10
1274	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Phoxocepha	Heterophoxus oculatus	1.61
1275	MOLLUSCA	BIVALVIA	MYOIDA	Hiatellida	Hiatella arctica	13.40
1276	CRUSTACEA	MYSIDACEA	MYSIDACEA	Mysidae	Holmesiella anomala	0.00
1277	MOLLUSCA	BIVALVIA	VENEROIDA	Veneridae	Humilaria kennerlyi	10.00
1278	MOLLUSCA	BIVALVIA	SOLEMYOIDA	Nuculellid	Huxleyia munita	3.30
1279	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Hyperiidae	Hyperia medusarum	0.00
1280	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Hyperiidae	Hyperia spinigera	0.40
1281	ANNELIDA	POLYCHAETA	TEREBELLID	Sabellarii	Idanthyrsus ornamentatus	20.20
1282	CRUSTACEA	ISOPODA	ISOPODA	Idoteidae	Idotea resecata	20.00
1283	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ischyrocer	Ischyrocerus anguipes	0.49
1284	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Isocirrus longiceps	85.00

Appendix 2. (continued)

1285	CRUSTACEA	ISOPODA	ISOPODA	Jaeropsida	Jaeropsis dubia	0.10
1286	CRUSTACEA	ISOPODA	ISOPODA	Janiridae	Janiralata solasteri	1.90
1287	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Jasmineira pacifica	2.27
1288	MOLLUSCA	BIVALVIA	VENEROIDA	Cardiidae	Keenecardium fucanum	229.15
1289	ANNELIDA	POLYCHAETA	PHYLLODOCI	Hesionidae	Kefersteinia cirrata	2.00
1290	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Kermystheus oclosa	0.69
1291	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Lysianassi	Koroga megalops	0.60
1292	MOLLUSCA	GASTROPODA	MESOGASTRO	Lacunidae	Lacuna carinata	17.50
1293	MOLLUSCA	GASTROPODA	MESOGASTRO	Lacunidae	Lacuna porrecta	10.00
1294	MOLLUSCA	SCAPHOPODA	DENTALIIDA	Leavidenta	Laevidentalium dalli	148.30
1295	CNIDARIA	HYDROZOA	LEPTOMEDUS	Lafoeidae	Lafoea dumosa	40.00
1296	CRUSTACEA	CUMACEA	CUMACEA	Lampropida	Lamprops quadriplicata	2.63
1297	CRUSTACEA	CUMACEA	CUMACEA	Lampropida	Lamprops triserrata	2.00
1298	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Lanassa venustavenusta	0.38
1299	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Laonice cirrata	26.45
1300	BRACHIOPODA	ARTICULATA	TEREBRATUL	Laqueidae	Laqueus californianus	368.50
1301	CRUSTACEA	DECAPODA	CARIDEA	Hippolytid	Lebbeus grandimanus	0.00
1302	ANNELIDA	POLYCHAETA	EUNICIDA	Orbiniidae	Leitoscoloplos pugettensis	2.20
1303	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Lepidasthenia berkeleyae	67.10
1304	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Lepidasthenia longicirrata	20.20
1305	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Lysianassi	Lepidepecreum garthi	101.60
1306	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Lysianassi	Lepidepecreum gurjanovae	1.50
1307	MOLLUSCA	POLYPLACOP	ISCHNOCHIT	Lepidochit	Lepidochitona flectens	1.00
1308	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Lepidonotus squamatus	9.99
1309	MOLLUSCA	POLYPLACOP	ISCHNOCHIT	Lepidochit	Lepidozona mertenzii	1.00
1310	CRUSTACEA	TANAIDACEA	TANAIDACEA	Leptognath	Leptochelia dubia	0.02*
1311	CRUSTACEA	TANAIDACEA	TANAIDACEA	Leptognath	Leptochelia savignyi	0.20
1312	CRUSTACEA	TANAIDACEA	TANAIDACEA	Leptognath	Leptognathia gracilis	0.05
1313	MOLLUSCA	GASTROPODA	MESOGASTRO	Vitrinelli	Leptogyra alaskana	1.45
1314	CNIDARIA	ANTHOZOA	PENNATULAC	Virgularii	Leptostylis villosa	0.85
1315	ECHINODERM	HOLOTHUROI	APODIDA	Synaptidae	Leptosynapta roxtana	0.00
1316	ECHINODERM	HOLOTHUROI	APODIDA	Synaptidae	Leptosynapta transgressor	0.00
1317	CRUSTACEA	CUMACEA	CUMACEA	Leuconidae	Leucon nasica	2.00
1318	CRUSTACEA	CUMACEA	CUMACEA	Leuconidae	Leucon subnasica	1.10
1319	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Levinsenia gracilis	0.28
1320	MOLLUSCA	GASTROPODA	CEPHALASPI	Limacinida	Limacina helicina	0.10
1321	ANNELIDA	OLIGOCHAET	TUBIFICIDA	Tubificida	Limnodriloides barnardi	0.05
1322	ANNELIDA	OLIGOCHAET	TUBIFICIDA	Tubificida	Limnodriloides victoriensis	0.05
1323	CRUSTACEA	ISOPODA	ISOPODA	Cymothoida	Limnoria lignorum	1.00
1324	MOLLUSCA	BIVALVIA	VENEROIDA	Lucinidae	Lucina tenuisculpta	33.70
1325	MOLLUSCA	BIVALVIA	VENEROIDA	Lucinidae	Lucinoma annulata	17.50
1326	ANNELIDA	POLYCHAETA	EUNICIDA	Lumbrineri	Lumbrineris acuta	3.00
1327	ANNELIDA	POLYCHAETA	EUNICIDA	Lumbrineri	Lumbrineris bicirrata	94.95
1328	ANNELIDA	POLYCHAETA	EUNICIDA	Lumbrineri	Lumbrineris cruzensis	2.07
1329	ANNELIDA	POLYCHAETA	EUNICIDA	Lumbrineri	Lumbrineris lagunae	51.90
1330	ANNELIDA	POLYCHAETA	EUNICIDA	Lumbrineri	Lumbrineris latreilli	107.10
1331	ANNELIDA	POLYCHAETA	EUNICIDA	Lumbrineri	Lumbrineris limicola	2.10
1332	ANNELIDA	POLYCHAETA	EUNICIDA	Lumbrineri	Lumbrineris luti	2.75
1333	ANNELIDA	POLYCHAETA	EUNICIIDA	Lumbrineri	Lumbrineris zonata	0.95

Appendix 2. (continued)

1334	MOLLUSCA	BIVALVIA	PHOLAD	Lyonsiidae	Lyonsia bracteata	58.20
1335	MOLLUSCA	BIVALVIA	PHOLAD.	Lyonsiidae	Lyonsia californica	4.07
1336	MOLLUSCA	BIVALVIA	PHOLAD.	Lyonsiidae	Lyonsia scammoni	[illegible]10
1337	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Lysippe labiata	3[illegible]0
1338	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Macoma brota	4785.61
1339	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Macoma calcarea	61.30
1340	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Macoma carlottensis	27.10
1341	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Macoma eliminata	193.73
1342	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Macoma inconspicua	2160.00
1343	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Macoma lipara	6400.00
1344	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Macoma moesta	538.30
1345	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Macoma yoldiformis	0.70
1346	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Melitidae	Maera danae	64.35
1347	ANNELIDA	POLYCHAETA	SPIONIDA	Magelonida	Magelona hobsonae	0.10*
1348	ANNELIDA	POLYCHAETA	SPIONIDA	Magelonida	Magelona longicornis	1.04
1349	ANNELIDA	POLYCHAETA	SPIONIDA	Magelonida	Magelona sacculata	1.00
1350	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Maldane glebifex	5.24
1351	MOLLUSCA	GASTROPODA	ARCHAEOGAS	Trochidae	Margarites helicinus	0.20
1352	MOLLUSCA	GASTROPODA	ARCHAEOGAS	Trochidae	Margarites pupillus	5.20
1353	CRUSTACEA	AMPHIPODA	CAPPRELLID	Aeginellid	Mayerella banksia	0.05
1354	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Mediomastus ambiseta	0.15
1355	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Mediomastus californiensis	1.01
1356	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Mediomastus capensis	1.80
1357	MOLLUSCA	BIVALVIA	MYTILLOIDA	Mytilidae	Megacrenella columbiana	32.00
1358	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Megalomma splendida	115.77
1359	ANNELIDA	POLYCHAETA	EUNICIDA	Dorvilleida	Meiodorvillea minuta	0.05
1360	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Melinna cristata	17.15
1361	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Melinna elisabethae	20.30
1362	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Melitidae	Melita dentata	0.45
1363	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Melitidae	Melita desdichada	0.33
1364	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Melphidipp	Melphisana bola	0.09
1365	ANNELIDA	POLYCHAETA	SPIONIDA	Chaetopter	Mesochaetopterus taylori	23.94
1366	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Phoxocepha	Metaphoxus frequens	0.05
1367	PORIFERA	DEMOSPONGI	POECILOSCL	Clathriida	Microciona primitiva	100.00
1368	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Ischyrocer	Microjassa litotes	0.52
1369	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Micromaldane ornithochaeta	0.10
1370	ANNELIDA	POLYCHAETA	PHYLLODOCI	Hesionidae	Micropodarke dubia	0.24
1371	MOLLUSCA	GASTROPODA	NEOGASTROP	Columbelli	Mitrella carinata	0.00
1372	MOLLUSCA	GASTROPODA	NEOGASTROP	Columbelli	Mitrella gausapata	56.56
1373	MOLLUSCA	GASTROPODA	NEOGASTROP	Columbelli	Mitrella tuberosa	18.00
1374	MOLLUSCA	BIVALVIA	MYTILLOIDA	Mytilidae	Modiolus difficilus	3.20
1375	MOLLUSCA	BIVALVIA	MYTILLOIDA	Mytilidae	Modiolus rectus	3.07
1376	ECHINODERM	HOLOTHUROI	MOLPADIDA	Molpadiida	Molpadia intermedia	1700.00
1377	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Oedoceroti	Monoculodes emarginatus	2.50
1378	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Oedoceroti	Monoculodes glyconica	1.10
1379	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Oedoceroti	Monoculodes recandesco	0.70
1380	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Oedoceroti	Monoculodes zernovi	0.04*
1381	CRUSTACEA	ISOPODA	ISOPODA	Munnidae	Munna fernaldi	0.05
1382	CRUSTACEA	ISOPODA	ISOPODA	Munnidae	Munna stephenseni	0.10

Appendix 2. (continued)

1383	CRUSTACEA	ISOPODA	ISOPODA	Munnidae	Munna ubiquita	0.04
1384	CRUSTACEA	ISOPODA	ISOPODA	Paramunnid	Munnogonium tillerae	0.05
1385	MOLLUSCA	BIVALVIA	MYTILLOIDA	Mytilidae	Musculus cultellus	0.00
1386	MOLLUSCA	BIVALVIA	MYOIDA	Myidae	Mya arenaria	15.35
1387	MOLLUSCA	BIVALVIA	VENEROIDA	Montacutid	Mysella tumida	1.13
1388	MOLLUSCA	BIVALVIA	MYTILLOIDA	Mytilidae	Mytilus edulis	25.20
1389	PORIFERA	DEMOSPONGI	POECILOSCL	Myxillidae	Myxilla incrustans	56.10
1390	MOLLUSCA	BIVALVIA	VENEROIDA	Montacutid	Naeromya compressa	8.83
1391	MOLLUSCA	BIVALVIA	VENEROIDA	Montaculid	Naeromya myaciformis	0.82
1392	MOLLUSCA	BIVALVIA	VENEROIDA	Montacutid	Naeromya rugifera	0.80
1393	ANNELIDA	POLYCHAETA	EUNICIDA	Orbiniidae	Naineris quadricuspida	0.05
1394	ANNELIDA	POLYCHAETA	EUNICIDA	Orbiniidae	Naineris uncinata	0.00
1395	MOLLUSCA	GASTROPODA	NEOGASTROP	Nassariida	Nassarius fossatus	98.96
1396	MOLLUSCA	GASTROPODA	NEOGASTROP	Nassariida	Nassarius mendicus	143.05
1397	MOLLUSCA	GASTROPODA	MESOGASTRO	Naticidae	Natica clausa	205.30
1398	CRUSTACEA	LEPTOSTRAC	LEPTOSTRAC	Nebaliidae	Nebalia pugettensis	0.10
1399	CRUSTACEA	EUPHAUSIAC	EUPHAUSIAC	Euphausiid	Nematobrachion flexipes	13.50
1400	MOLLUSCA	BIVALVIA	VENEROIDA	Cardiidae	Nemocardium centrifilosum	234.40
1401	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Neoamphitrites robusta	1.00
1402	CRUSTACEA	MYSIDACEA	MYSIDACEA	Mysidae	Neomysis kadiakensis	7.68
1403	CRUSTACEA	MYSIDACEA	MYSIDACEA	Mysidae	Neomysis rayi	185.00
1404	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys assignis	50.00
1405	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys caeca	1.00
1406	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys caecoides	0.30
1407	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys californiensis	106.80
1408	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys ciliata	90.00
1409	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys cornutacornuta	0.68
1410	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys cornutafranciscanum	0.47
1411	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys ferruginea	24.38
1412	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys longosetosa	0.85
1413	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys punctata	282.35
1414	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nephtyidae	Nephtys rickettsi	0.00
1415	MOLLUSCA	GASTROPODA	NEOGASTROP	Neptunidae	Neptunea lyrata	0.00
1416	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nereidae	Nereis brandti	1140.00
1417	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nereidae	Nereis procera	1.63
1418	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nereidae	Nereis zonata	7.60
1419	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Pardaliscl	Nicippe tumida	7.18
1420	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Nicolea zostericola	10.25
1421	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Nicomache lumbricalis	0.65
1422	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Nicomache personata	0.65
1423	ANNELIDA	POLYCHAETA	EUNICIDA	Lumbrineri	Ninoe gemmea	24.90
1424	MOLLUSCA	GASTROPODA	MESOGASTRO	Epitoniida	Nitidiscala indianorum	20.00
1425	ANNELIDA	POLYCHAETA	EUNICIDA	Onuphidae	Nothria elegans	62.00
1426	ANNELIDA	POLYCHAETA	EUNICIDA	Onuphidae	Nothria geophiliformis	0.01
1427	ANNELIDA	POLYCHAETA	EUNICIDA	Onuphidae	Nothria iridescens	62.44
1428	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Notomastus lineatus	10.00
1429	ANNELIDA	POLYCHAETA	CAPITELLID	Capitellid	Notomastus tenuis	10.00
1430	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Notoproctus pacificus	69.30
1431	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculidae	Nucula carlottensis	35.00

Appendix 2. (continued)

1432	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculidae	Nucula tenuis	45.00
1433	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanida	Nuculana extenuata	81.20
1434	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanida	Nuculana fossa	41.85
1435	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanida	Nuculana hamata	13.80
1436	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanida	Nuculana hindsii	29.80
1437	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanida	Nuculana minuta	0.30
1438	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanida	Nuculana pernula	10.00
1439	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanida	Nuculana radiata	3.30
1440	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanida	Nuculana taphria	244.00
1441	MOLLUSCA	BIVALVIA	NUCULOIDA	Nuculanid	Nuculana tenuisulcata	24.90
1442	MOLLUSCA	BIVALVIA	VENEROIDA	Veneridae	Nutricola tantilla	10.00
1443	PYCNOGINIDA	PYCNOGINIDA	PEGMATA	Nymphonid	Nymphon grossipes	0.10
1444	MOLLUSCA	GASTROPODA	NEOGASTROP	Muricidae	Ocenebra interfossa	32.30
1445	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Odontosyllis phosphorea	1.27
1446	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Odostomia avellana	9.00
1447	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Odostomia barkleyensis	5.00
1448	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Odostomia columbiana	9.40
1449	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Odostomia cypria	9.00
1450	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Odostomia oregonensis	0.00
1451	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Odostomia quadrae	2.30
1452	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Odostomia tenuisculpta	28.70
1453	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Odostomia vancouverensis	7.00
1454	MOLLUSCA	GASTROPODA	NEOGASTROP	Turridae	Oenopota elegans	0.00
1455	MOLLUSCA	GASTROPODA	NEOGASTROP	Turridae	Oenopota excurvata	10.00
1456	MOLLUSCA	GASTROPODA	NEOGASTROP	Turridae	Oenopota harpa	10.00
1457	MOLLUSCA	GASTROPODA	NEOGASTROP	Turridae	Oenopota turricula	17.80
1458	MOLLUSCA	GASTROPODA	NEOGASTROP	Olividae	Olivella baetica	166.30
1459	ANNELIDA	POLYCHAETA	EUNICIDA	Onuphidae	Onuphis conchylega	0.02
1460	ANNELIDA	POLYCHAETA	OPHELIIDA	Opheliidae	Ophelia limacina	1.00
1461	ANNELIDA	POLYCHAETA	OPHELIIDA	Opheliidae	Ophelina acuminata	42.28
1462	ANNELIDA	POLYCHAETA	OPHELIIDA	Opheliidae	Ophelina breviata	0.23
1463	ANNELIDA	POLYCHAETA	PHYLLODOCI	Hesionidae	Ophiodromus pugettensis	8.40
1464	ECHINODERM	OPHIUROIDE	OPHIURIDA	Ophiuridae	Ophiura leptoctenia	25.53
1465	ECHINODERM	OPHIUROIDE	OPHIURIDA	Ophiuridae	Ophiura leutkeni	174.00
1466	ECHINODERM	OPHIUROIDE	OPHIURIDA	Ophiuridae	Ophiura sarsi	60.43
1467	ANNELIDA	POLYCHAETA	EUNICIDA	Dorvilleid	Ophryotrocha pugettensis	0.10
1468	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Lysianassi	Opisa tridentata	0.10
1469	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Pontogenei	Oradarea longimana	1.40
1470	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Uristidae	Orchomene decipiens	0.40
1471	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Uristidae	Orchomene obtusa	67.00
1472	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Uristidae	Orchomene pinguis	2.10
1473	CRUSTACEA	DECAPODA	ANOMURA	Majidae	Oregonia gracilis	127.00
1474	ANNELIDA	POLYCHAETA	OWENIIDA	Oweniidae	Owenia fusiformis	4.74
1475	ANTHOZOA	HEXACORALL	CERIANTHAR	Cerianthid	Pachycerianthus fimbriatus	68.60
1476	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Lysianassi	Pachynus barnardi	0.16
1477	CRUSTACEA	MYSIDACEA	MYSIDACEA	Mysidae	Pacificanthomysis nephrophthal	1.40
1478	CRUSTACEA	DECAPODA	ANOMURA	Diogenidae	Paguristes turgidus	100.00
1479	CRUSTACEA	DECAPODA	ANOMURA	Paguridae	Pagurus armatus	10.00
1480	ANNELIDA	POLYCHAETA	PHYLLODOCI	Chrysopeta	Paleanotus bellis	0.05*

Appendix 2. (continued)

1481	MOLLUSCA	BIVALVIA	PHOLAD.	Pandoridae	Pandora bilirata	77.50
1482	MOLLUSCA	BIVALVIA	PHOLAD.	Pandoridae	Pandora filosa	85.23
1483	ANNELIDA	POLYCHAETA	PHYLLODOCI	Pilargiida	Parandalia fauveli	0.40
1484	ANNELIDA	POLYCHAETA	EUNICIDA	Lumbrineri	Paraninoe simpta	9.72
1485	ANNELIDA	POLYCHAETA	ORBINIIDA	Paraonidae	Paraonella platybranchia	1.00
1486	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Phoxocepha	Paraphoxus oculatus	1750.65
1487	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Pleustidae	Parapleustes pugettensis	1.30
1488	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Paraprionospio pinnata	12.85
1489	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Pardalisci	Pardaliscella symmetrica	0.10
1490	MOLLUSCA	BIVALVIA	OSTREOIDA	Propeamuss	Parvamussium alaskensis	30.00
1491	CRUSTACEA	DECAPODA	CARIDEA	Pasiphaeid	Pasiphaea pacifica	98.67
1492	ANNELIDA	POLYCHAETA	TEREBELLID	Pectinarii	Pectinaria californiensis	15.20
1493	ANNELIDA	POLYCHAETA	TEREBELLID	Pectinarii	Pectinaria moorei	9.00
1494	CRUSTACEA	CUMACEA	CUMACEA	Diastylida	Pentalosarsia declivis	0.00
1495	ECHINODERM	HOLOTHUROI	DENDROCHIR	Phyllophor	Pentamera populifera	82.50
1496	ECHINODERM	HOLOTHUROI	DENDROCHIR	Phyllophor	Pentamera pseudocalcigera	70.20
1497	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Petaloproctus tenuisborealis	0.05
1498	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Petaloproctus tenuistenuis	15.96
1499	ANNELIDA	POLYCHAETA	FLABELLIGE	Flabellige	Pherusa negligens	20.80
1500	ANNELIDA	POLYCHAETA	FLABELLIGE	Flabellige	Pherusa plumosa	20.80
1501	MOLLUSCA	GASTROPODA	CEPHALASPI	Philinidae	Philine polaris	1.12
1502	ANNELIDA	POLYCHAETA	PHYLLODOCI	Sigalionid	Pholoe minuta	8.81
1503	ANNELIDA	POLYCHAETA	PHYLLODOCI	Pholoidida	Pholoides aspera	7.97
1504	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Photis brevipes	1.10
1505	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Photis californica	0.90
1506	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Photis conchicola	0.88
1507	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Photis lacia	8.00
1508	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Photis macinerneyi	0.10
1509	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Photis pachydactyla	0.16
1510	PYCNOGONID	N/A	PEGMATA	Phoxichili	Phoxichilidium femoratum	0.20
1511	ANNELIDA	POLYCHAETA	SPIONIDA	Chaetopter	Phyllochaetopterus claparedi	15.42
1512	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Phyllodoce castanea	2.20
1513	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Phyllodoce papillosa	1.34
1514	ANNELIDA	POLYCHAETA	PHYLLODOCI	Phyllodoci	Phyllodoce polynoides	0.06
1515	ANNELIDA	POLYCHAETA	EUNICIDA	Orbiniidae	Phylo felix	0.00
1516	ANNELIDA	POLYCHAETA	PHYLLODOCI	Pilargiida	Pilargis berkeleyi	29.20
1517	CRUSTACEA	DECAPODA	BRACHYURA	Pinnotheri	Pinnixa eburna	0.80
1518	CRUSTACEA	DECAPODA	BRACHYURA	Pinnotheri	Pinnixa occidentalis	14.10
1519	CRUSTACEA	DECAPODA	BRACHYURA	Pinnotheri	Pinnixa schmitti	19.90
1520	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Pionosyllis uraga	0.40
1521	ANNELIDA	POLYCHAETA	PHYLLODOCI	Pisionidae	Pisione remota	0.00
1522	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Pista brevibranchiata	168.45
1523	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Pista cristata	98.14
1524	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Pista elongata	4.50
1525	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Pista moorei	126.80
1526	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Pista pacifica	2.10
1527	ANNELIDA	POLYCHAETA	PHYLLODOCI	Nereidae	Platynereis bicanaliculata	11.54
1528	CRUSTACEA	ISOPODA	ISOPODA	Paramunnid	Pleurogonium inerme	0.10
1529	CRUSTACEA	ISOPODA	ISOPODA	Paramunnid	Pleurogonium rubicundum	0.03

Appendix 2. (continued)

1530	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Pleustidae	Pleusirus secorrus	0.40
1531	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Pleustidae	Pleustes depressa	1.00
1532	MOLLUSCA	GASTROPODA	NEOGASTROP	Buccinidae	Plicifusus kroyeri	287.10
1533	ANNELIDA	POLYCHAETA	PHYLLODOCI	Hesionidae	Podarkeopsis brevipalpa	3.65
1534	MOLLUSCA	BIVALVIA	OSTREOIDA	Anomiidae	Pododesmus macroschisma	2.27
1535	MOLLUSCA	GASTROPODA	MESOGASTRO	Naticidae	Polinices lewisi	118.10
1536	MOLLUSCA	GASTROPODA	MESOGASTRO	Naticidae	Polinices pallidus	176.00
1537	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Polydora brachycephala	3.20
1538	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Polydora cardalia	2.93
1539	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Polydora giardi	0.05
1540	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Polydora socialis	2.41
1541	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Polynoe canadensis	10.00
1542	MOLLUSCA	SCAPHOPODA	GADILIDA	Siphonoden	Polyschides californicus	82.30
1543	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Pontogenei	Pontogeneia rostata	0.50
1544	MOLLUSCA	BIVALVIA	SEPTIBRANCH	Moromyidae	Poromya trosti	0.80
1545	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Potamilla intermedia	24.94
1546	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Lysianassi	Prachynella lodo	4.30
1547	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Praxillella affinisaffinis	4.60
1548	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Praxillella gracilis	82.77
1549	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Praxillella praetermissa	0.70
1550	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Prionospio lighti	0.70
1551	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Prionospio multibranchiata	0.10
1552	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Prionospio steenstrupi	2.87
1553	MOLLUSCA	APLACOPHOR	PROCHAETOD	Prochaetod	Prochaetoderma yongei	4.21
1554	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Proclea graffi	0.16
1555	ANNELIDA	POLYCHAETA	EUNICIDA	Dorvilleid	Protodorvillea gracilis	10.56
1556	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Protomedeia fasciata	5.00
1557	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Protomedeia grandimana	4.40
1558	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Isaeidae	Protomedeia prudens	420.10
1559	MOLLUSCA	BIVALVIA	VENEROIDA	Veneridae	Protothaca staminea	932.60
1560	MOLLUSCA	BIVALVIA	VENEROIDA	Veneridae	Psephidia lordi	9.57
1561	ANNELIDA	POLYCHAETA	SABELLIDA	Serpulidae	Pseudochitinopoma occidentalis	0.30
1562	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Pseudopolydora kempi	0.10
1563	CNIDARIA	ANTHOZOA	PENNATULAC	Pennatulid	Ptilosarcus guerneyi	36.00
1564	CRUSTACEA	DECAPODA	ANOMURA	Majidae	Pugettia richi	0.00
1565	MOLLUSCA	SCAPHOPODA	GADILIDA	Pulsellida	Pulsellum salishorum	5.10
1566	MOLLUSCA	GASTROPODA	ARCHAEOGAS	Fissurelli	Punctarella galeata	4.40
1567	KINORHYNCH	N/A	HOMALORHAG	Pycnophyid	Pycnophyes sanjuanensis	0.00
1568	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Pygospio elegans	0.05
1569	MOLLUSCA	SCAPHOPODA	DENTALIIDA	Leavidenta	Rhabdus rectius	47.77
1570	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Phoxocepha	Rhepoxynius episburi	0.10
1571	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Phoxocepha	Rhepoxynius variatus	0.10
1572	ANNELIDA	POLYCHAETA	CAPITELLID	Maldanidae	Rhodine bitorquata	4.40
1573	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Rhynchospio glutaea	1.00
1574	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Pardalisci	Rhynohalicella halona	0.68
1575	MOLLUSCA	GASTROPODA	CEPHALASPI	Acteonidae	Rictaxis punctocoelatus	23.78
1576	MOLLUSCA	GASTROPODA	MESOGASTRO	Rissoidae	Rissoina newcombei	0.10
1577	CRUSTACEA	ISOPODA	ISOPODA	Aegidae	Rocinela angustata	0.00
1578	CRUSTACEA	ISOPODA	ISOPODA	Aegidae	Rocinela belliceps	0.00*

Appendix 2. (continued)

1579	CRUSTACEA	OSTRACODA	MYODOCOPIDA	Rutidermat	Rutiderma lomae	1.90
1580	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Sabella pacifica	18.80
1581	ANNELIDA	POLYCHAETA	TEREBELLID	Sabellaria	Sabellaria cementarium	21.62
1582	CRUSTACEA	OSTRACODA	MYODOCOPID	Sarsiellid	Sarsiella pseudospinosa	0.00
1583	ANNELIDA	POLYCHAETA	OPHELIIDA	Scalibregm	Scalibregma inflatum	7.25
1584	ANNELIDA	POLYCHAETA	TEREBELLID	Ampharetid	Schistocomus hiltoni	0.10
1585	ANNELIDA	POLYCHAETA	EUNICIDA	Dorvilleid	Schistomeringos annulata	0.00
1586	ANNELIDA	POLYCHAETA	EUNICIDA	Dorvilleid	Schistomeringos caeca	1.00
1587	ANNELIDA	POLYCHAETA	EUNICIDA	Dorvilleid	Schistomeringos longicornis	1.10
1588	ANNELIDA	POLYCHAETA	SABELLIDA	Sabellidae	Schizobranchia insignus	2.20
1589	CRUSTACEA	AMPHIPODA	HYPERIIDEA	Scinidae	Scina borealis	0.40
1590	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Scionella estevanica	17.53
1591	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Scionella japonica	101.67
1592	CRUSTACEA	OSTRACODA	MYODOCOPOI	Philomedid	Scleroconcha trituberculatus	1.20
1593	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Scolelepis foliosa	1.00
1594	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Scolelepis squamata	1.35
1595	ANNELIDA	POLYCHAETA	EUNICIDA	Orbiniidae	Scoloplos acmeceps	0.08
1596	ANNELIDA	POLYCHAETA	EUNICIDA	Orbiniidae	Scoloplos armiger	0.10
1597	ANNELIDA	POLYCHAETA	PHYLLODOCI	Pilargiida	Sigambra tentaculata	0.20
1598	CRUSTACEA	TANAIDACEA	TANAIDACEA	Tanaidae	Sinelobus stanfordi	0.01
1599	MOLLUSCA	GASTROPODA	ARCHAEOGAS	Trochidae	Solariella obscura	0.05
1600	MOLLUSCA	GASTROPODA	ARCHAEOGAS	Trochidae	Solariella peramabilis	110.60
1601	MOLLUSCA	GASTROPODA	ARCHAEOGAS	Trochidae	Solariella varicosa	95.20
1602	MOLLUSCA	BIVALVIA	VENEROIDA	Solenidae	Solen sicarius	3.80
1603	CRUSTACEA	CIRRIPEDIA	THORACICA	Archaeobal	Solidobalanus hesperius	0.00
1604	MOLLUSCA	APLACOPHORA	CHAETODERMA	Chaetoderm	Spathoderma denchi	4.01
1605	ANNELIDA	POLYCHAETA	PHYLLODOCI	Sphaerodor	Sphaerodoropsis minuta	0.10
1606	ANNELIDA	POLYCHAETA	PHYLLODOCI	Sphaerodor	Sphaerodoropsis sphaerulifer	0.78
1607	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Sphaerosyllis brandhorsti	0.08
1608	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Sphaerosyllis hystrix	1.60
1609	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Sphaerosyllis pirifera	1.00
1610	CRUSTACEA	OSTRACODA	HALOCYPRID	Halocyprid	Spinoecia spinirostris	0.10
1611	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Spio butleri	3.05
1612	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Spio cirrifera	0.10
1613	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Spio filicornis	2.10
1614	ANNELIDA	POLYCHAETA	SPIONIDA	Chaetopter	Spiochaetopterus costarum	0.10
1615	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Spiophanes berkeleyorum	2.72
1616	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Spiophanes bombyx	5.20
1617	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Spiophanes kroyeri	10.42
1618	MOLLUSCA	BIVALVIA	VENEROIDA	Mactridae	Spisula falcata	5.70
1619	CNIDARIA	ANTHOZOA	PENNATULAC	Stachyopti	Stachyoptilum superbum	0.00
1620	ANNELIDA	POLYCHAETA	STERNASPID	Sternaspid	Sternaspis scutata	37.23
1621	ANNELIDA	POLYCHAETA	PHYLLODOCI	Sigalionid	Sthenelais berkelyi	0.10
1622	ANNELIDA	POLYCHAETA	PHYLLODOCI	Sigalionid	Sthenelais tertiaglabra	35.00
1623	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Streblosoma bairdi	68.60
1624	ANNELIDA	POLYCHAETA	SPIONIDA	Spionidae	Streblospio benedicti	0.11
1625	ECHINODERM	ECHINOIDEA	CLYPEASTER	Strongyloc	Strongylocentrotus pallidus	0.10
1626	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Syllides longocirrata	0.05
1627	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Syllis alternata	1.80

Appendix 2. (continued)

1628	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Syllis elongata	1.94
1629	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Syllis harti	7.40
1630	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Syllis heterochaeta	0.93
1631	ANNELIDA	POLYCHAETA	PHYLLODOCI	Syllidae	Syllis hyalina	4.60
1632	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Oedoceroti	Synchelidium rectipalmum	0.90
1633	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Oedoceroti	Synchelidium shoemakeri	0.20
1634	CRUSTACEA	ISOPODA	ISOPODA	Idoteidae	Synidotea angulata	4.88
1635	CRUSTACEA	ISOPODA	ISOPODA	Idoteidae	Synidotea bicuspida	10.00
1636	CRUSTACEA	ISOPODA	ISOPODA	Idoteidae	Synidotea media	10.00
1637	CRUSTACEA	ISOPODA	ISOPODA	Idoteidae	Synidotea nebulosa	3.80
1638	CRUSTACEA	ISOPODA	ISOPODA	Idoteidae	Synidotea nodulosa	0.60
1639	CRUSTACEA	ISOPODA	ISOPODA	Idoteidae	Synidotea picta	3.70
1640	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Synopiidae	Syrrhoe longifrons	1.00
1641	MOLLUSCA	BIVALVIA	VENEROIDA	Veneridae	Tapes philippinarum	217.90
1642	ANNELIDA	OLIGOCHAET	TUBIFICIDA	Tubificida	Tectidrilus diversus	0.05
1643	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Tellina carpenteri	52.95
1644	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Tellina modesta	1.60
1645	MOLLUSCA	BIVALVIA	VENEROIDA	Tellinidae	Tellina nuculoides	15.65
1646	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Tenonia kitsapensis	1.02
1647	ANNELIDA	POLYCHAETA	PHYLLODOCI	Polynoidae	Tenonia priops	7.13
1648	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Terebellides californica	2.15
1649	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Terebellides stroemi	111.10
1650	BRACHIOPODA	ARTICULATA	TEREBRATUL	Cancelloth	Terebratulina unguicula	33.00
1651	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Tharyx multifilis	7.56
1652	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Tharyx secundus	8.19
1653	ANNELIDA	POLYCHAETA	SPIONIDA	Cirratulid	Tharyx tessalata	1.20
1654	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Thelepus cincinnatus	1.00
1655	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Thelepus japonicus	223.00
1656	ANNELIDA	POLYCHAETA	TEREBELLID	Terebellid	Thelepus setosus	22.85
1657	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Hyperiidae	Themisto pacifica	2.03
1658	MOLLUSCA	BIVALVIA	VENEROIDA	Thyasirida	Thyasira gouldi	37.81
1659	SIPUNCULA	SIPUNCULA	SIPUNCULID	Golfingiid	Thysanocardia nigra	9.14
1660	CRUSTACEA	EUPHAUSIAC	EUPHAUSIAC	Euphausiid	Thysanoessa spinifera	40.03
1661	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Synopiidae	Tiron biocellata	0.30
1662	ANNELIDA	POLYCHAETA	OPHELIIDA	Opheliidae	Travisia brevis	5.40
1663	ANNELIDA	POLYCHAETA	OPHELIIDA	Opheliidae	Travisia pupa	1545.10
1664	MOLLUSCA	BIVALVIA	VENEROIDA	Mactridae	Tresus nuttalli	108.40
1665	ANNELIDA	POLYCHAETA	TEREBELLID	Trichobran	Trichobranchus glacialis	0.10
1666	MOLLUSCA	GASTROPODA	MESOGASTRO	Trichotrop	Trichotropis borealis	33.60
1667	MOLLUSCA	GASTROPODA	NEOGASTROP	Capulidae	Trichotropis cancellata	10.00
1668	MOLLUSCA	BIVALVIA	VENEROIDA	Astartidae	Tridonta alaskensis	64.90
1669	MOLLUSCA	BIVALVIA	VENEROIDA	Astartidae	Tridonta borealis	265.70
1670	MOLLUSCA	BIVALVIA	VENEROIDA	Astartidae	Tridonta montagui	0.10
1671	CRUSTACEA	AMPHIPODA	CAPPRELLID	Aeginellid	Tritella pilimana	0.16
1672	ANNELIDA	POLYCHAETA	SPIONIDA	Trochochae	Trochochaeta multisetosa	19.80
1673	MOLLUSCA	GASTROPODA	NEOGASTROP	Muricidae	Trophonopsis orpheus	2.20
1674	ANNELIDA	OLIGOCHAET	TUBIFICIDA	Tubificida	Tubificoides bakeri	0.05
1675	ANNELIDA	OLIGOCHAET	TUBIFICIDA	Tubificida	Tubificoides benedii	0.05*
1676	ANNELIDA	OLIGOCHAET	TUBIFICIDA	Tubificida	Tubificoides brownae	0.05*

Appendix 2. (continued)

1677	ANNELIDA	OLIGOCHAET	TUBIFICIDA	Tubificida	Tubificoides diazi	0.05*
1678	ANNELIDA	OLIGOCHAET	TUBIFICIDA	Tubificida	Tubificoides pseudogaster	0.05
1679	ANNELIDA	OLIGOCHAET	TUBIFICIDA	Tubificida	Tubificoides wasselli	0.05
1680	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Turbonilla aurantia	1.50
1681	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Turbonilla lordi	1.45
1682	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Turbonilla lyalli	2.10
1683	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Turbonilla pedroana	1.50
1684	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Turbonilla pugetensis	1.50
1685	MOLLUSCA	GASTROPODA	OPISTHOBRA	Pyramidell	Turbonilla vancouverensis	2.40
1686	CRUSTACEA	COPEPODA	HARPACTICO	Diosaccida	Typhanlamphiascus typhlops	0.00
1687	MOLLUSCA	GASTROPODA	NEOGASTROP	Muricidae	Urosalpinx cinerea	1.00
1688	CRUSTACEA	AMPHIPODA	CAPRELLIDA	Aeginellid	Urothoe denticulata	1.00
1689	CNIDARIA	HYDROZOA	ANTHOMEDUS	Velellidae	Velella velella	0.00
1690	ANTHOZOA	OCTOCORALL	PENNATULAC	Virgularlid	Virgularia cystiferum	146.50
1691	MOLLUSCA	GASTROPODA	MESOGASTRO	Vitrinelli	Vitrinella columbiana	1.50
1692	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Lysianassid	Wecomedon wecomus	0.05
1693	CRUSTACEA	AMPHIPODA	GAMMARIDEA	Oedoceroti	Westwoodilla caecula	1.30
1694	MOLLUSCA	BIVALVIA	NUCULOIDA	Yoldiidae	Yoldia amygdalea	960.83
1695	MOLLUSCA	BIVALVIA	NUCULOIDA	Yoldiidae	Yoldia beringiana	476.00
1696	MOLLUSCA	BIVALVIA	NUCULOIDA	Yoldiidae	Yoldia hyperboria	358.15
1697	MOLLUSCA	BIVALVIA	NUCULOIDA	Yoldiidae	Yoldia martyria	262.97
1698	MOLLUSCA	BIVALVIA	NUCULOIDA	Yoldiidae	Yoldia myalis	0.10
1699	MOLLUSCA	BIVALVIA	NUCULOIDA	Yoldiidae	Yoldia scissurata	88.50
1700	MOLLUSCA	BIVALVIA	NUCULOIDA	Yoldiidae	Yoldia thraciaeformis	10.00

Appendix 3a. Comtre2 comparison of Alice Arm/Hastings Arm raw abundance (Tree 1) and biomass weighted abundance (Tree 2) dendrograms. Linkages for each tree are given, followed by the Fowlkes-Mallows statistics for each linkage, probability, mean and standard deviations for the Fowlkes-Mallows statistics.

Tree 1: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	6EN	6EM	0.17
2	2EN	2ES	0.19
3	6ES	3ES	0.21
4	3ZE	3ZM	0.23
5	6ZE	6ZM	0.28
6	9CN	9CM	0.29
7	3ZE	3ZW	0.30
8	65N	65M	0.30
9	2ZE	2ZW	0.31
10	6EN	3EM	0.31
11	65N	65S	0.33
12	6CN	6CM	0.34
13	6ES	2EN	0.35
14	2EM	2ZM	0.38
15	6ZE	3ZE	0.38
16	9EN	9EM	0.39
17	9DN	9DM	0.39
18	3DN	3DS	0.40
19	6EN	3EN	0.41
20	6DN	65N	0.42
21	2CM	2DM	0.42
22	6DN	6DS	0.43
23	6CN	6DM	0.45
24	2EM	2ZE	0.46
25	6CS	6DN	0.47
26	9DN	9EN	0.48
27	6EN	6ES	0.50
28	9CN	9CS	0.50
29	3CS	3DN	0.55
30	6ZE	6ZW	0.55
31	35N	35M	0.56
32	9ZE	9ZW	0.56
33	6CN	6CS	0.56
34	9DN	9ES	0.57
35	3CN	3DM	0.58
36	2DS	35S	0.59
37	9CN	9DS	0.60
38	2DN	2EM	0.61
39	3CN	3CS	0.62
40	9DN	35N	0.63
41	9ZM	3CN	0.64
42	6CN	2DN	0.67

Appendix 3a. (continued)

43	9CN	9DN	0.69
44	9ZM	3CM	0.73
45	9CN	6CN	0.73
46	6EN	6ZE	0.73
47	9CN	6EN	0.76
48	9ZE	9ZM	0.79
49	9ZE	2DS	0.82
50	2CN	2CM	0.85
51	9CN	9ZE	0.86
52	9CN	2CS	0.87
53	9CN	2CN	0.95

Tree 2: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	3FM	3ES	0.18
2	9CN	9CM	0.21
3	2EN	3EM	0.24
4	6CM	6EN	0.24
5	9EM	9ES	0.27
6	9CN	6CN	0.27
7	9CN	9DN	0.29
8	9DM	9EN	0.29
9	3DN	3DS	0.30
10	6EM	6ES	0.30
11	6ZE	6ZM	0.31
12	2EN	2ES	0.31
13	2ZE	2ZM	0.33
14	2EM	35M	0.33
15	3ZE	3ZW	0.33
16	65S	6EM	0.34
17	9DS	35S	0.36
18	9CN	9CS	0.37
19	6CM	65S	0.37
20	2EN	3EN	0.37
21	6ZE	3ZM	0.38
22	9DM	9EM	0.39
23	6ZE	3ZE	0.42
24	6?M	65N	0.42
25	9ZE	9ZW	0.42
26	2EN	2EM	0.43
27	6DM	6DS	0.43
28	6DN	65M	0.44
29	9DM	35N	0.48
30	9ZM	6ZW	0.48
31	6CM	6CS	0.48
32	6CM	6DN	0.50
33	9CN	6DM	0.50
34	9DM	2ZW	0.51

Appendix 3a. (continued)

35	9CN	6CM	0.54
36	3CN	3DN	0.55
37	2CM	2DS	0.56
38	9CN	9DM	0.57
39	9DS	9ZM	0.58
40	9CN	6ZE	0.60
41	2EN	2ZE	0.60
42	9ZE	2DN	0.63
43	3CN	3CS	0.63
44	9DS	2EN	0.63
45	9CN	9DS	0.65
46	9CN	9ZE	0.72
47	2CM	3DM	0.72
48	2CS	3CN	0.73
49	2CM	3CM	0.75
50	9CN	2CS	0.85
51	2CN	2CM	0.90
52	9CN	2CN	0.96
53	9CN	2DM	0.99

H0: Tree 1 and Tree 2 are generated by the same probability model.

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	Mean	Std.Dev.
1	1	0.000	0.980	0.020	0.141
2	2	0.000	0.800	0.094	0.192
3	3	0.000	0.720	0.098	0.172
4	4	0.000	0.560	0.117	0.146
5	5	0.000	0.520	0.102	0.119
6	6	0.144	0.580	0.116	0.105
7	7	0.107	0.360	0.112	0.093
8	8	0.096	0.340	0.118	0.091
9	9	0.088	0.380	0.130	0.095
10	10	0.077	0.360	0.128	0.085
11	11	0.138	0.520	0.137	0.083
12	12	0.183	0.680	0.143	0.084
13	13	0.263	0.900	0.146	0.076
14	14	0.250	0.880	0.148	0.071
15	15	0.257	0.900	0.150	0.069
16	16	0.241	0.900	0.159	0.062
17	17	0.231	0.900	0.163	0.058
18	18	0.246	0.860	0.170	0.064
19	19	0.243	0.860	0.171	0.059
20	20	0.247	0.880	0.177	0.066
21	21	0.290	0.960	0.182	0.072
22	22	0.286	0.960	0.179	0.068
23	23	0.393	0.980	0.186	0.071
24	24	0.398	0.980	0.183	0.066

Appendix 3a. (continued)

25	25	0.374	0.980	0.193	0.065
26	26	0.365	0.980	0.202	0.059
27	27	0.435	1.000	0.205	0.057
28	28	0.468	1.000	0.214	0.062
29	29	0.449	1.000	0.221	0.065
30	30	0.432	0.980	0.223	0.070
31	31	0.438	0.980	0.238	0.073
32	32	0.481	0.980	0.242	0.072
33	33	0.493	0.980	0.263	0.075
34	34	0.500	1.000	0.276	0.074
35	35	0.530	1.000	0.286	0.076
36	36	0.524	0.980	0.305	0.087
37	37	0.516	0.980	0.328	0.084
38	38	0.429	0.780	0.349	0.094
39	39	0.426	0.660	0.385	0.108
40	40	0.368	0.400	0.416	0.104
41	41	0.364	0.220	0.447	0.097
42	42	0.348	0.040	0.476	0.081
43	43	0.395	0.060	0.508	0.074
44	44	0.376	0.000	0.523	0.064
45	45	0.605	0.920	0.535	0.058
46	46	0.648	0.940	0.546	0.053
47	47	0.896	1.000	0.549	0.050
48	48	0.888	1.000	0.562	0.050
49	49	0.883	1.000	0.569	0.048
50	50	0.811	1.000	0.582	0.051
51	51	0.918	1.000	0.595	0.053
52	52	0.962	0.940	0.695	0.115
53	53	1.000	1.000	1.000	0.000

Appendix 3b. Co rel comparison of Alice Arm raw abundance dendrogram (Tree 1) with environmental dendrogram (Tree 2). Linkages for each dendrogram are given, followed by the Fowlkes-Mallows statistics, probabilities and means and standard deviations for each linkage.

	Tree 1 Linkages		Tree 2 Linkages	
Linkage(i)	A(i)	B(i)	A(i)	B(i)
1	6EN	6EM	6ZW	3ZW
2	2EN	2ES	6ZM	3ZM
3	6ES	3ES	6ZE	3ZE
4	3ZE	3ZM	6ES	3ES
5	6ZE	6ZM	6EM	3EM
6	9CN	9CM	6EN	3EN
7	3ZE	3ZW	65S	35S
8	65N	65M	65M	35M
9	2ZE	2ZW	6DS	3DS
10	6EN	3EM	6DM	3DM
11	65N	65S	6DN	3DN
12	6CN	6CM	6CS	3CS
13	6ES	2EN	6CM	3CM
14	2EM	2ZM	6CN	3CN
15	6ZE	3ZE	6ZE	6ZM
16	9EN	9EM	6EN	6EM
17	9DN	9DM	2ZE	2ZM
18	3DN	3DS	6ZE	2ZW
19	6EN	3EN	9ZE	9ZM
20	6DN	65N	6ES	2ES
21	2CM	2DM	6CM	2CM
22	6DN	6DS	2EN	2EM
23	6CN	6DM	9EN	9EM
24	2EM	2ZE	6ZE	2ZE
25	6CS	6DN	9DS	65S
26	9DN	9EN	6ZE	6ZW
27	6EN	6ES	6EN	2EN
28	9CN	9CS	9DM	65M
29	3CS	3DN	9DN	65N
30	6ZE	6ZW	6DN	6DM
31	35N	35M	9CN	6CM
32	9ZE	9ZW	9ES	6ZE
33	6CN	6CS	6CN	2CN
34	9DN	9ES	6EN	6ES
35	3CN	3DM	9EN	9ES
36	2DS	35S	6DS	2DM
37	9CN	9DS	9ZW	6CN
38	2DN	2EM	9DN	2DN
39	3CN	3CS	9CN	9CM
40	9DN	35N	9EN	6EN
41	9ZM	3CN	9ZE	35N
42	6CN	2DN	9CN	9ZW
43	9CN	9DN	9DM	9DS

Appendix 3b. (continued)

44	9ZM	3CM	9DN	6DS
45	9CN	6CN	6CS	2CS
46	6EN	6ZE	9DM	2DS
47	9CN	6EN	9DN	9DM
48	9ZE	9ZM	9CS	6CS
49	9ZE	2DS	9DN	9EN
50	2CN	2CM	9CN	9ZE
51	9CN	9ZE	9CN	9CS
52	9CN	2CS	9DN	6DN
53	9CN	2CN	9CN	9DN

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.001	0.026	0.001	0.026
2	2	0.000	1.000	0.001	0.019	0.001	0.026
3	3	0.000	1.000	0.001	0.016	0.002	0.026
4	4	0.250	0.885	0.247	0.015	0.003	0.026
5	5	0.200	0.847	0.198	0.012	0.003	0.026
6	6	0.167	0.807	0.165	0.012	0.004	0.026
7	7	0.134	0.988	0.141	0.011	0.005	0.026
8	8	0.118	0.762	0.117	0.010	0.006	0.026
9	9	0.105	0.721	0.104	0.009	0.007	0.026
10	10	0.183	0.007	0.094	0.009	0.008	0.026
11	11	0.161	0.898	0.165	0.009	0.009	0.026
12	12	0.149	0.665	0.147	0.009	0.009	0.026
13	13	0.127	0.977	0.137	0.009	0.011	0.026
14	14	0.120	0.652	0.118	0.008	0.012	0.026
15	15	0.370	0.001	0.203	0.010	0.015	0.026
16	16	0.410	0.636	0.405	0.013	0.017	0.026
17	17	0.394	0.588	0.388	0.012	0.018	0.026
18	18	0.357	0.539	0.352	0.012	0.020	0.026
19	19	0.434	0.002	0.340	0.012	0.021	0.026
20	20	0.463	0.792	0.469	0.014	0.023	0.026
21	21	0.442	0.467	0.435	0.013	0.024	0.026
22	22	0.413	0.896	0.422	0.013	0.025	0.026
23	23	0.423	0.720	0.421	0.013	0.026	0.026
24	24	0.422	0.007	0.384	0.014	0.031	0.026
25	25	0.392	0.903	0.401	0.014	0.034	0.026
26	26	0.400	0.820	0.405	0.016	0.040	0.026
27	27	0.389	0.019	0.367	0.015	0.049	0.027
28	28	0.378	0.627	0.375	0.014	0.050	0.027
29	29	0.370	0.566	0.367	0.015	0.051	0.026
30	30	0.413	0.007	0.352	0.014	0.054	0.026
31	31	0.403	0.431	0.396	0.016	0.056	0.026
32	32	0.379	0.364	0.372	0.016	0.059	0.026
33	33	0.350	0.926	0.365	0.017	0.066	0.026
34	34	0.455	0.671	0.454	0.018	0.074	0.026
35	35	0.433	0.284	0.425	0.018	0.081	0.026

Appendix 3b. (continued)

36	36	0.428	0.211	0.419	0.019	0.082	0.026
37	37	0.417	0.425	0.412	0.019	0.084	0.026
38	38	0.406	0.507	0.402	0.020	0.086	0.025
39	39	0.406	0.158	0.396	0.020	0.090	0.025
40	40	0.314	0.543	0.316	0.030	0.124	0.025
41	41	0.307	0.484	0.309	0.030	0.127	0.024
42	42	0.265	0.949	0.298	0.031	0.153	0.029
43	43	0.255	0.864	0.266	0.025	0.167	0.027
44	44	0.259	0.346	0.262	0.024	0.172	0.026
45	45	0.274	0.133	0.262	0.027	0.227	0.036
46	46	0.395	0.028	0.280	0.027	0.244	0.031
47	47	0.505	0.036	0.422	0.019	0.354	0.031
48	48	0.506	0.333	0.503	0.008	0.359	0.029
49	49	0.646	0.800	0.649	0.020	0.488	0.039
50	50	0.647	0.500	0.647	0.008	0.499	0.035
51	51	0.667	0.167	0.651	0.009	0.642	0.020
52	52	0.739	1.000	0.747	0.009	0.717	0.015
53	53	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters linked at L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3c. Comtrel comparison of Alice Arm biomass weighted abundance dendrogram (Tree 1) and environmental dendrogram (Tree 2). Linkages for the two trees are given, followed by the Fowlkes-Mallows statistics and errors.

	Tree 1 Linkages		Tree 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	3EM	3ES	6ZW	3ZW
2	9CN	9CM	6ZM	3ZM
3	2EN	3EM	6ZE	3ZE
4	6CM	6EN	6ES	3ES
5	9EM	9ES	6EM	3EM
6	9DN	6CN	6EN	3EN
7	9DM	9EN	65S	35S
8	3DN	D3	65M	35M
9	6EM	6ES	6DS	3DS
10	6ZE	6ZM	6DM	3DM
11	2EN	2ES	6DN	3DN
12	9CN	9DN	6CS	3CS
13	2ZE	2ZM	6CM	3CM
14	2EM	35M	6CN	3CN
15	3ZE	3ZW	6ZE	6ZM
16	65S	6EM	6EN	6EM
17	9DS	35S	2ZE	2ZM
18	9CN	9CS	6ZE	2ZW
19	2EN	3EN	9ZE	9ZM
20	6CM	65S	6ES	2ES
21	6ZE	3ZM	6CM	2CM
22	9DM	9EM	2EN	2EM
23	6ZE	3ZE	9EN	9EM
24	9ZE	9ZW	6ZE	2ZE
25	6CM	65N	9DS	65S
26	2EN	2EM	6ZE	6ZW
27	6DM	6DS	6EN	2EN
28	6DN	65M	9DM	65M
29	9DM	35N	9DN	65N
30	9ZM	6ZW	6DN	6DM
31	6CM	6CS	9CN	6CM
32	6CM	6DN	9ES	6ZE
33	9CN	6DM	6CN	2CN
34	9DM	2ZW	6EN	6ES
35	9CN	6CM	9EN	9ES
36	3CN	3DN	6DS	2DM
37	2CM	2DS	9ZW	6CN
38	9CN	9DM	9DN	2DN
39	9DS	9ZM	9CN	9CM
40	9CN	6ZE	9EN	6EN
41	2EN	2ZE	9ZE	35N
42	9ZE	2DN	9CN	9ZW
43	3CN	3CS	9DM	9DS

Appendix 3c. (continued)

44	9DS	2EN	9DN	6DS
45	9CN	9DS	6CS	2CS
46	9CN	9ZE	9DM	2DS
47	2CM	3DM	9DN	9DM
48	2CS	3CN	9CS	6CS
49	2CM	3CM	9DN	9EN
50	9CN	2CS	9CN	9ZE
51	2CN	2CM	9CN	9CS
52	9CN	2CN	9DN	6DN
53	9CN	2DM	9CN	9DN

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.001	0.026	0.001	0.026
2	2	0.000	1.000	0.001	0.019	0.001	0.026
3	3	0.000	1.000	0.001	0.016	0.002	0.026
4	4	0.000	1.000	0.001	0.012	0.003	0.026
5	5	0.000	1.000	0.001	0.011	0.004	0.026
6	6	0.000	1.000	0.001	0.010	0.005	0.026
7	7	0.000	1.000	0.001	0.010	0.005	0.026
8	8	0.000	1.000	0.001	0.010	0.006	0.026
9	9	0.000	1.000	0.001	0.010	0.007	0.026
10	10	0.000	1.000	0.001	0.010	0.007	0.026
11	11	0.000	1.000	0.001	0.010	0.009	0.026
12	12	0.000	1.000	0.001	0.009	0.010	0.026
13	13	0.000	1.000	0.001	0.008	0.011	0.026
14	14	0.000	1.000	0.001	0.008	0.012	0.026
15	15	0.051	0.569	0.052	0.008	0.014	0.026
16	16	0.044	0.858	0.046	0.008	0.016	0.026
17	17	0.085	0.522	0.085	0.008	0.016	0.026
18	18	0.073	0.961	0.077	0.008	0.019	0.026
19	19	0.100	0.029	0.070	0.006	0.021	0.026
20	20	0.148	0.032	0.126	0.008	0.024	0.026
21	21	0.196	0.005	0.140	0.008	0.025	0.026
22	22	0.184	0.824	0.188	0.009	0.027	0.026
23	23	0.267	0.006	0.202	0.009	0.029	0.026
24	24	0.232	0.525	0.230	0.011	0.033	0.026
25	25	0.236	0.929	0.242	0.011	0.035	0.026
26	26	0.270	0.677	0.270	0.013	0.044	0.027
27	27	0.311	0.489	0.307	0.013	0.047	0.027
28	28	0.304	0.433	0.301	0.013	0.048	0.026
29	29	0.294	0.720	0.296	0.013	0.050	0.026
30	30	0.284	0.360	0.280	0.013	0.052	0.026
31	31	0.268	0.812	0.272	0.013	0.055	0.026
32	32	0.233	0.968	0.249	0.012	0.063	0.026
33	33	0.219	0.926	0.227	0.011	0.067	0.026
34	34	0.298	0.067	0.290	0.013	0.075	0.026
35	35	0.265	0.979	0.302	0.016	0.103	0.031

Appendix 3c. (continued)

36	36	0.261	0.620	0.261	0.013	0.104	0.030
37	37	0.257	0.340	0.256	0.013	0.106	0.030
38	38	0.210	1.000	0.254	0 014	0.133	0.032
39	39	0.216	0.700	0.218	0.008	0.136	0.031
40	40	0.290	0.029	0.211	0.017	0.215	0.050
41	41	0.321	0.033	0.290	0.017	0.220	0 047
42	42	0.318	0.615	0.319	0.019	0.229	0.043
43	43	0.317	0.621	0.320	0.021	0.233	0.041
44	44	0.333	0.036	0.320	0.022	0.248	0.035
45	45	0.495	0.022	0.334	0.025	0.333	0.038
46	46	0.474	0.972	0.488	0.005	0.361	0.034
47	47	0.486	0.821	0.486	0.003	0.387	0.029
48	48	0.486	0.476	0.485	0.003	0.389	0.028
49	49	0.643	0.400	0.643	0.008	0.524	0.041
50	50	0.637	1.000	0.650	0.009	0.595	0.029
51	51	0.656	0.500	0.661	0.009	0.618	0.023
52	52	0.738	0.333	0.720	0.016	0.744	0.009
53	53	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3d. Comtre2 comparison of Hecate Strait raw abundance (Tree 1) and biomass-weighted abundance (Tree 2) dendrograms. Linkages for each tree are given, followed by the Fowlkes-Mallows statistics for each linkage, probability, mean and standard deviations for the Fowlkes-Mallows statistics.

Tree 1: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	H1B1	H1B2	0.14
2	H3B2	H3B3	0.15
3	H2B1	H3B2	0.18
4	H1B1	H2B1	0.20
5	H1B1	H3B1	0.25
6	H2C1	H3C1	0.29
7	H2C3	H3C3	0.29
8	H1B1	H1B3	0.34
9	H3A1	H3A3	0.34
10	H2B2	H2B3	0.35
11	H1A2	H1A3	0.36
12	H2A1	H3A1	0.37
13	H1A1	H2A2	0.39
14	H3D1	H3D3	0.40
15	H1B1	H2B2	0.41
16	H1A1	H2A3	0.41
17	H2C2	H2C3	0.42
18	H1A1	H2A1	0.44
19	H1C1	H1C2	0.44
20	H2C2	H3C2	0.45
21	H2D1	H2D3	0.46
22	H1C1	H2C1	0.49
23	H1A1	H1A2	0.50
24	H1A1	H3A2	0.50
25	H2D2	H3D2	0.52
26	H1C1	H2C2	0.52
27	H2D1	H3D1	0.58
28	H2D1	H2D2	0.62
29	H1A1	H1C1	0.70
30	H1A1	H2D1	0.81
31	H1A1	H1C3	0.85
32	H1A1	H1B1	0.96

Tree 2: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	H3A1	H3A2	0.22
2	H2B2	H3B2	0.23
3	H2B1	H3B3	0.23
4	H2B1	H2B3	0.30
5	H2B1	H2B2	0.31

Appendix 3d. (continued)

6	H1B1	H1B3	0.31
7	H2A2	H2A3	0.33
8	H1B2	H2B1	0.36
9	H3C1	H3C2	0.38
10	H1B1	H1B2	0.38
11	H2A1	H2A2	0.40
12	H2C3	H3C3	0.41
13	H2C1	H2C2	0.44
14	H2C1	H3C1	0.47
15	H3D1	H3D3	0.50
16	H1A1	H2A1	0.51
17	H3A1	H3A3	0.51
18	H1C1	H1C2	0.52
19	H1C1	H2C1	0.56
20	H2D1	H2D3	0.57
21	H1A2	H1A3	0.61
22	H1B1	H3B1	0.64
23	H1A1	H1A2	0.66
24	H2D1	H2D2	0.68
25	H3D1	H3D2	0.68
26	H1C1	H2C3	0.68
27	H1A1	H1C1	0.77
28	H1A1	H3D1	0.82
29	H1A1	H1C3	0.88
30	H1A1	H3A1	0.92
31	H1A1	H1B1	0.95
32	H1A1	H2D1	0.96

H0: Tree 1 and Tree 2 are generated by the same probability model.

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	Mean	Std.Dev.
1	1	0.000	0.880	0.120	0.328
2	2	0.000	0.820	0.077	0.170
3	3	0.288	0.920	0.126	0.149
4	4	0.141	0.400	0.150	0.142
5	5	0.233	0.520	0.246	0.140
6	6	0.216	0.200	0.306	0.129
7	7	0.201	0.140	0.372	0.146
8	8	0.344	0.340	0.451	0.181
9	9	0.327	0.160	0.481	0.166
10	10	0.574	0.600	0.508	0.170
11	11	0.546	0.620	0.517	0.161
12	12	0.550	0.540	0.549	0.145
13	13	0.533	0.380	0.592	0.131
14	14	0.526	0.340	0.598	0.135
15	15	0.738	0.840	0.609	0.132

Appendix 3d. (continued)

16	16	0.764	0.880	0.639	0.126
17	17	0.753	0.880	0.651	0.113
18	18	0.742	0.720	0.661	0.112
19	19	0.696	0.480	0.679	0.113
20	20	0.690	0.360	0.697	0.109
21	21	0.712	0.420	0.704	0.098
22	22	0.830	0.880	0.711	0.093
23	23	0.827	0.900	0.715	0.089
24	24	0.802	0.860	0.703	0.097
25	25	0.787	0.700	0.727	0.095
26	26	0.882	0.960	0.750	0.096
27	27	0.696	0.180	0.779	0.094
28	28	0.615	0.080	0.773	0.097
29	29	0.712	0.220	0.784	0.105
30	30	0.853	0.680	0.806	0.109
31	31	0.673	0.300	0.760	0.132
32	32	1.000	1.000	1.000	0.000

Appendix 3e. Comtrel comparison of Hecate Strait raw abundance dendrogram (Tree 1) and environmental dendrogam (Tree 2). Linkages for the two trees are given, followed by the Fowlkes-Mallows statistic and errors.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	H1B1	H1B2	H2D2	H3D2
2	H3B2	H3B3	H1C2	H2C2
3	H2B1	H3B2	H1B2	H2B2
4	H1B1	H2B1	H1B1	H1B2
5	H1B1	H3B1	H1C3	H3C3
6	H2C1	H3C1	H2D1	H3D1
7	H2C3	H3C3	H1A3	H3A1
8	H1B1	H1B3	H1B3	H2B1
9	H3A1	H3A3	H1C1	H2C1
10	H2B2	H2B3	H1A2	H3A2
11	H1A2	H1A3	H1C3	H2A2
12	H2A1	H3A1	H1C2	H3C2
13	H1A1	H2A2	H1B3	H2B3
14	H3D1	H3D3	H2A3	H3A3
15	H1B1	H2B2	H1C1	H2A1
16	H1A1	H2A3	H1C3	H2C3
17	H2C2	H2C3	H1C1	H3C1
18	H1C1	H1C2	H1B1	H3B3
19	H1A1	H2A1	H1A3	H2A3
20	H2C2	H3C2	H1B3	H3B1
21	H2D1	H2D3	H1A3	H1C2
22	H1C1	H2C1	H1B1	H3B2
23	H1A1	H1A2	H1A2	H1C3
24	H1A1	H3A2	H1A3	H1C1
25	H2D2	H3D2	H1B1	H1B3
26	H1C1	H2C2	H1A1	H1A2
27	H2D1	H3D1	H2D1	H3D3
28	H2D1	H2D2	H1A1	H1A3
29	H1A1	H1C1	H2D1	H2D3
30	H1A1	H2D1	H2D1	H2D2
31	H1A1	H1C3	H1A1	H2D1
32	H1A1	H1B1	H1A1	H1B1

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.001	0.043	0.001	0.043
2	2	0.000	1.000	0.002	0.031	0.003	0.043
3	3	0.000	1.000	0.002	0.025	0.006	0.043
4	4	0.141	1.000	0.198	0.023	0.013	0.044
5	5	0.105	1.000	0.123	0.014	0.017	0.043
6	6	0.094	0.931	0.095	0.012	0.020	0.042
7	7	0.085	0.857	0.086	0.013	0.022	0.042

Appendix 3e. (continued)

8	8	0.139	0.021	0.079	0.012	0.027	0.041
9	9	0.129	0.780	0.129	0.011	0.029	0.041
10	10	0.120	0.702	0.120	0.011	0.031	0.040
11	11	0.108	0.624	0.109	0.011	0.034	0.040
12	12	0.097	0.874	0.100	0.011	0.038	0.040
13	13	0.090	0.528	0.091	0.013	0.042	0.040
14	14	0.086	0.452	0.087	0.014	0.044	0.040
15	15	0.202	0.005	0.082	0.014	0.056	0.038
16	16	0.215	0.751	0.216	0.013	0.061	0.039
17	17	0.226	0.669	0.227	0.014	0.066	0.039
18	18	0.291	0.400	0.287	0.015	0.071	0.039
19	19	0.320	0.066	0.291	0.016	0.082	0.038
20	20	0.384	0.087	0.362	0.018	0.088	0.038
21	21	0.329	0.346	0.325	0.020	0.103	0.040
22	22	0.409	0.060	0.376	0.023	0.110	0.039
23	23	0.409	0.054	0.370	0.025	0.129	0.038
24	24	0.425	0.200	0.412	0.036	0.164	0.039
25	25	0.598	0.138	0.570	0.040	0.183	0.037
26	26	0.636	0.107	0.584	0.045	0.205	0.035
27	27	0.646	0.142	0.607	0.054	0.211	0.034
28	28	0.698	0.400	0.685	0.091	0.282	0.028
29	29	0.934	0.100	0.668	0.113	0.362	0.036
30	30	0.770	0.833	0.866	0.102	0.459	0.032
31	31	1.000	0.333	0.894	0.114	0.590	0.029
32	32	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3f. Comtrel comparison of Hecate Strait biomass weighted abundance dendrogam (Tree 1) and environmental dendrogram (Tree 2). Linkages for the two trees are given, followed by the Fowlkes-Mallows statistic and errors.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	H3A1	H3A2	H2D2	H3D2
2	H2B2	H3B2	H1C2	H2C2
3	H2B1	H3B3	H1B2	H2B2
4	H2B1	H2B3	H1B1	H1B2
5	H2B1	H2B2	H1C3	H3C3
6	H1B1	H1B3	H2D1	H3D1
7	H2A2	H2A3	H1A3	H3A1
8	H1B2	H2B1	H1B3	H2B1
9	H3C1	H3C2	H1C1	H2C1
10	H1B1	H1B2	H1A2	H3A2
11	H2A1	H2A2	H1C3	H2A2
12	H2C3	H3C3	H1C2	H3C2
13	H2C1	H2C2	H1B3	H2B3
14	H2C1	H3C1	H2A3	H3A3
15	H3D1	H3D3	H1C1	H2A1
16	H1A1	H2A1	H1C3	H2C3
17	H3A1	H3A3	H1C1	H3C1
18	H1C1	H1C2	H1B1	H3B3
19	H1C1	H2C1	H1A3	H2A3
20	H2D1	H2D3	H1B3	H3B1
21	H1A2	H1A3	H1A3	H1C2
22	H1B1	H3B1	H1B1	H3B2
23	H1A1	H1A2	H1A2	H1C3
24	H2D1	H2D2	H1A3	H1C1
25	H3D1	H3D2	H1B1	H1B3
26	H1C1	H2C3	H1A1	H1A2
27	H1A1	H1C1	H2D1	H3D3
28	H1A1	H3D1	H1A1	H1A3
29	H1A1	H1C3	H2D1	H2D3
30	H1A1	H3A1	H2D1	H2D2
31	H1A1	H1B1	H1A1	H2D1
32	H1A1	H2D1	H1A1	H1B1

Fowlkes-Mallows Statistics

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.001	0.043	0.001	0.043
2	2	0.000	1.000	0.002	0.031	0.003	0.043
3	3	0.000	1.000	0.002	0.025	0.005	0.043
4	4	0.000	1.000	0.002	0.022	0.009	0.043
5	5	0.000	1.000	0.002	0.019	0.015	0.043
6	6	0.000	1.000	0.001	0.014	0.017	0.043

Appendix 3f. (continued)

7	7	0.000	1.000	0.002	0.013	0.019	0.042
8	8	0.078	0.024	0.002	0.014	0.024	0.041
9	9	0.072	0.706	0.073	0.013	0.026	0.041
10	10	0.216	0.003	0.068	0.014	0.034	0.039
11	11	0.193	0.901	0.195	0.011	0.039	0.040
12	12	0.177	0.688	0.176	0.011	0.042	0.040
13	13	0.245	0.604	0.243	0.012	0.046	0.040
14	14	0.264	0.057	0.233	0.012	0.050	0.039
15	15	0.247	0.590	0.245	0.012	0.053	0.039
16	16	0.254	0.771	0.257	0.014	0.059	0.039
17	17	0.263	0.698	0.262	0.015	0.064	0.040
18	18	0.328	0.458	0.323	0.017	0.069	0.039
19	19	0.402	0.009	0.323	0.018	0.079	0.039
20	20	0.382	0.406	0.374	0.020	0.084	0.039
21	21	0.327	0.346	0.322	0.021	0.098	0.040
22	22	0.416	0.075	0.376	0.023	0.109	0.039
23	23	0.395	0.218	0.375	0.025	0.124	0.038
24	24	0.458	0.444	0.450	0.036	0.152	0.039
25	25	0.629	0.361	0.607	0.043	0.171	0.037
26	26	0.589	0.642	0.598	0.049	0.189	0.035
27	27	0.668	0.047	0.561	0.053	0.237	0.035
28	28	0.706	0.933	0.771	0.075	0.351	0.041
29	29	0.746	0.200	0.684	0.073	0.370	0.039
30	30	0.865	0.166	0.711	0.089	0.426	0.034
31	31	0.673	1.000	0.840	0.133	0.700	0.026
32	32	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3g. Comtre2 comparison of Shelf raw (Tree 1) and biomass-weighted (Tree 2) abundance dendrograms. Linkages for both trees are given, followed by the Fowlkes-Mallows statistic, probability and mean and standard error for each linkage level.

Tree 1: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	S1D2	S1D4	0.22
2	S1D1	S1D2	0.26
3	S1A1	S1A4	0.27
4	S2B1	S1B1	0.29
5	S2B1	S1B2	0.29
6	S2A1	S2A4	0.31
7	S2B2	S2B3	0.31
8	S1B3	S1C1	0.32
9	S2D1	S2D2	0.33
10	S1A2	S1A5	0.35
11	S2B2	S2C2	0.35
12	S2A1	S2C1	0.36
13	S1B3	S1C2	0.37
14	S2D1	S2D4	0.37
15	S1A1	S1A2	0.40
16	S2A1	S2B1	0.41
17	S2B2	S1B3	0.42
18	S2A2	S1A1	0.43
19	S2D1	S1D1	0.45
20	S2A1	S2A2	0.46
21	S2A1	S2A5	0.49
22	S2A1	S2B2	0.50
23	S2C4	S1C4	0.55
24	S2C4	S2D1	0.58
25	S2A1	S2C4	0.69

Tree 2: Cluster Analysis

Linkage	Clusters Linked		Linkagevel
1	S2B2	S1B2	0.28
2	S1A2	S1A5	0.31
3	S2A2	S2A4	0.31
4	S1D1	S1D2	0.33
5	S2D1	S2D2	0.36
6	S2A1	S1A4	0.36
7	S2B1	S1B1	0.36
8	S1D1	S1D4	0.37
9	S2A1	S1A1	0.38
10	S2A5	S1A2	0.39
11	S2B3	S1B3	0.39
12	S1C1	S1C2	0.43
13	S2A2	S2A5	0.44

Appendix 3g. (continued)

14	S2B2	S2C2	0.44
15	S2B2	S2B3	0.46
16	S2D1	S2D4	0.47
17	S2A1	S2A2	0.52
18	S2D1	S1D1	0.52
19	S2B1	S2B2	0.52
20	S2A1	S2B1	0.55
21	S2C4	S1C4	0.62
22	S2C4	S2D1	0.65
23	S2A1	S2C1	0.66
24	S2A1	S1C1	0.73
25	S2A1	S2C4	0.74

H0: Tree 1 and Tree 2 are generated by the same probability model.

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	Mean	Std.Dev.
1	1	0.000	0.960	0.040	0.196
2	2	0.000	0.840	0.076	0.181
3	3	0.000	0.674	0.102	0.155
4	4	0.223	0.814	0.128	0.152
5	5	0.169	0.646	0.140	0.134
6	6	0.144	0.622	0.156	0.127
7	7	0.251	0.796	0.167	0.122
8	8	0.421	0.980	0.173	0.110
9	9	0.545	0.998	0.183	0.106
10	10	0.560	1.000	0.194	0.101
11	11	0.500	0.992	0.204	0.097
12	12	0.451	0.986	0.218	0.091
13	13	0.411	0.968	0.235	0.084
14	14	0.419	0.948	0.261	0.086
15	15	0.416	0.906	0.288	0.092
16	16	0.406	0.834	0.317	0.096
17	17	0.477	0.880	0.354	0.100
18	18	0.497	0.844	0.389	0.104
19	19	0.602	0.928	0.426	0.108
20	20	0.660	0.966	0.456	0.101
21	21	0.711	0.974	0.473	0.096
22	22	0.806	0.998	0.476	0.090
23	23	0.863	1.000	0.525	0.088
24	24	1.000	1.000	0.617	0.067
25	25	1.000	1.000	1.000	0.000

Appendix 3h. Comtrel comparison of Shelf raw abundance dendrogram (Tree 1) and environmental dendrogram (Tree 2). Linkages for the two trees are given, followed by the Fowlkes-Mallows statistic and errors.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	S1D2	S1D4	S2A1	S1A1
2	S1D1	S1D2	S1D2	S1D4
3	S1A1	S1A4	S2D2	S1D1
4	S2B1	S1B1	S2A4	S1A4
5	S2B1	S1B2	S2A5	S1C2
6	S2A1	S2A4	S2D1	S2D4
7	S2B2	S2B3	S2A4	S1B2
8	S1B3	S1C1	S2A2	S2C1
9	S2D1	S2D2	S2D2	S1D2
10	S1A2	S1A5	S2C4	S1C4
11	S2B2	S2C2	S2A4	S1B3
12	S2A1	S2C1	S2A1	S2B1
13	S1B3	S1C2	S2D1	S2D2
14	S2D1	S2D4	S2A2	S1C1
15	S1A1	S1A2	S2A4	S2B2
16	S2A1	S2B1	S2A1	S1B1
17	S2B2	S1B3	S2C2	S1A2
18	S2A2	S1A1	S2A4	S2B3
19	S2D1	S1D1	S2A5	S2C2
20	S2A1	S2A2	S2A2	S2A4
21	S2A1	S2A5	S2A1	S2A2
22	S2A1	S2B2	S2C4	S2D1
23	S2C4	S1C4	S2A1	S2A5
24	S2C4	S2D1	S2A1	S1A5
25	S2A1	S2C4	S2A1	S2C4

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.003	0.055	0.003	0.055
2	2	0.408	1.000	0.494	0.038	0.007	0.054
3	3	0.288	0.920	0.286	0.025	0.010	0.054
4	4	0.223	0.841	0.221	0.022	0.013	0.054
5	5	0.169	0.909	0.180	0.022	0.018	0.054
6	6	0.144	0.742	0.143	0.021	0.021	0.054
7	7	0.117	0.652	0.118	0.021	0.026	0.054
8	8	0.105	0.555	0.106	0.022	0.029	0.053
9	9	0.250	0.457	0.245	0.026	0.036	0.053
10	10	0.231	0.367	0.226	0.025	0.039	0.053
11	11	0.194	0.691	0.198	0.024	0.047	0.052
12	12	0.172	0.600	0.176	0.025	0.053	0.052
13	13	0.181	0.527	0.186	0.033	0.067	0.050
14	14	0.249	0.038	0.171	0.033	0.074	0.050

Appendix 3h. (continued)

15	15	0.213	0.757	0.225	0.037	0.086	0.049
16	16	0.290	0.036	0.231	0.036	0.106	0.049
17	17	0.279	0.311	0.278	0.035	0.121	0.048
18	18	0.295	0.694	0.302	0.035	0.135	0.048
19	19	0.457	0.035	0.299	0.038	0.154	0.046
20	20	0.515	0.142	0.468	0.040	0.226	0.044
21	21	0.602	0.733	0.608	0.061	0.301	0.046
22	22	0.721	0.100	0.560	0.073	0.422	0.042
23	23	0.913	0.500	0.868	0.075	0.512	0.041
24	24	1.000	0.333	0.877	0.100	0.556	0.031
25	25	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3i. Comtrel comparison of Shelf biomass-weighted abundance dendrogram (Tree 1) and environmental dendrogram (Tree 2). Linkages for the two trees are given, followed by the Fowlkes-Mallows statistic and errors.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage(i)	A(i)	B(i)	A(i)	B(i)
1	S2B2	S1B2	S2A1	S1A1
2	S1A2	S1A5	S1D2	S1D4
3	S2A2	S2A4	S2D2	S1D1
4	S1D1	S1D2	S2A4	S1A4
5	S2D1	S2D2	S2A5	S1C2
6	S2A1	S1A4	S2D1	S2D4
7	S2B1	S1B1	S2A4	S1B2
8	S1D1	S1D4	S2A2	S2C1
9	S2A1	S1A1	S2D2	S1D2
10	S2A5	S1A2	S2C4	S1C4
11	S2B3	S1B3	S2A4	S1B3
12	S1C1	S1C2	S2A1	S2B1
13	S2A2	S2A5	S2D1	S2D2
14	S2B2	S2C2	S2A2	S1C1
15	S2B2	S2B3	S2A4	S2B2
16	S2D1	S2D4	S2A1	S1B1
17	S2A1	S2A2	S2C2	S1A2
18	S2D1	S1D1	S2A4	S2B3
19	S2B1	S2B2	S2A5	S2C2
20	S2A1	S2B1	S2A2	S2A4
21	S2C4	S1C4	S2A1	S2A2
22	S2C4	S2D1	S2C4	S2D1
23	S2A1	S2C1	S2A1	S2A5
24	S2A1	S1C1	S2A1	S1A5
25	S2A1	S2C4	S2A1	S2C4

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.003	0.055	0.003	0.055
2	2	0.000	1.000	0.003	0.040	0.006	0.055
3	3	0.000	1.000	0.003	0.034	0.009	0.055
4	4	0.000	1.000	0.003	0.030	0.012	0.055
5	5	0.000	1.000	0.004	0.027	0.015	0.054
6	6	0.000	1.000	0.004	0.025	0.018	0.054
7	7	0.000	1.000	0.005	0.024	0.023	0.054
8	8	0.111	0.029	0.005	0.023	0.027	0.054
9	9	0.334	0.032	0.256	0.024	0.036	0.053
10	10	0.296	0.727	0.299	0.024	0.041	0.053
11	11	0.259	0.383	0.253	0.023	0.047	0.052
12	12	0.236	0.304	0.231	0.023	0.051	0.052
13	13	0.209	0.967	0.235	0.033	0.073	0.052

Appendix 3i. (continued)

14	14	0.193	0.576	0.198	0.030	0.079	0.051
15	15	0.258	0.075	0.213	0.031	0.095	0.050
16	16	0.329	0.072	0.270	0.032	0.102	0.049
17	17	0.290	0.800	0.311	0.039	0.126	0.049
18	18	0.499	0.027	0.332	0.035	0.147	0.047
19	19	0.457	0.857	0.475	0.031	0.168	0.045
20	20	0.511	0.047	0.410	0.040	0.270	0.045
21	21	0.669	0.200	0.648	0.046	0.339	0.054
22	22	0.702	0.100	0.621	0.060	0.376	0.041
23	23	0.857	0.333	0.785	0.099	0.480	0.037
24	24	1.000	0.333	0.842	0.137	0.556	0.031
25	25	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3j. Comtre2 comparison of Vancouver Harbour and Port Moody Arm raw abundance (Tree 1) and biomass-weighted abundance (Tree 2) dendrograms. Linkages for each tree are given, followed by the Fowlkes-Mallows statistics for each linkage, probability, mean and standard deviations for the Fowlkes-Mallows statistics.

Tree 1: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	V233	V236	0.15
2	V122E	V125E	0.17
3	V122E	V125D	0.26
4	V233	V239E	0.26
5	V115	V122D	0.28
6	V11	V12	0.29
7	V225E	V222E	0.30
8	V115	V122E	0.31
9	V21	V241B	0.31
10	V233	V237B	0.31
11	V136	V137B	0.32
12	V115	V119	0.35
13	V115	V122	0.37
14	V21	V225D	0.37
15	V237A	V137A	0.37
16	V240	V239A	0.39
17	V233	V239C	0.39
18	V216	V225E	0.40
19	V237A	V139E	0.40
20	V237A	V136	0.44
21	V245	V139A	0.44
22	V111	V115	0.46
23	V13B	V14A	0.46
24	V246	V245	0.48
25	V216	V240	0.49
26	V241A	V139C	0.49
27	V233	V237A	0.52
28	V111	V116	0.55
29	V211	V216	0.57
30	V11	V13A	0.59
31	V21	V125B	0.60
32	V246	V141	0.62
33	V211	V233	0.63
34	V241A	V246	0.68
35	V11	V13B	0.69
36	V211	V241A	0.71
37	V111	V114	0.72
38	V141B	V145	0.73
39	V21	V222B	0.75
40	V111	V1PE	0.77
41	V211	V111	0.80
42	V211	V215	0.82

Appendix 3j. (continued)

43	V211	V140	0.82
44	V21	V11	0.84
45	V21	V211	0.87
46	V141B	V146	0.94
47	V21	V141B	0.97

Tree 2: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	V233	V236	0.24
2	V115	V122E	0.25
3	V122D	V125D	0.25
4	V225E	V222E	0.25
5	V122D	V125E	0.27
6	V233	V239E	0.30
7	V115	V122D	0.33
8	V241B	V245	0.34
9	V116	V122	0.36
10	V233	V237B	0.36
11	V136	V137B	0.38
12	V137A	V139E	0.39
13	V225E	V115	0.40
14	V13A	V125B	0.45
15	V237A	V239C	0.45
16	V241A	V241B	0.45
17	V111	V116	0.46
18	V225E	V111	0.46
19	V139C	V140	0.47
20	V240	V241A	0.48
21	V225E	V119	0.48
22	V12	V13A	0.49
23	V233	V237A	0.50
24	V240	V239A	0.52
25	V211	V215	0.53
26	V12	V14A	0.54
27	V137A	V139C	0.55
28	V216	V136	0.59
29	V216	V240	0.61
30	V225D	V222B	0.61
31	V225E	V114	0.63
32	V139A	V141	0.63
33	V216	V233	0.67
34	V12	V13B	0.68
35	V225E	V1PE	0.68
36	V216	V137A	0.70
37	V211	V225E	0.70
38	V211	V216	0.75
39	V12	V1391	0.79
40	V211	V12	0.81

Appendix 3j. (continued)

41	V211	V2253	0.82
42	V211	V246	0.86
43	V1413	V145	0.89
44	V211	V11	0.92
45	V21	V211	0.93
46	V21	V1413	0.95
47	V21	V146	0.99

H0: Tree 1 and Tree 2 are generated by thesame probability model.

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	Mean	Std.Dev.
1	1	1.000	1.000	0.100	0.300
2	2	0.500	0.986	0.134	0.234
3	3	0.288	0.728	0.147	0.186
4	4	0.204	0.520	0.171	0.166
5	5	0.308	0.754	0.188	0.149
6	6	0.500	0.970	0.199	0.140
7	7	0.712	1.000	0.210	0.129
8	8	0.933	1.000	0.215	0.123
9	9	0.875	1.000	0.222	0.118
10	10	0.894	1.000	0.226	0.114
11	11	0.900	1.000	0.232	0.111
12	12	0.785	1.000	0.241	0.112
13	13	0.580	0.990	0.249	0.106
14	14	0.553	0.990	0.257	0.105
15	15	0.537	0.990	0.264	0.100
16	16	0.514	0.988	0.277	0.095
17	17	0.473	0.946	0.292	0.097
18	18	0.471	0.946	0.305	0.096
19	19	0.476	0.932	0.322	0.096
20	20	0.435	0.846	0.341	0.097
21	21	0.500	0.926	0.354	0.096
22	22	0.569	0.968	0.365	0.096
23	23	0.594	0.980	0.378	0.098
24	24	0.584	0.968	0.384	0.098
25	25	0.554	0.940	0.392	0.096
26	26	0.540	0.930	0.397	0.095
27	27	0.505	0.864	0.397	0.095
28	28	0.561	0.958	0.396	0.094
29	29	0.527	0.894	0.399	0.093
30	30	0.529	0.916	0.394	0.091
31	31	0.498	0.876	0.389	0.089
32	32	0.498	0.880	0.388	0.089
33	33	0.550	0.956	0.388	0.088
34	34	0.543	0.946	0.384	0.084
35	35	0.538	0.942	0.398	0.085
36	36	0.624	0.972	0.414	0.090

Appendix 3j. (continued)

37	37	0.623	0.940	0.448	0.098
38	38	0.560	0.774	0.479	0.097
39	39	0.554	0.648	0.519	0.096
40	40	0.557	0.522	0.555	0.093
41	41	0.733	0.956	0.589	0.083
42	42	0.790	0.974	0.618	0.080
43	43	0.814	0.968	0.647	0.079
44	44	0.811	0.868	0.705	0.099
45	45	1.000	1.000	0.832	0.115
46	46	0.956	0.116	0.981	0.038
47	47	1.000	1.000	1.000	0.000

Appendix 3k. Comtrel comparison of Vancouver Harbour and Port Moody Arm abundance dendrogram (Tree 1) and environmental dendrogram (Tree 2). Linkages for the two trees are given, followed by the Fowlkes-Mallows statistic and errors.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	V233	V236	V236	V245
2	V122E	V125E	V136	V137B
3	V122E	V125D	V21	V11
4	V233	V239E	V141	V141B
5	V115	V122D	V222B	V122E
6	V11	V12	V236	V145
7	V225E	V222E	V237A	V240
8	V115	V122E	V236	V139A
9	V21	V241B	V239C	V241B
10	V233	V237B	V239C	V241A
11	V136	V137B	V215	V1255
12	V115	V119	V211	V116
13	V115	V122	V137A	V139E
14	V21	V225D	V236	V239A
15	V237A	V137A	V236	V239F
16	V240	V239A	V237B	V246
17	V233	V239C	V236	V237A
18	V216	V225E	V12	V13B
19	V237A	V139E	V236	V139C
20	V237A	V136	V233	V137A
21	V245	V139A	V236	V239C
22	V111	V115	V211	V119
23	V13B	V14A	V140	V141
24	V246	V245	V222B	V122D
25	V216	V240	V236	V237B
26	V241A	V139C	V215	V115
27	V233	V237A	V233	V136
28	V111	V116	V211	V222E
29	V211	V216	V13A	V125
30	V11	V13A	V215	V125D
31	V21	V125	V233	V140
32	V246	V141	V225D	V146
33	V211	V233	V14A	V122
34	V241A	V246	V216	V222B
35	V11	V13B	V225E	V13A
36	V211	V241A	V233	V236
37	V111	V114	V211	V111
38	V141B	V145	V21	V233
39	V21	V222B	V211	V215
40	V111	V1PE	V14A	V114
41	V211	V111	V211	V225E
42	V211	V215	V216	V225D
43	V211	V140	V12	V14A

Appendix 3k. (continued)

44	V21	V11	V21	V216
45	V21	V211	V21	V211
46	V141B	V146	V21	V1PE
47	V21	V141B	V21	V12

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.000	0.029	0.000	0.029
2	2	0.000	1.000	0.000	0.019	0.001	0.029
3	3	0.000	1.000	0.000	0.017	0.003	0.029
4	4	0.000	1.000	0.000	0.013	0.004	0.029
5	5	0.000	1.000	0.000	0.011	0.005	0.029
6	6	0.000	1.000	0.000	0.011	0.006	0.029
7	7	0.000	1.000	0.001	0.010	0.007	0.029
8	8	0.000	1.000	0.001	0.010	0.011	0.030
9	9	0.000	1.000	0.001	0.008	0.012	0.029
10	10	0.000	1.000	0.001	0.008	0.014	0.029
11	11	0.057	0.010	0.001	0.008	0.015	0.029
12	12	0.050	0.986	0.054	0.007	0.017	0.029
13	13	0.043	0.985	0.048	0.007	0.020	0.029
14	14	0.037	0.889	0.039	0.006	0.023	0.030
15	15	0.067	0.689	0.067	0.007	0.026	0.031
16	16	0.065	0.638	0.065	0.007	0.027	0.030
17	17	0.076	0.925	0.080	0.008	0.034	0.032
18	18	0.074	0.819	0.075	0.008	0.035	0.032
19	19	0.088	0.057	0.067	0.008	0.040	0.032
20	20	0.080	0.921	0.086	0.008	0.043	0.031
21	21	0.112	0.071	0.098	0.009	0.055	0.033
22	22	0.104	0.965	0.111	0.010	0.059	0.034
23	23	0.102	0.569	0.103	0.010	0.060	0.033
24	24	0.113	0.700	0.115	0.010	0.062	0.032
25	25	0.154	0.902	0.161	0.013	0.074	0.033
26	26	0.175	0.098	0.164	0.012	0.075	0.032
27	27	0.262	0.021	0.214	0.013	0.091	0.035
28	28	0.257	0.128	0.256	0.012	0.096	0.035
29	29	0.259	0.121	0.254	0.012	0.099	0.034
30	30	0.271	0.614	0.271	0.013	0.101	0.033
31	31	0.252	0.738	0.254	0.013	0.108	0.031
32	32	0.248	0.676	0.250	0.014	0.110	0.030
33	33	0.264	0.083	0.245	0.015	0.137	0.036
34	34	0.293	0.028	0.261	0.015	0.142	0.034
35	35	0.292	0.175	0.289	0.018	0.145	0.032
36	36	0.594	0.012	0.399	0.027	0.238	0.049
37	37	0.587	0.833	0.590	0.021	0.244	0.046
38	38	0.549	0.181	0.543	0.020	0.264	0.046
39	39	0.557	0.622	0.556	0.022	0.275	0.042
40	40	0.550	0.750	0.553	0.024	0.280	0.039
41	41	0.445	1.000	0.531	0.024	0.390	0.042

Appendix 3k (continued)

42	42	0.449	0.190	0.448	0.015	0.406	0.039
43	43	0.475	0.200	0.458	0.016	0.421	0.036
44	44	0.510	1.000	0.529	0.029	0.507	0.033
45	45	0.809	0.166	0.730	0.038	0.823	0.021
46	46	0.832	1.000	0.854	0.017	0.844	0.018
47	47	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 31. Comtrel comparison of Vancouver Harbour and Port Moody Arm biomass-weighted abundance dendrogram (Tree 1) with environmental dendrogram (Tree 2). Linkages for the two trees are given, followed by Fowlkes- Mallows statistics, means and errors.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	V233	V236	V236	V245
2	V115	V122E	V136	V137B
3	V122D	V125D	V21	V11
4	V225E	V222E	V141	V141B
5	V122D	V125E	V222B	V122E
6	V233	V239E	V236	V145
7	V115	V122D	V237A	V240
8	V241B	V245	V236	V139A
9	V116	V122B	V239C	V241B
10	V233	V237B	V239C	V241A
11	V136	V137B	V215	V125E
12	V137A	V139E	V211	V116
13	V225E	V115	V137A	V139E
14	V13A	V125B	V236	V239A
15	V237A	V239C	V236	V239E
16	V241A	V241B	V237B	V246
17	V111	V116	V236	V237A
18	V225E	V111	V12	V13B
19	V139C	V140	V236	V139C
20	V240	V241A	V233	V137A
21	V225E	V119	V236	V239C
22	V12	V13A	V211	V119
23	V233	V237A	V140	V141
24	V240	V239A	V222B	V122D
25	V211	V215	V236	V237B
26	V12	V14A	V215	V115
27	V137A	V139C	V233	V136
28	V216	V136	V211	V222E
29	V216	V240	V13A	V125B
30	V225D	V222B	V215	V125D
31	V225E	V114	V233	V140
32	V139A	V141	V225D	V146
33	V216	V233	V14A	V122B
34	V12	V13B	V216	V222B
35	V225E	V1PE	V225E	V13A
36	V216	V137A	V233	V236
37	V211	V225E	V211	V111
38	V211	V216	V21	V233
39	V12	V139A	V211	V215
40	V211	V12	V14A	V114
41	V211	V225D	V211	V225E
42	V211	V246	V216	V225D
43	V141B	V145	V12	V14A

Appendix 31. (continued)

44	V211	V11	V21	V216
45	V21	V211	V21	V211
46	V21	V141B	V21	V1PE
47	V21	V146	V21	V12

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.000	0.029	0.000	0.029
2	2	0.000	1.000	0.000	0.019	0 001	0.029
3	3	0.000	1.000	0.000	0.017	0.002	0.029
4	4	0.000	1.000	0.000	0.015	0.003	0.029
5	5	0.000	1.000	0.001	0.014	0.004	0.029
6	6	0.000	1.000	0.001	0.012	0.006	0.029
7	7	0.000	1.000	0.001	0.010	0.009	0.029
8	8	0.000	1.000	0.001	0.008	0.011	0.030
9	9	0.000	1.000	0.001	0.008	0 012	0.029
10	10	0.000	1.000	0.001	0.008	0.014	0.029
11	11	0.057	0.008	0.001	0.008	0.015	0.029
12	12	0.054	0.713	0.054	0.007	0.016	0.029
13	13	0.087	0.998	0.103	0.007	0.020	0.029
14	14	0.077	0.702	0.077	0.006	0.022	0.030
15	15	0.102	0.647	0.102	0.007	0.025	0.031
16	16	0.130	0.030	0.099	0.007	0.027	0.030
17	17	0.105	0.826	0.106	0.008	0.033	0.032
18	18	0.083	0.997	0.102	0.008	0.042	0.035
19	19	0.075	0.632	0.076	0.006	0.047	0.037
20	20	0.089	0.073	0.074	0.006	0.049	0.035
21	21	0.134	0.981	0.144	0.010	0.066	0.042
22	22	0.143	0.806	0.145	0.010	0.067	0.040
23	23	0.184	0.021	0.141	0.010	0.072	0.039
24	24	0.236	0.013	0.192	0.012	0.074	0.037
25	25	0.248	0.558	0.248	0.015	0.085	0.039
26	26	0.252	0.758	0.254	0.016	0.087	0.038
27	27	0.240	0.779	0.243	0.016	0.092	0.036
28	28	0.253	0.657	0.254	0.016	0.094	0.035
29	29	0.243	0.957	0.259	0.017	0.101	0.034
30	30	0.256	0.555	0.256	0.016	0.103	0.033
31	31	0.246	0.928	0.256	0.017	0.115	0.032
32	32	0.244	0.485	0.244	0.017	0.115	0.032
33	33	0.381	0.008	0.242	0.018	0.137	0.034
34	34	0.379	0.161	0.373	0.016	0.140	0.032
35	35	0.364	0.868	0.372	0.018	0.145	0.032
36	36	0.584	0.012	0.425	0.028	0.221	0.042
37	37	0.588	0.575	0.584	0.028	0.234	0.039
38	38	0.389	1.000	0.540	0.030	0.359	0.055
39	39	0.421	0.933	0.428	0.014	0.374	0.048
40	40	0.430	0.166	0.426	0.010	0.447	0.042
41	41	0.448	1.000	0.468	0.010	0.488	0.033

Appendix 31. (continued)

42	42	0.472	0.238	0.456	0.009	0.506	0.029
43	43	0.480	0.666	0.485	0.009	0.510	0.027
44	44	0.577	0.400	0.567	0.014	0.616	0.026
45	45	0.809	0.500	0.802	0.016	0.823	0.021
46	46	0.876	0.333	0.854	0.017	0.880	0.011
47	47	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3m. Comtrel comparison of Vancouver Harbour and Port Moody Arm abundance dendrogram (Tree 1) with sediment chemistry dendrogram (Tree 2). Linkages for each tree are shown, followed by the Fowlkes-Mallows statistics, means and standard errors.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	V233	V236	V125D	V125E
2	V122E	V125E	V122D	V122E
3	V122E	V125D	V139C	V139E
4	V233	V239E	V241A	V141
5	V115	V122D	V240	V140
6	V11	V12	V239C	V239A
7	V225E	V222E	V241A	V241B
8	V115	V122E	V236	V239E
9	V21	V241B	V136	V137B
10	V233	V237B	V137A	V139C
11	V136	V137B	V111	V116
12	V115	V119	V225E	V115
13	V115	V122B	V211	V215
14	V21	V225D	V237A	V136
15	V237A	V137A	V246	V146
16	V240	V239A	V237B	V237A
17	V233	V239C	V225E	V222E
18	V216	V225E	V239C	V137A
19	V237A	V139E	V114	V119
20	V237A	V136	V236	V237B
21	V245	V139A	V211	V216
22	V111	V115	V240	V125B
23	V13B	V14A	V111	V1PE
24	V246	V245	V211	V114
25	V216	V240	V236	V239C
26	V241A	V139C	V245	V145
27	V233	V237A	V240	V241A
28	V111	V116	V21	V13A
29	V211	V216	V211	V225E
30	V11	V13A	V236	V125D
31	V21	V125B	V122B	V122D
32	V246	V141	V225D	V246
33	V211	V233	V240	V139A
34	V241A	V246	V21	V13B
35	V11	V13B	V225D	V236
36	V211	V241A	V222B	V122B
37	V111	V114	V211	V233
38	V141B	V145	V225D	V240
39	V21	V222B	V211	V111
40	V111	V1PE	V21	V14A
41	V211	V111	V225D	V245
42	V211	V215	V225D	V222B
43	V211	V140	V21	V12

Appendix 3m. (continued)

44	V21	V11	V225D	V141B
45	V21	V211	V211	V225D
46	V141B	V146	V21	V211
47	V21	V141B	V21	V11

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.000	0.029	0.000	0.029
2	2	0.000	1.000	0.000	0.021	0.001	0.029
3	3	0.288	0.002	0.000	0.016	0.003	0.029
4	4	0.204	0.956	0.221	0.013	0.004	0.029
5	5	0.169	0.911	0.167	0.012	0.005	0.029
6	6	0.144	0.864	0.143	0.011	0.006	0.029
7	7	0.117	0.817	0.117	0.010	0.007	0.029
8	8	0.258	0.008	0.208	0.011	0.010	0.029
9	9	0.237	0.807	0.235	0.010	0.011	0.029
10	10	0.198	0.940	0.208	0.009	0.013	0.029
11	11	0.248	0.011	0.184	0.009	0.014	0.029
12	12	0.213	0.988	0.230	0.009	0.016	0.029
13	13	0.185	0.987	0.200	0.008	0.019	0.028
14	14	0.168	0.879	0.170	0.007	0.020	0.028
15	15	0.161	0.680	0.160	0.007	0.021	0.028
16	16	0.147	0.630	0.146	0.007	0.024	0.029
17	17	0.166	0.921	0.172	0.008	0.026	0.028
18	18	0.145	0.812	0.146	0.007	0.030	0.029
19	19	0.167	0.029	0.140	0.007	0.031	0.029
20	20	0.231	0.012	0.194	0.010	0.038	0.029
21	21	0.223	0.589	0.221	0.011	0.039	0.029
22	22	0.204	0.957	0.213	0.011	0.043	0.029
23	23	0.197	0.520	0.196	0.011	0.044	0.029
24	24	0.182	0.666	0.182	0.011	0.048	0.029
25	25	0.261	0.891	0.269	0.016	0.064	0.031
26	26	0.257	0.494	0.255	0.015	0.065	0.030
27	27	0.428	0.004	0.240	0.015	0.080	0.032
28	28	0.419	0.752	0.418	0.013	0.084	0.032
29	29	0.436	0.021	0.410	0.013	0.093	0.031
30	30	0.393	0.614	0.390	0.010	0.103	0.031
31	31	0.409	0.104	0.399	0.011	0.106	0.030
32	32	0.401	0.632	0.399	0.012	0.108	0.030
33	33	0.381	0.891	0.392	0.013	0.136	0.033
34	34	0.383	0.104	0.374	0.011	0.141	0.032
35	35	0.344	0.197	0.342	0.010	0.162	0.033
36	36	0.378	0.025	0.339	0.012	0.201	0.037
37	37	0.390	0.181	0.386	0.010	0.208	0.035
38	38	0.477	0.527	0.476	0.017	0.263	0.042
39	39	0.473	0.688	0.475	0.019	0.277	0.038
40	40	0.485	0.166	0.476	0.019	0.283	0.035
41	41	0.515	0.178	0.501	0.021	0.403	0.042

Appendix 3m. (continued)

42	42	0.580	0.333	0.578	0.024	0.467	0.041
43	43	0.607	0.200	0.587	0.028	0.483	0.039
44	44	0.587	0.800	0.599	0.035	0.507	0.033
45	45	0.809	1.000	0.829	0.019	0.823	0.021
46	46	0.915	1.000	0.936	0.016	0.918	0.009
47	47	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes

Appendix 3n. Comtrel comparison of Vancouver Harbour and Port Moody Arm biomass-weighted abundance dendrogram (Tree 1) with sediment chemistry dendrogram (Tree 2). Linkages for both trees are given, followed by Fowlkes-Mallows statistics, means and standard errors.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	V233	V236	V125D	V125E
2	V115	V122E	V122D	V122E
3	V122D	V125D	V139C	V139E
4	V225E	V222E	V241A	V141
5	V122D	V125E	V240	V140
6	V233	V239E	V239C	V239A
7	V115	V122D	V241A	V241B
8	V241B	V245	V236	V239E
9	V116	V122B	V136	V137A
10	V233	V237B	V137A	V139C
11	V136	V137B	V111	V116
12	V137A	V139E	V225E	V115
13	V225E	V115	V211	V215
14	V13A	V125B	V237A	V136
15	V237A	V239C	V246	V146
16	V241A	V241B	V237B	V237A
17	V111	V116	V225E	V2225
18	V225E	V111	V239C	V137A
19	V139C	V140	V114	V119
20	V240	V241A	V236	V237B
21	V225E	V119	V211	V216
22	V12	V13A	V240	V125B
23	V233	V237A	V111	V1PE
24	V240	V239A	V211	V114
25	V211	V215	V236	V239C
26	V12	V14A	V245	V145
27	V137A	V139C	V240	V241A
28	V216	V136	V21	V13A
29	V216	V240	V211	V225E
30	V225D	V222B	V236	V125D
31	V225E	V114	V122B	V122D
32	V139A	V141	V225D	V246
33	V216	V233	V240	V139A
34	V12	V13B	V21	V13B
35	V225E	V1PE	V225D	V236
36	V216	V137A	V222B	V122
37	V211	V225E	V211	V233
38	V211	V216	V225D	V240
39	V12	V139A	V211	V111
40	V211	V12	V21	V14A
41	V211	V225D	V225D	V245
42	V211	V246	V225D	V222B
43	V141B	V145	V21	V12

Appendix 3n. (continued)

44	V211	V11	V225D	V141B
45	V21	V211	V211	V225D
46	V21	V141B	V21	V211
47	V21	V146	V21	V11

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.000	0.029	0.000	0.029
2	2	0.000	1.000	0.000	0.021	0.001	0.029
3	3	0.000	1.000	0.000	0.017	0.002	0.029
4	4	0.000	1.000	0.000	0.014	0.003	0.029
5	5	0.182	0.004	0.000	0.013	0.004	0.029
6	6	0.144	0.951	0.152	0.011	0.006	0.029
7	7	0.188	0.008	0.117	0.010	0.009	0.029
8	8	0.258	0.857	0.256	0.010	0.010	0.029
9	9	0.237	0.810	0.235	0.010	0.011	0.029
10	10	0.198	0.940	0.208	0.009	0.013	0.029
11	11	0.248	0.010	0.184	0.009	0.014	0.029
12	12	0.291	0.009	0.230	0.009	0.015	0.029
13	13	0.278	0.014	0.271	0.010	0.019	0.028
14	14	0.257	0.690	0.255	0.009	0.020	0.028
15	15	0.246	0.634	0.243	0.009	0.021	0.028
16	16	0.258	0.020	0.222	0.009	0.024	0.029
17	17	0.342	0.018	0.309	0.010	0.025	0.029
18	18	0.243	0.997	0.297	0.011	0.036	0.030
19	19	0.237	0.602	0.236	0.008	0.037	0.029
20	20	0.247	0.842	0.249	0.010	0.043	0.031
21	21	0.223	0.978	0.237	0.009	0.047	0.031
22	22	0.215	0.789	0.215	0.009	0.049	0.030
23	23	0.249	0.006	0.207	0.009	0.053	0.029
24	24	0.228	0.860	0.231	0.009	0.058	0.029
25	25	0.239	0.054	0.227	0.011	0.073	0.035
26	26	0.234	0.774	0.235	0.012	0.075	0.034
27	27	0.260	0.043	0.242	0.012	0.081	0.032
28	28	0.256	0.628	0.256	0.014	0.082	0.032
29	29	0.267	0.100	0.264	0.014	0.096	0.031
30	30	0.242	0.555	0.241	0.011	0.106	0.031
31	31	0.276	0.032	0.254	0.012	0.112	0.031
32	32	0.273	0.426	0.272	0.012	0.113	0.031
33	33	0.331	0.016	0.272	0.013	0.136	0.032
34	34	0.331	0.104	0.325	0.013	0.139	0.031
35	35	0.294	0.197	0.292	0.014	0.162	0.032
36	36	0.384	0.012	0.291	0.014	0.186	0.033
37	37	0.406	0.045	0.378	0.011	0.200	0.031
38	38	0.445	0.981	0.474	0.015	0.358	0.050
39	39	0.491	0.266	0.491	0.010	0.377	0.042
40	40	0.514	0.083	0.494	0.008	0.451	0.036
41	41	0.536	0.142	0.521	0.009	0.505	0.033

Appendix 3n. (continued)

42	42	0.639	0.142	0.615	0.010	0.582	0.030
43	43	0.640	0.800	0.641	0.010	0.585	0.029
44	44	0.609	1.000	0.628	0.017	0.616	0.026
45	45	0.809	1.000	0.832	0.019	0.823	0.021
46	46	0.957	0.333	0.936	0.016	0.958	0.006
47	47	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3o. Comtre2 comparison of Boundary Bay raw abundance (Tree 1) and biomass weighted abundance (Tree 2) dendrograms. Linkages for each tree are given, followed by the Fowlkes-Mallows statistics for each linkage, probability, mean and standard deviations for the Fowlkes-Mallows statistics.

Tree 1: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	BC5	BC6	0.35
2	BBO	BD2	0.39
3	BE8	BE9	0.42
4	BD4	BE1	0.43
5	BE7	BE8	0.46
6	BC5	BD4	0.48
7	BCM	BD3	0.53
8	BCM	BC5	0.62
9	BBNW	BBSE	0.69
10	BBO	BCM	0.73
11	BASR	BANR	0.73
12	BASR	BBNW	0.80
13	BASR	BBO	0.86
14	BASR	BE7	0.95

Tree 2: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	BE7	BE8	0.33
2	BE7	BE9	0.41
3	BC5	BD4	0.47
4	BC5	BE1	0.49
5	BANR	BBSE	0.55
6	BC5	BC6	0.56
7	BBO	BD2	0.59
8	BBO	BD3	0.66
9	BCM	BC5	0.72
10	BASR	BBNW	0.72
11	BASR	BANR	0.79
12	BBO	BCM	0.86
13	BASR	BBO	0.91
14	BASR	BE7	0.97

H0: Tree 1 and Tree 2 are generated by the same probability model.

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	Mean	Std.Dev.
1	1	0.000	0.900	0.100	0.303
2	2	0.000	0.500	0.256	0.290

Appendix 3o. (continued)

3	3	0.288	0.680	0.313	0.236
4	4	0.223	0.500	0.346	0.223
5	5	0.500	0.760	0.369	0.193
6	6	0.900	1.000	0.372	0.174
7	7	0.909	1.000	0.381	0.150
8	8	0.636	0.940	0.430	0.135
9	9	0.759	0.980	0.446	0.119
10	10	0.666	0.900	0.472	0.118
11	11	0.668	0.760	0.568	0.131
12	12	1.000	1.000	0.660	0.131
13	13	1.000	1.000	0.764	0.144
14	14	1.000	1.000	1.000	0.000

Appendix 3p. Comtrel comparison of Boundary Bay raw abundance dendrogram (Tree 1) with environmental dendrogram (Tree 2). Linkages for each tree are shown, followed by the Fowlkes-Mallows statistic, probability, means and standard deviations for each linkage.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	BE7	BE8	BC5	BD4
2	BE7	BE9	BBNW	BBSE
3	BC6	BD4	BC5	BD3
4	BC5	BE1	BC5	BC6
5	BANR	BBSE	BBNW	BD2
6	BC5	BC6	BC5	BE1
7	BBO	BD2	BBO	BC5
8	BBO	BD3	BBO	BCM
9	BCM	BC5	BASR	BBNW
10	BASR	BBNW	BASR	BBO
11	BASR	BANR	BE8	BE9
12	BBO	BCM	BASR	BANR
13	BASR	BBO	BE7	BE8
14	BASR	BE7	BASR	BE7

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.009	0.097	0.009	0.097
2	2	0.000	1.000	0.010	0.073	0.023	0.094
3	3	0.000	1.000	0.012	0.055	0.038	0.095
4	4	0.169	0.712	0.176	0.059	0.056	0.093
5	5	0.136	0.563	0.147	0.054	0.069	0.090
6	6	0.526	0.022	0.218	0.067	0.108	0.091
7	7	0.426	0.527	0.423	0.063	0.134	0.086
8	8	0.396	0.285	0.360	0.062	0.168	0.078
9	9	0.513	0.095	0.368	0.070	0.204	0.078
10	10	0.444	0.533	0.446	0.083	0.299	0.056
11	11	0.484	0.600	0.493	0.106	0.334	0.042
12	12	0.702	0.333	0.564	0.147	0.474	0.060
13	13	1.000	0.333	0.735	0.188	0.657	0.059
14	14	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3q. Comtrel comparison of Boundary Bay biomass weighted abundance dendrogram (Tree 1) with environmental dendrogram (Tree 2). Linkages for both trees are shown, followed by the Fowlkes-Mallows statistic, probability, means and standard deviations for each linkage.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	BC5	BC6	BC5	BD4
2	BBO	BD2	BBNW	BBSE
3	BE8	BE9	BC5	BD3
4	BD4	BE1	BC5	BC6
5	BE7	BE8	BBNW	BD2
6	BC5	BD4	BC5	BE1
7	BCM	BD3	BBO	BC5
8	BCM	BC5	BBO	BCM
9	BBNW	BBSE	BASR	BBNW
10	BBO	BCM	BASR	BBO
11	BASR	BANR	BE8	BE9
12	BASR	BBNW	BASR	BANR
13	BASR	BBO	BE7	BE8
14	BASR	BE7	BASR	BE7

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.009	0.097	0.009	0.097
2	2	0.000	1.000	0.009	0.066	0.019	0.096
3	3	0.000	1.000	0.013	0.059	0.032	0.093
4	4	0.188	0.575	0.194	0.066	0.050	0.089
5	5	0.136	0.909	0.158	0.057	0.069	0.090
6	6	0.526	0.022	0.218	0.067	0.108	0.091
7	7	0.426	0.555	0.422	0.055	0.134	0.086
8	8	0.702	0.035	0.410	0.070	0.203	0.097
9	9	0.688	0.190	0.628	0.055	0.221	0.086
10	10	0.691	0.133	0.521	0.087	0.399	0.098
11	11	0.697	0.400	0.698	0.090	0.409	0.087
12	12	0.702	0.500	0.676	0.117	0.474	0.060
13	13	1.000	0.333	0.735	0.188	0.657	0.059
14	14	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3r. Comtre2 comparison of Fjord raw abundance (Tree 1) and biomass-weighted abundance (Tree 2) dendrograms. Linkages for each tree are given, followed by the fowlkes-Mallows statistics for each linkage, probability, mean and standard deviations for the Fowlkes-Mallows statistics.

Tree 1: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	F118	F1205	0.34
2	F15A	F1143	0.43
3	F15A	F1203	0.44
4	F15C	F1201	0.50
5	F1145	F115	0.51
6	F15A	F113	0.55
7	F15A	F1145	0.61
8	F15A	F15C	0.67
9	F15A	F118	0.70
10	F19	F110	0.73
11	F15A	F19	0.78
12	F15A	F1141	0.80
13	F15A	F15D	0.90
14	F15A	F15B	0.95

Tree 2: Cluster Analysis

Linkage	Clusters Linked		Linkage Level
1	F118	F1205	0.43
2	F1201	F1203	0.56
3	F1143	F1145	0.57
4	F113	F1201	0.62
5	F1143	F115	0.64
6	F110	F113	0.66
7	F110	F1143	0.68
8	F15A	F110	0.73
9	F15A	F15C	0.77
10	F1141	F118	0.81
11	F15B	F15D	0.84
12	F15A	F19	0.86
13	F15A	F1141	0.88
14	F15A	F15B	0.93

H0: Tree 1 and Tree 2 are generated by the same probability model.

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	Mean	Std.Dev.
1	1	1.000	1.000	0.100	0.303
2	2	0.500	1.000	0.108	0.206

Appendix 3r. (continued)

3	3	0.288	0.760	0.127	0.182
4	4	0.200	0.700	0.146	0.198
5	5	0.308	0.820	0.217	0.180
6	6	0.316	0.800	0.236	0.134
7	7	0.568	0.920	0.276	0.169
8	8	0.758	0.980	0.323	0.140
9	9	0.710	1.000	0.361	0.125
10	10	0.684	0.960	0.438	0.148
11	11	0.720	0.940	0.506	0.133
12	12	0.776	0.980	0.544	0.111
13	13	0.919	1.000	0.589	0.097
14	14	1.000	1.000	1.000	0.000

Appendix 3s. Comtrel comparison of fjord raw abundance dendrogram (Tree 1) with environmental dendrogram (Tree 2). Linkages for each tree are given, followed by the Fowlkes-Mallows statistic, means and standard deviations for each linkage.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	F118	F1205	F15D	F1145
2	F1201	F1203	F15D	F115
3	F1143	F1145	F118	F1201
4	F113	F1201	F15B	F15D
5	F1143	F115	F15C	F110
6	F110	F113	F118	F1203
7	F110	F1143	F15C	F19
8	F15A	F110	F15B	F1205
9	F15A	F15C	F1141	F1143
10	F1141	F118	F15B	F15C
11	F15B	F15D	F15A	F1141
12	F15A	F19	F15B	F118
13	F15A	F1141	F15A	F15B
14	F15A	F15B	F15A	F113

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.009	0.097	0.009	0.097
2	2	0.000	1.000	0.013	0.072	0.023	0.094
3	3	0.000	1.000	0.013	0.059	0.032	0.093
4	4	0.000	1.000	0.018	0.053	0.056	0.093
5	5	0.133	0.127	0.019	0.048	0.071	0.091
6	6	0.200	0.955	0.228	0.050	0.095	0.090
7	7	0.123	1.000	0.185	0.045	0.154	0.085
8	8	0.092	1.000	0.123	0.036	0.205	0.087
9	9	0.119	0.476	0.113	0.033	0.238	0.075
10	10	0.198	1.000	0.236	0.036	0.336	0.096
11	11	0.244	0.700	0.267	0.034	0.351	0.083
12	12	0.450	0.500	0.452	0.047	0.507	0.079
13	13	0.790	0.333	0.724	0.057	0.807	0.044
14	14	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3t. Comtrel comparison of fjord biomass-weighted abundance dendrogram (Tree 1) with environmental dendrogram (Tree 2). Linkages for both trees are given, followed by the Fowlkes-Mallows statistics, means and standard deviations for each linkage.

	TREE 1 Linkages		TREE 2 Linkages	
Linkage (i)	A(i)	B(i)	A(i)	B(i)
1	F118	F1205	F15D	F1145
2	F15A	F1143	F15D	F115
3	F15A	F1203	F118	F1201
4	F15C	F1201	F15B	F15D
5	F1145	F115	F15C	F110
6	F15A	F113	F118	F1203
7	F15A	F1145	F15C	F19
8	F15A	F15C	F15B	F1205
9	F15A	F118	F1141	F1143
10	F19	F110	F15B	F15C
11	F15A	F19	F15A	F1141
12	F15A	F1141	F15B	F118
13	F15A	F15D	F15A	F15B
14	F15A	F15B	F15A	F113

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.009	0.097	0.009	0.097
2	2	0.000	1.000	0.013	0.072	0.023	0.094
3	3	0.000	1.000	0.014	0.061	0.038	0.095
4	4	0.000	1.000	0.017	0.051	0.056	0.093
5	5	0.144	0.109	0.020	0.049	0.065	0.090
6	6	0.105	0.933	0.132	0.053	0.090	0.090
7	7	0.070	1.000	0.110	0.048	0.136	0.086
8	8	0.092	0.392	0.084	0.037	0.205	0.087
9	9	0.216	0.047	0.113	0.033	0.263	0.071
10	10	0.260	0.666	0.265	0.028	0.365	0.100
11	11	0.401	0.100	0.315	0.038	0.451	0.077
12	12	0.579	1.000	0.624	0.043	0.640	0.070
13	13	0.857	0.666	0.834	0.031	0.866	0.035
14	14	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3u. Comtre2 comparison of ABUNBASE and BIOBASE. Options used are shown followed by linkages compared, Fowlkes-Mallows statistics, probabilities means and standard deviations.

H0: Tree 1 and Tree 2 are generated by the same probability model.

Fowlkes-Mallows Statistic

L1	L2	FM(L1,L2)	PROB	Mean	Std.Dev.
1	1	0.000	0.970	0.030	0.170
2	2	0.000	0.900	0.050	0.160
3	3	0.000	0.780	0.070	0.140
4	4	0.000	0.670	0.090	0.130
5	5	0.000	0.570	0.100	0.120
6	6	0.150	0.750	0.100	0.110
7	7	0.270	0.940	0.110	0.100
8	8	0.180	0.750	0.110	0.100
9	9	0.160	0.690	0.120	0.100
10	10	0.140	0.620	0.120	0.090
11	11	0.130	0.560	0.120	0.080
12	12	0.110	0.480	0.120	0.080
13	13	0.160	0.740	0.130	0.080
14	14	0.150	0.660	0.130	0.080
15	15	0.130	0.600	0.130	0.080
16	16	0.200	0.780	0.140	0.080
17	17	0.190	0.760	0.140	0.080
18	18	0.180	0.720	0.140	0.080
19	19	0.180	0.690	0.150	0.070
20	20	0.170	0.670	0.150	0.070
21	21	0.200	0.750	0.150	0.070
22	22	0.250	0.890	0.160	0.070
23	23	0.230	0.860	0.160	0.070
24	24	0.230	0.830	0.160	0.070
25	25	0.220	0.800	0.160	0.070
26	26	0.260	0.920	0.170	0.070
27	27	0.280	0.940	0.170	0.070
28	28	0.320	0.980	0.170	0.060
29	29	0.310	0.980	0.180	0.060
30	30	0.300	0.970	0.180	0.060
31	31	0.320	0.970	0.180	0.060
32	32	0.300	0.960	0.180	0.060
33	33	0.300	0.950	0.190	0.060
34	34	0.310	0.970	0.190	0.060
35	35	0.320	0.980	0.190	0.060
36	36	0.320	0.970	0.190	0.060
37	37	0.390	0.000	0.200	0.060
38	38	0.430	0.000	0.200	0.060
39	39	0.420	0.000	0.200	0.060
40	40	0.420	0.000	0.210	0.060
41	41	0.410	0.990	0.210	0.060
42	42	0.420	0.990	0.210	0.060

Appendix 3u (continued)

43	43	0.430	0.000	0.210	0.060
44	44	0.460	0.000	0.210	0.060
45	45	0.480	0.000	0.220	0.060
46	46	0.500	0.000	0.220	0.060
47	47	0.510	0.000	0.220	0.060
48	48	0.510	0.000	0.220	0.060
49	49	0.500	0.000	0.220	0.060
50	50	0.490	0.000	0.220	0.060
51	51	0.490	0.000	0.230	0.060
52	52	0.480	0.000	0.230	0.060
53	53	0.480	0.000	0.230	0.060
54	54	0.470	0.000	0.230	0.060
55	55	0.470	0.000	0.230	0.060
56	56	0.460	0.000	0.230	0.060
57	57	0.460	0.000	0.230	0.060
58	58	0.460	0.000	0.240	0.060
59	59	0.450	0.000	0.240	0.060
60	60	0.450	0.000	0.240	0.060
61	61	0.450	0.000	0.240	0.060
62	62	0.450	0.000	0.240	0.050
63	63	0.430	0.000	0.240	0.050
64	64	0.420	0.000	0.250	0.050
65	65	0.420	0.000	0.250	0.050
66	66	0.460	0.000	0.250	0.050
67	67	0.460	0.000	0.250	0.050
68	68	0.470	0.000	0.250	0.050
69	69	0.470	0.000	0.260	0.050
70	70	0.510	0.000	0.260	0.050
71	71	0.510	0.000	0.260	0.050
72	72	0.520	0.000	0.260	0.050
73	73	0.510	0.000	0.260	0.050
74	74	0.510	0.000	0.270	0.050
75	75	0.510	0.000	0.270	0.050
76	76	0.500	0.000	0.270	0.050
77	77	0.510	0.000	0.270	0.050
78	78	0.510	0.000	0.280	0.050
79	79	0.490	0.000	0.280	0.050
80	80	0.490	0.000	0.280	0.050
81	81	0.490	0.000	0.280	0.050
82	82	0.480	0.000	0.290	0.050
83	83	0.480	0.000	0.290	0.050
84	84	0.490	0.000	0.290	0.050
85	85	0.490	0.000	0.290	0.050
86	86	0.500	0.000	0.290	0.050
87	87	0.500	0.000	0.300	0.050
88	88	0.530	0.000	0.300	0.050
89	89	0.510	0.000	0.300	0.050
90	90	0.520	0.000	0.300	0.050
91	91	0.510	0.000	0.310	0.050
92	92	0.500	0.000	0.310	0.050

Appendix 3u (continued)

93	93	0.500	0.000	0.310	0.050
94	94	0.490	0.000	0.310	0.050
95	95	0.500	0.000	0.310	0.050
96	96	0.520	0.000	0.320	0.050
97	97	0.510	0.000	0.320	0.040
98	98	0.510	0.000	0.320	0.050
99	99	0.500	0.000	0.320	0.050
100	100	0.510	0.000	0.330	0.050
101	101	0.520	0.000	0.330	0.050
102	102	0.520	0.000	0.330	0.050
103	103	0.520	0.000	0.330	0.050
104	104	0.510	0.000	0.340	0.050
105	105	0.450	0.990	0.340	0.050
106	106	0.480	0.000	0.340	0.050
107	107	0.480	0.000	0.340	0.050
108	108	0.510	0.000	0.350	0.050
109	109	0.520	0.000	0.350	0.050
110	110	0.530	0.000	0.350	0.050
111	111	0.540	0.000	0.350	0.050
112	112	0.540	0.000	0.360	0.050
113	113	0.520	0.000	0.360	0.050
114	114	0.510	0.000	0.360	0.050
115	115	0.510	0.990	0.360	0.040
116	116	0.600	0.000	0.360	0.040
117	117	0.600	0.000	0.370	0.040
118	118	0.630	0.000	0.370	0.050
119	119	0.620	0.000	0.370	0.050
120	120	0.630	0.000	0.370	0.050
121	121	0.630	0.000	0.370	0.050
122	122	0.630	0.000	0.380	0.050
123	123	0.580	0.000	0.380	0.050
124	124	0.580	0.000	0.380	0.050
125	125	0.570	0.000	0.390	0.050
126	126	0.520	0.980	0.390	0.050
127	127	0.520	0.980	0.390	0.050
128	128	0.510	0.960	0.400	0.050
129	129	0.510	0.960	0.400	0.050
130	130	0.510	0.940	0.410	0.050
131	131	0.520	0.950	0.410	0.050
132	132	0.520	0.950	0.410	0.050
133	133	0.510	0.940	0.420	0.060
134	134	0.500	0.910	0.420	0.050
135	135	0.480	0.840	0.430	0.060
136	136	0.490	0.840	0.430	0.060
137	137	0.490	0.830	0.440	0.050
138	138	0.500	0.860	0.440	0.050
139	139	0.490	0.800	0.440	0.050
140	140	0.500	0.870	0.440	0.050
141	141	0.520	0.920	0.450	0.050
142	142	0.530	0.940	0.450	0.050

Appendix 3u (continued)

143	143	0.500	0.840	0.450	0.050
144	144	0.520	0.910	0.450	0.050
145	145	0.540	0.960	0.460	0.050
146	146	0.530	0.910	0.460	0.050
147	147	0.520	0.900	0.460	0.050
148	148	0.490	0.670	0.470	0.050
149	149	0.490	0.640	0.470	0.050
150	150	0.490	0.650	0.470	0.050
151	151	0.510	0.810	0.480	0.050
152	152	0.510	0.780	0.480	0.050
153	153	0.510	0.740	0.480	0.050
154	154	0.510	0.730	0.480	0.050
155	155	0.570	0.960	0.480	0.050
156	156	0.590	0.980	0.480	0.050
157	157	0.580	0.970	0.480	0.050
158	158	0.580	0.970	0.490	0.050
159	159	0.590	0.980	0.490	0.050
160	160	0.720	0.000	0.490	0.050
161	161	0.690	0.000	0.490	0.050
162	162	0.690	0.000	0.500	0.050
163	163	0.770	0.000	0.500	0.050
164	164	0.680	0.000	0.510	0.050
165	165	0.750	0.000	0.510	0.050
166	166	0.730	0.000	0.520	0.050
167	167	0.830	0.000	0.520	0.050
168	168	0.830	0.000	0.520	0.050
169	169	0.760	0.000	0.530	0.050
170	170	0.760	0.000	0.530	0.050
171	171	0.770	0.000	0.530	0.050
172	172	0.740	0.000	0.530	0.050
173	173	0.730	0.000	0.520	0.050
174	174	0.770	0.000	0.510	0.060
175	175	0.750	0.000	0.500	0.060
176	176	0.800	0.000	0.490	0.070
177	177	0.800	0.000	0.470	0.070
178	178	0.640	0.990	0.460	0.080
179	179	0.640	0.980	0.470	0.080
180	180	0.650	0.980	0.500	0.090
181	181	0.510	0.390	0.540	0.080
182	182	0.520	0.210	0.570	0.070
183	183	0.660	0.900	0.600	0.060
184	184	0.660	0.860	0.620	0.050
185	185	0.650	0.660	0.630	0.060
186	186	0.890	0.980	0.670	0.080
187	187	0.890	0.860	0.760	0.110
188	188	0.940	0.490	0.890	0.110
189	189	0.990	0.700	0.980	0.050
190	190	1.000	0.000	0.000	0.000

Appendix 3v. Comtrel comparison of ABUNBASE with ENVIROBASE. Fowlkes-Mallows statistics are shown, followed by probabilities, means and standard deviations for each linkage.

		Fowlkes-Mallows Statistic					
L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.000	0.007	0.000	0.007
2	2	0.000	1.000	0.000	0.005	0.000	0.007
3	3	0.000	1.000	0.000	0.004	0.000	0.007
4	4	0.000	1.000	0.000	0.003	0.000	0.007
5	5	0.000	1.000	0.000	0.003	0.000	0.007
6	6	0.000	1.000	0.000	0.003	0.000	0.007
7	7	0.000	1.000	0.000	0.002	0.000	0.007
8	8	0.000	1.000	0.000	0.002	0.000	0.007
9	9	0.000	1.000	0.000	0.002	0.000	0.007
10	10	0.000	1.000	0.000	0.002	0.000	0.007
11	11	0.073	0.892	0.072	0.002	0.000	0.007
12	12	0.068	0.881	0.067	0.002	0.000	0.007
13	13	0.062	0.870	0.061	0.002	0.000	0.007
14	14	0.053	0.859	0.053	0.001	0.001	0.007
15	15	0.092	0.001	0.050	0.001	0.001	0.007
16	16	0.120	0.001	0.086	0.002	0.001	0.007
17	17	0.116	0.867	0.115	0.000	0.001	0.007
18	18	0.103	0.998	0.109	0.002	0.001	0.007
19	19	0.098	0.855	0.098	0.002	0.001	0.007
20	20	0.125	0.972	0.126	0.000	0.001	0.007
21	21	0.119	0.961	0.121	0.000	0.001	0.007
22	22	0.116	0.841	0.115	0.001	0.001	0.007
23	23	0.112	0.830	0.112	0.001	0.001	0.007
24	24	0.097	0.999	0.109	0.000	0.002	0.007
25	25	0.094	0.948	0.095	0.002	0.002	0.007
26	26	0.079	0.999	0.089	0.000	0.002	0.007
27	27	0.078	0.837	0.077	0.001	0.002	0.007
28	28	0.107	0.987	0.113	0.000	0.003	0.007
29	29	0.104	0.835	0.104	0.000	0.003	0.007
30	30	0.102	0.935	0.102	0.001	0.003	0.007
31	31	0.100	0.822	0.100	0.000	0.003	0.007
32	32	0.097	0.810	0.097	0.001	0.003	0.007
33	33	0.091	0.797	0.091	0.001	0.003	0.007
34	34	0.105	0.003	0.090	0.000	0.003	0.007
35	35	0.118	0.772	0.118	0.001	0.003	0.007
36	36	0.116	0.917	0.116	0.000	0.003	0.007
37	37	0.110	0.968	0.112	0.001	0.003	0.007
38	38	0.133	0.951	0.134	0.000	0.004	0.007
39	39	0.131	0.767	0.131	0.001	0.004	0.007
40	40	0.124	0.996	0.129	0.001	0.004	0.007
41	41	0.121	0.891	0.121	0.001	0.004	0.007
42	42	0.114	0.936	0.115	0.001	0.004	0.007
43	43	0.113	0.750	0.113	0.001	0.004	0.007
44	44	0.111	0.736	0.111	0.000	0.004	0.007
45	45	0.112	0.006	0.110	0.000	0.005	0.007

Appendix 3v. (continued)

46	46	0.111	0.734	0.111	0.001	0.005	0.007
47	47	0.107	0.720	0.107	0.000	0.005	0.007
48	48	0.120	0.882	0.120	0.001	0.005	0.007
49	49	0.153	0.705	0.153	0.001	0.006	0.007
50	50	0.148	0.691	0.148	0.000	0.006	0.007
51	51	0.147	0.678	0.146	0.002	0.006	0.007
52	52	0.139	0.957	0.140	0.002	0.006	0.007
53	53	0.136	0.861	0.137	0.001	0.006	0.007
54	54	0.140	0.007	0.132	0.000	0.007	0.007
55	55	0.139	0.646	0.138	0.001	0.007	0.007
56	56	0.137	0.842	0.137	0.002	0.007	0.007
57	57	0.136	0.829	0.136	0.001	0.007	0.007
58	58	0.175	0.816	0.176	0.000	0.007	0.007
59	59	0.174	0.626	0.174	0.002	0.007	0.007
60	60	0.180	0.800	0.180	0.000	0.007	0.007
61	61	0.185	0.009	0.178	0.003	0.007	0.007
62	62	0.173	0.996	0.183	0.000	0.008	0.007
63	63	0.170	0.617	0.169	0.000	0.008	0.007
64	64	0.179	0.001	0.167	0.000	0.008	0.007
65	65	0.178	0.612	0.178	0.003	0.008	0.007
66	66	0.176	0.597	0.176	0.002	0.008	0.007
67	67	0.173	0.932	0.175	0.001	0.008	0.007
68	68	0.171	0.750	0.171	0.002	0.008	0.007
69	69	0.175	0.577	0.174	0.001	0.009	0.007
70	70	0.173	0.561	0.173	0.001	0.009	0.007
71	71	0.172	0.546	0.172	0.000	0.009	0.007
72	72	0.189	0.014	0.183	0.002	0.009	0.007
73	73	0.203	0.528	0.202	0.002	0.010	0.007
74	74	0.200	0.836	0.201	0.001	0.010	0.007
75	75	0.203	0.009	0.197	0.001	0.010	0.007
76	76	0.198	0.817	0.198	0.002	0.010	0.007
77	77	0.196	0.707	0.196	0.002	0.010	0.007
78	78	0.200	0.015	0.195	0.002	0.010	0.007
79	79	0.202	0.010	0.196	0.001	0.010	0.007
80	80	0.199	0.469	0.198	0.001	0.011	0.007
81	81	0.193	0.774	0.193	0.000	0.011	0.007
82	82	0.226	0.000	0.191	0.002	0.011	0.007
83	83	0.225	0.458	0.224	0.003	0.011	0.007
84	84	0.222	0.869	0.222	0.003	0.011	0.007
85	85	0.225	0.440	0.224	0.001	0.013	0.007
86	86	0.226	0.020	0.223	0.001	0.013	0.007
87	87	0.224	0.673	0.224	0.002	0.013	0.007
88	88	0.221	0.898	0.223	0.002	0.013	0.007
89	89	0.227	0.423	0.226	0.003	0.014	0.007
90	90	0.223	0.648	0.223	0.002	0.014	0.007
91	91	0.226	0.404	0.225	0.002	0.014	0.007
92	92	0.227	0.021	0.223	0.002	0.014	0.007
93	93	0.233	0.005	0.225	0.002	0.014	0.007
94	94	0.231	0.596	0.231	0.001	0.014	0.007
95	95	0.233	0.015	0.228	0.002	0.014	0.007

Appendix 3v. (continued)

96	96	0.235	0.572	0.235	0.002	0.014	0.007
97	97	0.247	0.001	0.232	0.002	0.015	0.007
98	98	0.243	0.551	0.242	0.002	0.015	0.007
99	99	0.254	0.004	0.243	0.002	0.015	0.007
100	100	0.253	0.336	0.252	0.003	0.015	0.007
101	101	0.251	0.523	0.250	0.003	0.015	0.007
102	102	0.249	0.661	0.248	0.003	0.016	0.007
103	103	0.246	0.310	0.245	0.003	0.016	0.007
104	104	0.248	0.027	0.245	0.002	0.016	0.007
105	105	0.244	0.721	0.244	0.003	0.017	0.007
106	106	0.249	0.027	0.245	0.003	0.017	0.007
107	107	0.253	0.290	0.251	0.003	0.017	0.007
108	108	0.289	0.880	0.292	0.003	0.019	0.007
109	109	0.293	0.011	0.287	0.003	0.019	0.007
110	110	0.289	0.867	0.291	0.003	0.020	0.007
111	111	0.293	0.008	0.284	0.003	0.020	0.007
112	112	0.292	0.263	0.290	0.004	0.020	0.007
113	113	0.310	0.005	0.299	0.003	0.020	0.007
114	114	0.317	0.824	0.319	0.003	0.020	0.007
115	115	0.305	0.972	0.315	0.003	0.021	0.007
116	116	0.270	0.998	0.302	0.003	0.025	0.008
117	117	0.280	0.004	0.269	0.003	0.025	0.008
118	118	0.273	0.913	0.274	0.003	0.026	0.007
119	119	0.275	0.272	0.274	0.003	0.026	0.007
120	120	0.280	0.007	0.272	0.003	0.027	0.007
121	121	0.279	0.551	0.279	0.003	0.027	0.007
122	122	0.279	0.257	0.278	0.003	0.027	0.007
123	123	0.275	0.909	0.278	0.003	0.028	0.007
124	124	0.274	0.665	0.273	0.003	0.028	0.007
125	125	0.273	0.443	0.272	0.003	0.028	0.007
126	126	0.278	0.010	0.271	0.003	0.028	0.007
127	127	0.279	0.010	0.271	0.003	0.030	0.007
128	128	0.275	0.852	0.277	0.004	0.030	0.007
129	129	0.281	0.009	0.273	0.004	0.030	0.007
130	130	0.281	0.021	0.278	0.004	0.030	0.007
131	131	0.280	0.448	0.279	0.004	0.031	0.007
132	132	0.280	0.244	0.278	0.004	0.031	0.007
133	133	0.281	0.016	0.277	0.004	0.031	0.007
134	134	0.279	0.229	0.277	0.004	0.031	0.007
135	135	0.281	0.356	0.279	0.004	0.033	0.007
136	136	0.281	0.042	0.278	0.004	0.033	0.007
137	137	0.295	0.007	0.278	0.004	0.034	0.007
138	138	0.320	0.002	0.292	0.004	0.035	0.007
139	139	0.289	0.216	0.287	0.005	0.039	0.008
140	140	0.290	0.196	0.288	0.005	0.039	0.008
141	141	0.285	0.801	0.287	0.005	0.042	0.008
142	142	0.298	0.006	0.277	0.004	0.043	0.008
143	143	0.309	0.021	0.305	0.005	0.044	0.008
144	144	0.303	0.868	0.305	0.005	0.045	0.008
145	145	0.301	0.698	0.301	0.005	0.045	0.008

Appendix 3v. (continued)

146	146	0.298	0.504	0.296	0.005	0.046	0.008
147	147	0.328	0.318	0.326	0.006	0.050	0.007
148	148	0.362	0.547	0.360	0.006	0.053	0.008
149	149	0.365	0.190	0.362	0.007	0.053	0.007
150	150	0.365	0.033	0.360	0.007	0.053	0.007
151	151	0.368	0.028	0.363	0.007	0.053	0.007
152	152	0.368	0.035	0.363	0.007	0.054	0.007
153	153	0.397	0.005	0.365	0.007	0.055	0.007
154	154	0.397	0.254	0.393	0.008	0.055	0.007
155	155	0.404	0.382	0.400	0.008	0.059	0.007
156	156	0.405	0.074	0.400	0.008	0.059	0.007
157	157	0.403	0.206	0.399	0.008	0.060	0.007
158	158	0.394	0.828	0.398	0.009	0.070	0.009
159	159	0.429	0.003	0.389	0.008	0.073	0.008
160	160	0.428	0.397	0.425	0.009	0.074	0.008
161	161	0.473	0.030	0.468	0.010	0.078	0.009
162	162	0.475	0.266	0.471	0.010	0.079	0.008
163	163	0.491	0.007	0.472	0.010	0.082	0.008
164	164	0.483	0.039	0.475	0.011	0.089	0.009
165	165	0.559	0.008	0.533	0.012	0.099	0.009
166	166	0.549	0.036	0.540	0.013	0.102	0.009
167	167	0.548	0.100	0.542	0.014	0.102	0.009
168	168	0.552	0.036	0.541	0.015	0.104	0.008
169	169	0.553	0.632	0.550	0.016	0.107	0.008
170	170	0.552	0.069	0.544	0.016	0.108	0.008
171	171	0.551	0.252	0.543	0.017	0.108	0.008
172	172	0.536	0.794	0.542	0.017	0.111	0.008
173	173	0.530	0.508	0.524	0.018	0.113	0.008
174	174	0.484	0.346	0.478	0.019	0.127	0.008
175	175	0.496	0.058	0.477	0.020	0.129	0.008
176	176	0.513	0.158	0.504	0.023	0.139	0.008
177	177	0.515	0.171	0.503	0.024	0.146	0.008
178	178	0.500	0.670	0.504	0.026	0.151	0.007
179	179	0.558	0.051	0.491	0.028	0.161	0.007
180	180	0.576	0.075	0.543	0.033	0.170	0.007
181	181	0.639	0.036	0.564	0.035	0.199	0.009
182	182	0.644	0.066	0.607	0.036	0.209	0.008
183	183	0.730	0.222	0.705	0.044	0.229	0.008
184	184	0.566	0.250	0.557	0.050	0.307	0.012
185	185	0.579	0.238	0.562	0.058	0.312	0.012
186	186	0.599	0.266	0.565	0.066	0.342	0.009
187	187	0.539	0.400	0.531	0.046	0.509	0.009
188	188	0.557	1.000	0.622	0.064	0.551	0.005
189	189	0.672	1.000	0.726	0.041	0.675	0.001
190	190	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 3w. Comtrel comparison of BIOBASE with ENVIROBASE. Fowlkes-Mallows statistics are shown, followed by probabilities, means and standard errors for each linkage.

		Fowlkes-Mallows Statistic					
L1	L2	FM(L1,L2)	PROB	M1	S1	M2	S2
1	1	0.000	1.000	0.000	0.007	0.000	0.007
2	2	0.000	1.000	0.000	0.005	0.000	0.007
3	3	0.000	1.000	0.000	0.004	0.000	0.007
4	4	0.000	1.000	0.000	0.003	0.000	0.007
5	5	0.000	1.000	0.000	0.003	0.000	0.007
6	6	0.000	1.000	0.000	0.003	0.000	0.007
7	7	0.000	1.000	0.000	0.002	0.000	0.007
8	8	0.000	1.000	0.000	0.002	0.000	0.007
9	9	0.000	1.000	0.000	0.002	0.000	0.007
10	10	0.000	1.000	0.000	0.002	0.000	0.007
11	11	0.000	1.000	0.000	0.002	0.000	0.007
12	12	0.000	1.000	0.000	0.002	0.000	0.007
13	13	0.000	1.000	0.000	0.002	0.000	0.007
14	14	0.000	1.000	0.000	0.002	0.000	0.007
15	15	0.000	1.000	0.000	0.002	0.000	0.007
16	16	0.000	1.000	0.000	0.001	0.001	0.007
17	17	0.000	1.000	0.000	0.001	0.001	0.007
18	18	0.000	1.000	0.000	0.001	0.001	0.007
19	19	0.000	1.000	0.000	0.001	0.001	0.007
20	20	0.000	1.000	0.000	0.001	0.001	0.007
21	21	0.000	1.000	0.000	0.001	0.001	0.007
22	22	0.000	1.000	0.000	0.001	0.001	0.007
23	23	0.000	1.000	0.000	0.001	0.001	0.007
24	24	0.000	1.000	0.000	0.001	0.002	0.007
25	25	0.025	0.948	0.025	0.001	0.002	0.007
26	26	0.042	0.999	0.047	0.001	0.002	0.007
27	27	0.041	0.837	0.040	0.001	0.002	0.007
28	28	0.056	0.002	0.039	0.001	0.002	0.007
29	29	0.073	0.835	0.073	0.000	0.002	0.007
30	30	0.071	0.935	0.072	0.001	0.003	0.007
31	31	0.070	0.829	0.070	0.001	0.003	0.007
32	32	0.069	0.810	0.069	0.001	0.003	0.007
33	33	0.085	0.797	0.084	0.001	0.003	0.007
34	34	0.083	0.785	0.083	0.000	0.003	0.007
35	35	0.074	0.772	0.074	0.001	0.003	0.007
36	36	0.072	0.917	0.072	0.001	0.003	0.007
37	37	0.067	0.968	0.068	0.001	0.004	0.007
38	38	0.065	0.951	0.066	0.000	0.004	0.007
39	39	0.064	0.767	0.064	0.001	0.004	0.007
40	40	0.060	0.996	0.063	0.000	0.004	0.007
41	41	0.071	0.891	0.072	0.000	0.004	0.007
42	42	0.082	0.004	0.070	0.001	0.004	0.007
43	43	0.081	0.750	0.080	0.001	0.004	0.007
44	44	0.080	0.737	0.080	0.000	0.004	0.007
45	45	0.121	0.000	0.076	0.000	0.005	0.007

Appendix 3w. (continued)

46	46	0.119	0.734	0.119	0.000	0.005	0.007
47	47	0.117	0.720	0.117	0.001	0.005	0.007
48	48	0.115	0.882	0.115	0.001	0.005	0.007
49	49	0.150	0.705	0.149	0.000	0.005	0.007
50	50	0.163	0.691	0.162	0.003	0.006	0.007
51	51	0.169	0.678	0.169	0.000	0.006	0.007
52	52	0.163	0.958	0.165	0.000	0.006	0.007
53	53	0.161	0.861	0.161	0.000	0.006	0.007
54	54	0.167	0.660	0.167	0.002	0.006	0.007
55	55	0.190	0.005	0.181	0.001	0.006	0.007
56	56	0.188	0.843	0.188	0.002	0.006	0.007
57	57	0.185	0.830	0.185	0.000	0.006	0.007
58	58	0.183	0.816	0.183	0.002	0.006	0.007
59	59	0.181	0.626	0.181	0.000	0.006	0.007
60	60	0.185	0.800	0.185	0.002	0.007	0.007
61	61	0.198	0.000	0.183	0.002	0.007	0.007
62	62	0.192	0.008	0.189	0.001	0.008	0.007
63	63	0.190	0.616	0.189	0.002	0.008	0.007
64	64	0.200	0.000	0.188	0.000	0.008	0.007
65	65	0.199	0.611	0.198	0.003	0.008	0.007
66	66	0.233	0.595	0.232	0.001	0.008	0.007
67	67	0.229	0.932	0.230	0.000	0.008	0.007
68	68	0.226	0.749	0.226	0.003	0.008	0.007
69	69	0.222	0.575	0.221	0.000	0.008	0.007
70	70	0.244	0.560	0.243	0.002	0.009	0.007
71	71	0.238	0.544	0.238	0.000	0.009	0.007
72	72	0.242	0.855	0.242	0.001	0.009	0.007
73	73	0.240	0.526	0.239	0.000	0.009	0.007
74	74	0.238	0.836	0.238	0.002	0.009	0.007
75	75	0.242	0.007	0.235	0.001	0.009	0.007
76	76	0.239	0.817	0.239	0.000	0.009	0.007
77	77	0.233	0.707	0.233	0.000	0.010	0.007
78	78	0.235	0.010	0.230	0.001	0.010	0.007
79	79	0.239	0.007	0.233	0.002	0.010	0.007
80	80	0.238	0.468	0.237	0.002	0.010	0.007
81	81	0.236	0.775	0.236	0.000	0.010	0.007
82	82	0.240	0.014	0.238	0.002	0.010	0.007
83	83	0.238	0.456	0.237	0.002	0.010	0.007
84	84	0.237	0.867	0.238	0.002	0.011	0.007
85	85	0.235	0.436	0.234	0.001	0.011	0.007
86	86	0.227	0.978	0.232	0.002	0.011	0.007
87	87	0.225	0.673	0.225	0.002	0.011	0.007
88	88	0.211	0.898	0.213	0.002	0.012	0.007
89	89	0.219	0.420	0.218	0.002	0.012	0.007
90	90	0.217	0.647	0.217	0.002	0.012	0.007
91	91	0.215	0.401	0.214	0.001	0.012	0.007
92	92	0.221	0.018	0.216	0.002	0.012	0.007
93	93	0.227	0.001	0.218	0.002	0.013	0.007
94	94	0.225	0.593	0.224	0.002	0.013	0.007
95	95	0.224	0.370	0.223	0.002	0.013	0.007

Appendix 3w. (continued)

96	96	0.220	0.571	0.219	0.002	0.013	0.007
97	97	0.222	0.002	0.214	0.002	0.013	0.007
98	98	0.220	0.550	0.220	0.002	0.013	0.007
99	99	0.237	0.022	0.233	0.002	0.014	0.007
100	100	0.235	0.335	0.234	0.002	0.014	0.007
101	101	0.239	0.520	0.238	0.002	0.014	0.007
102	102	0.237	0.660	0.236	0.002	0.014	0.007
103	103	0.230	0.310	0.229	0.001	0.015	0.007
104	104	0.228	0.030	0.225	0.002	0.015	0.007
105	105	0.235	0.722	0.235	0.003	0.015	0.007
106	106	0.237	0.026	0.233	0.002	0.015	0.007
107	107	0.234	0.292	0.233	0.002	0.016	0.007
108	108	0.257	0.000	0.237	0.003	0.017	0.007
109	109	0.284	0.028	0.280	0.003	0.017	0.007
110	110	0.276	0.869	0.277	0.003	0.017	0.007
111	111	0.283	0.003	0.273	0.003	0.018	0.007
112	112	0.282	0.263	0.281	0.003	0.018	0.007
113	113	0.286	0.034	0.283	0.003	0.018	0.007
114	114	0.279	0.826	0.280	0.003	0.018	0.007
115	115	0.270	0.953	0.276	0.003	0.019	0.007
116	116	0.224	0.998	0.257	0.003	0.024	0.008
117	117	0.229	0.004	0.222	0.002	0.024	0.008
118	118	0.223	0.452	0.222	0.002	0.025	0.008
119	119	0.222	0.288	0.221	0.002	0.025	0.008
120	120	0.238	0.010	0.233	0.003	0.028	0.008
121	121	0.236	0.558	0.236	0.002	0.028	0.008
122	122	0.236	0.064	0.235	0.003	0.028	0.008
123	123	0.242	0.063	0.241	0.003	0.029	0.008
124	124	0.245	0.673	0.245	0.003	0.032	0.008
125	125	0.244	0.454	0.243	0.003	0.032	0.008
126	126	0.242	0.525	0.241	0.002	0.032	0.008
127	127	0.243	0.013	0.240	0.003	0.033	0.008
128	128	0.275	0.857	0.277	0.004	0.036	0.008
129	129	0.278	0.007	0.271	0.003	0.036	0.008
130	130	0.279	0.033	0.276	0.003	0.036	0.008
131	131	0.288	0.461	0.287	0.003	0.037	0.008
132	132	0.290	0.035	0.287	0.004	0.037	0.008
133	133	0.289	0.241	0.287	0.004	0.037	0.008
134	134	0.291	0.034	0.288	0.004	0.037	0.008
135	135	0.290	0.367	0.289	0.004	0.037	0.008
136	136	0.296	0.048	0.293	0.004	0.038	0.008
137	137	0.303	0.006	0.292	0.004	0.039	0.008
138	138	0.318	0.003	0.300	0.004	0.040	0.008
139	139	0.318	0.228	0.315	0.005	0.040	0.008
140	140	0.327	0.207	0.324	0.005	0.040	0.008
141	141	0.333	0.963	0.345	0.005	0.044	0.008
142	142	0.335	0.010	0.329	0.005	0.045	0.008
143	143	0.341	0.038	0.338	0.005	0.046	0.008
144	144	0.396	0.870	0.399	0.007	0.055	0.009
145	145	0.416	0.642	0.415	0.007	0.056	0.009

Appendix 3w. (continued)

146	146	0.413	0.695	0.412	0.007	0.057	0.009
147	147	0.419	0.010	0.408	0.007	0.059	0.009
148	148	0.418	0.551	0.416	0.007	0.059	0.009
149	149	0.416	0.200	0.413	0.008	0.060	0.009
150	150	0.417	0.027	0.412	0.008	0.060	0.009
151	151	0.420	0.017	0.414	0.008	0.060	0.009
152	152	0.433	0.064	0.429	0.008	0.061	0.009
153	153	0.451	0.004	0.427	0.009	0.063	0.008
154	154	0.451	0.078	0.447	0.009	0.064	0.008
155	155	0.440	0.385	0.437	0.009	0.067	0.008
156	156	0.449	0.055	0.443	0.010	0.068	0.008
157	157	0.450	0.047	0.444	0.010	0.068	0.008
158	158	0.550	0.001	0.452	0.010	0.080	0.011
159	159	0.546	0.613	0.544	0.011	0.083	0.011
160	160	0.549	0.022	0.541	0.011	0.084	0.011
161	161	0.527	0.086	0.522	0.011	0.088	0.010
162	162	0.501	0.119	0.496	0.011	0.095	0.010
163	163	0.516	0.014	0.496	0.012	0.098	0.010
164	164	0.542	0.034	0.531	0.013	0.100	0.009
165	165	0.560	0.011	0.535	0.013	0.102	0.009
166	166	0.562	0.064	0.555	0.014	0.102	0.009
167	167	0.558	0.103	0.551	0.015	0.107	0.009
168	168	0.541	0.039	0.527	0.016	0.116	0.009
169	169	0.536	0.071	0.525	0.017	0.131	0.009
170	170	0.532	0.134	0.524	0.018	0.133	0.009
171	171	0.532	0.161	0.525	0.018	0.133	0.008
172	172	0.561	0.026	0.530	0.019	0.138	0.009
173	173	0.567	0.526	0.562	0.022	0.145	0.009
174	174	0.575	0.346	0.567	0.023	0.146	0.008
175	175	0.568	0.573	0.563	0.024	0.147	0.008
176	176	0.561	0.225	0.551	0.025	0.150	0.008
177	177	0.564	0.238	0.552	0.027	0.151	0.008
178	178	0.545	0.670	0.548	0.028	0.157	0.007
179	179	0.450	0.294	0.442	0.027	0.202	0.008
180	180	0.478	0.121	0.446	0.029	0.213	0.008
181	181	0.411	0.072	0.357	0.024	0.346	0.015
182	182	0.423	0.311	0.423	0.027	0.354	0.014
183	183	0.431	0.444	0.437	0.031	0.357	0.013
184	184	0.450	0.428	0.460	0.036	0.363	0.013
185	185	0.461	0.523	0.472	0.041	0.372	0.013
186	186	0.451	0.600	0.467	0.025	0.455	0.008
187	187	0.553	0.400	0.550	0.040	0.535	0.006
188	188	0.587	1.000	0.643	0.046	0.587	0.002
189	189	0.705	1.000	0.748	0.031	0.704	0.000
190	190	1.000	1.000	1.000	0.000	1.000	0.000

PROB = probability given the clusters defined at level L1-1
M1 = mean given the clusters at level L1-1
S1 = standard deviation given the clusters at level L1-1
M2 = mean given the cluster sizes
S2 = standard deviation given the cluster sizes

Appendix 4. Taxa collected in various studies. Classes and taxa are listed alphabetically. Trawl data and data pertaining to non specific taxa were not included in the master database.

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
AMPHIPODA	Accedomoera vagor		x	x					
AMPHIPODA	Allorchestes angusta								x
AMPHIPODA	Ampelisca		x		x				x
AMPHIPODA	Ampelisca agassizi								x
AMPHIPODA	Ampelisca brevisimulata		x	x					
AMPHIPODA	Ampelisca careyi								x
AMPHIPODA	Ampelisca cristata								
AMPHIPODA	Ampelisca hancocki								
AMPHIPODA	Ampelisca lobata								x
AMPHIPODA	Ampelisca pugetica		x			x	x		x
AMPHIPODA	Ampeliscidae		x						
AMPHIPODA	Amphipoda		x						
AMPHIPODA	Anonyx		x		x				
AMPHIPODA	Anonyx lilljeborgi							x	x
AMPHIPODA	Aoroides							x	
AMPHIPODA	Aoroides columbiae		x	x					
AMPHIPODA	Aoroides inermis			x					x
AMPHIPODA	Aoroides intermedius	x	x			x	x		x
AMPHIPODA	Argissa hamatipes				x				
AMPHIPODA	Atylus collingi							x	
AMPHIPODA	Atylus tridens		x						
AMPHIPODA	Bathymedon nepos				x				
AMPHIPODA	Bathymedon pumilis	x				x	x		
AMPHIPODA	Byblis							x	
AMPHIPODA	Byblis galmardi	x							
AMPHIPODA	Byblis millsi			x					
AMPHIPODA	Byblis mulleni							x	
AMPHIPODA	Byblis pearcyi	x			x				
AMPHIPODA	Byblis veleronis							x	x
AMPHIPODA	Caprella		x						
AMPHIPODA	Caprella gracilior							x	
AMPHIPODA	Caprella irregularis		x						
AMPHIPODA	Cheirimedia zotea			x					
AMPHIPODA	Corophiidae		x					x	x
AMPHIPODA	Corophium ascherusicum			x					x
AMPHIPODA	Cyphocaris challengerii				x				
AMPHIPODA	Deutella californica		x		x	x	x	x	x
AMPHIPODA	Diasterope pilosa			x					
AMPHIPODA	Dulichia rhabdoplastis						x		
AMPHIPODA	Dulichiidae		x			x			
AMPHIPODA	Dyopedos	x							
AMPHIPODA	Dyopedos monacanthus			x					

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjo1	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
AMPHIPODA	Dyopedos normani				x				
AMPHIPODA	Eohaustorius								x
AMPHIPODA	Eusiridae								x
AMPHIPODA	Eusirus					x	x		
AMPHIPODA	Foxiphalus	x	x						
AMPHIPODA	Foxiphalus obtusidens	x							
AMPHIPODA	Gammaridea							x	
AMPHIPODA	Gammaropsis					x			x
AMPHIPODA	Grandifoxus	x	x		x	x	x	x	x
AMPHIPODA	Guernea reduncans		x						
AMPHIPODA	Haploops tubicola		x						
AMPHIPODA	Harpinia		x						
AMPHIPODA	Harpiniopsis					x	x	x	
AMPHIPODA	Heterophoxus oculatus	x		x			x		
AMPHIPODA	Hyperia medusarum	x	x		x		x	x	x
AMPHIPODA	Hyperia spinigera			x					
AMPHIPODA	Ischyroceridae					x	x		
AMPHIPODA	Ischyrocerus anguipes	x	x	x	x	x	x	x	x
AMPHIPODA	Jassa	x							
AMPHIPODA	Kermystheus ociosa							x	
AMPHIPODA	Koroga megalops						x		x
AMPHIPODA	Lepidepecreum							x	
AMPHIPODA	Lepidepecreum garthi						x		x
AMPHIPODA	Lepidepecreum gurjanovae	x	x		x			x	x
AMPHIPODA	Lysianassidae				x	x			
AMPHIPODA	Maera danae	x							x
AMPHIPODA	Mayerella	x	x		x	x	x	x	x
AMPHIPODA	Mayerella banksia	x		x	x				x
AMPHIPODA	Melita dentata	x							
AMPHIPODA	Melita desdichada	x		x				x	
AMPHIPODA	Melphisana bola								x
AMPHIPODA	Menigratopsis?	x							
AMPHIPODA	Metaphoxus frequens	x							
AMPHIPODA	Metopa		x		x				
AMPHIPODA	Microjassa litotes								
AMPHIPODA	Monoculodes							x	
AMPHIPODA	Monoculodes emarginatus								
AMPHIPODA	Monoculodes glyconica						x		
AMPHIPODA	Monoculodes zernovi	x				x	x		
AMPHIPODA	Neomegamphus								
AMPHIPODA	Nicippe tumida							x	
AMPHIPODA	Oediceroides		x		x				
AMPHIPODA	Oedicerotidae							x	
AMPHIPODA	Opisa tridentata								
AMPHIPODA	Oradarea longimana						x		
AMPHIPODA	Orchomene	x	x			x	x	x	x
AMPHIPODA	Orchomene decipiens								
AMPHIPODA	Orchomene obtusa		x				x		

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjo1	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelt
AMPHIPODA	Orchomene pacifica				x				x
AMPHIPODA	Orchomene pinguis	x		x					
AMPHIPODA	Pachynus		x						x
AMPHIPODA	Pachynus barnardi			x	x				
AMPHIPODA	Paraphoxus oculatus								
AMPHIPODA	Parapleustes							x	x
AMPHIPODA	Parathemisto		x			x			x
AMPHIPODA	Parathemisto pacifica	x		x		x	x		
AMPHIPODA	Pardaliscella cuspidata								
AMPHIPODA	Pardaliscella symmetrica								
AMPHIPODA	Photis								
AMPHIPODA	Photis brevipes		x		x				
AMPHIPODA	Photis californica			x					
AMPHIPODA	Photis conchicola								
AMPHIPODA	Photis fischmanni	x							
AMPHIPODA	Photis lacia								
AMPHIPODA	Photis macinerneyi		x					x	x
AMPHIPODA	Photis macinerneyi				x				x
AMPHIPODA	Phoxocephalidae								
AMPHIPODA	Pleusirus secorrus	x	x					x	x
AMPHIPODA	Pleustes								
AMPHIPODA	Pleustes depressa							x	
AMPHIPODA	Pleustidae								
AMPHIPODA	Pontogeneia rostata								x
AMPHIPODA	Prachynella lodo								
AMPHIPODA	Protomedeia							x	x
AMPHIPODA	Protomedeia fasciata		x						x
AMPHIPODA	Protomedeia grandimana				x				
AMPHIPODA	Protomedeia prudens			x					
AMPHIPODA	Rhachotropis							x	
AMPHIPODA	Rhepoxynius								
AMPHIPODA	Rhepoxynius episburi	x							
AMPHIPODA	Rhepoxynius variatus		x	x					x
AMPHIPODA	Rhynohalicella halona							x	
AMPHIPODA	Scina borealis						x		
AMPHIPODA	Synchelidium rectipalmum		x	x					
AMPHIPODA	Synchelidium shoemakeri				x				
AMPHIPODA	Syrrhoe								
AMPHIPODA	Syrrhoe longifrons	x				x	x		x
AMPHIPODA	Tiron biocellata				x				
AMPHIPODA	Tritella							x	x
AMPHIPODA	Tritella pilimana			x					
AMPHIPODA	Wecomedon								
AMPHIPODA	Westwoodilla caecula			x				x	
ANOPLA	Cerebratulus				x				
ANOPLA	Heteronemertea	x	x		x	x		x	x
ANOPLA	Micrura								
ANOPLA	Micrura alaskensis		x			x	x	x	x

Appendix 4. (continued)

CLASS	GENUS, SPECIES	Fjo1	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
ANOPLA	Paleonemertea								
ANTHOMEDUSA	Stegopoma	x	x		x	x		x	x
ANTHOZOA	Actinaria								
ANTHOZOA	Anthozoa		x						
ANTHOZOA	Edwardsia sipunculoides								
ANTHOZOA	Leptostylis villosa		x						
ANTHOZOA	Pennatulacea								
ANTHOZOA	Pennatulidae							x	
ANTHOZOA	Ptilosarcus guerneyi								
ANTHOZOA	Stachyoptilum superbum	x	x		x				
ANTHOZOA	Virgularia		x						
ANTHOZOA	Virgularia cystiferum		x				x		
APLACOPHOR	Aplacophora				x				
APLACOPHOR	Chaetoderma							x	
APLACOPHOR	Chaetoderma A						x		
APLACOPHOR	Chaetoderma argenteum		x		x				
APLACOPHOR	Chaetoderma B						x		
APLACOPHOR	Chaetodermatidae								
APLACOPHOR	Limifossor talpoideus				x			x	
APLACOPHOR	Scutopus		x		x				
APLACOPHORA	Chaetoderma attenuatum	x	x					x	x
APLACOPHORA	Chaetoderma whitlachi							x	
APLACOPHORA	Spathoderma denchi	x							
ARCHIANNEL	Archiannelida							x	
ARCHIANNEL	Polygordius					x	x		
ARTICULATA	Laqueus californianus	x						x	
ARTICULATA	Terebratulina unguicula	x							x
ASCIDIACEA	Aplidium								x
ASCIDIACEA	Mogula pugetiensis					x	x	x	x
ASTEROIDEA	Asteroidea								x
ASTEROIDEA	Ctenodiscus crispatus	x				x	x	x	x
ASTEROIDEA	Henricia sanguinolenta		x		x			x	x
ASTEROIDEA	Luidia foliolata								
ASTEROIDEA	Solasteridae	x							
ASTEROIDEA	Stylasterias forreri	x							
BIVALVIA	Acila castrensis			x				x	x
BIVALVIA	Adontorhina cyclia	x	x			x	x	x	x
BIVALVIA	Astarte esquimalti	x				x	x		
BIVALVIA	Astartidae								
BIVALVIA	Axinopsida serricata			x				x	x
BIVALVIA	Bivalvia				x			x	
BIVALVIA	Cardiidae	x				x	x	x	x
BIVALVIA	Cardiomya californica								
BIVALVIA	Cardiomya oldroydi								x
BIVALVIA	Cardiomya planetica					x	x		x
BIVALVIA	Cardiomya pseustes	x	x			x	x		x
BIVALVIA	Chlamys hastata			x					
BIVALVIA	Chlamys rubida	x							

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
BIVALVIA	Ciliatocardium ciliatum			x				x	
BIVALVIA	Clinocardium nuttalli			x	x			x	
BIVALVIA	Compsomyax subdiaphana			x					x
BIVALVIA	Cooperella subdiaphana								
BIVALVIA	Cuspidaria apodema	x	x		x	x	x		
BIVALVIA	Cuspidariidae								
BIVALVIA	Cyclocardia ventricosa							x	
BIVALVIA	Dacrydium vitreum								
BIVALVIA	Delectopecten vancouverensis							x	
BIVALVIA	Delectopecten v.teus						x		
BIVALVIA	Diplodonta orbella				x				
BIVALVIA	Gari californica	x						x	
BIVALVIA	Glycymeris subobsoleta				x				
BIVALVIA	Hiatella arctica			x					x
BIVALVIA	Humilaria kennerlyi				x				
BIVALVIA	Huxleyia munita	x	x		x	x	x		x
BIVALVIA	Lasaea cistula		x						x
BIVALVIA	Lucina tenuisculpta			x					
BIVALVIA	Lucinidae				x				
BIVALVIA	Lucinoma annulata			x					
BIVALVIA	Lyonsia bracteata	x			x				
BIVALVIA	Lyonsia californica								
BIVALVIA	Lyonsia scammoni							x	
BIVALVIA	Lyonsiidae					x	x		
BIVALVIA	Macoma		x						x
BIVALVIA	Macoma brota						x		
BIVALVIA	Macoma calcarea				x				
BIVALVIA	Macoma eliminata							x	x
BIVALVIA	Macoma inconspicua								
BIVALVIA	Macoma lipara				x			x	
BIVALVIA	Macoma nasuta		x						
BIVALVIA	Macoma yoldiformis				x			x	
BIVALVIA	Megacrenella columbiana				x				
BIVALVIA	Modiolus difficilus							x	
BIVALVIA	Modiolus rectus			x				x	
BIVALVIA	Musculista senhousei	x			x	x	x		
BIVALVIA	Musculus cultellus		x			x	x		x
BIVALVIA	Musculus niger					x	x		
BIVALVIA	Mya arenaria			x				x	
BIVALVIA	Mysella tumida			x					
BIVALVIA	Mytilidae	x	x		x				
BIVALVIA	Mytilus edulis			x					
BIVALVIA	Naeromya							x	
BIVALVIA	Naeromya compressa	x	x		x	x	x	x	x
BIVALVIA	Naeromya myaciformis						x		
BIVALVIA	Naeromya rugifer		x					x	x
BIVALVIA	Nemocardium centrifilosum	x			x			x	x
BIVALVIA	Nucula	x							

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA62	AA3-9	Hec	Shelf
BIVALVIA	Nucula carlottensis					x	x		
BIVALVIA	Nucula tenuis			x	x		x	x	
BIVALVIA	Nuculana	x				x	x		
BIVALVIA	Nuculana amiata								
BIVALVIA	Nuculana extenuata							x	
BIVALVIA	Nuculana fossa	x	x	x		x	x		x
BIVALVIA	Nuculana hindsii								
BIVALVIA	Nuculana leonina	x	x						x
BIVALVIA	Nuculana minuta							x	
BIVALVIA	Nuculana navisa							x	x
BIVALVIA	Nuculana pernula							x	
BIVALVIA	Nuculana radiata						x		
BIVALVIA	Nuculana taphria				x	x		x	x
BIVALVIA	Nuculana tenuisulcata		x		x			x	
BIVALVIA	Nuculanidae		x					x	x
BIVALVIA	Nutricola tantilla				x				
BIVALVIA	Pandora	x						x	x
BIVALVIA	Pandora bilirata								x
BIVALVIA	Pandora filosa	x	x	x		x	x	x	x
BIVALVIA	Pandora grandis					x		x	
BIVALVIA	Parvamussium alaskensis				x				
BIVALVIA	Patinopecten caurinus		x		x				
BIVALVIA	Pectinilidae	x	x			x	x	x	x
BIVALVIA	Pododesmus macroschisma	x		x					
BIVALVIA	Propeamussium					x	x		
BIVALVIA	Protothaca staminea			x	x				
BIVALVIA	Psephidia lordi			x			x		x
BIVALVIA	Solen sicarius	x							
BIVALVIA	Spisula falcata					x			x
BIVALVIA	Tapes philippinarum		x						
BIVALVIA	Tellina carpenteri			x		x	x		
BIVALVIA	Tellina modesta		x						
BIVALVIA	Tellina nuculoides			x				x	
BIVALVIA	Tellinidae								
BIVALVIA	Thyasira	x							
BIVALVIA	Thyasira cygnus								x
BIVALVIA	Thyasira gouldi			x			x	x	
BIVALVIA	Tresus nuttalli		x					x	x
BIVALVIA	Tridonta alaskensis		x		x			x	x
BIVALVIA	Tridonta borealis		x		x				
BIVALVIA	Tridonta montagui		x						
BIVALVIA	Tridonta rollandi		x		x			x	
BIVALVIA	Veneridae								x
BIVALVIA	Yoldia amygdalea				x		x		
BIVALVIA	Yoldia beringiana							x	x
BIVALVIA	Yoldia hyperboria					x	x		
BIVALVIA	Yoldia martyria			x	x		x		
BIVALVIA	Yoldia myalis	x				x	x		

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelt
BIVALVIA	Yoldia scissurata			x				x	
BIVALVIA	Yoldia thraciaeformis	x							
CALCAREA	Scypha							x	
CEPHALOPOD	Octopus					x	x		
CEPHALOPOD	Rossia pacifica							x	x
CIRRIPEDIA	Balanidae								
CIRRIPEDIA	Balanus crenatus			x				x	
CIRRIPEDIA	Lepas anatifera		x						
CIRRIPEDIA	Solidobalanus hesperius	x	x		x			x	x
COPEPODA	Ancorabolus				x			x	x
COPEPODA	Bradya typica								x
COPEPODA	Bulbamphiascus imus							x	x
COPEPODA	Cervinia synartha							x	
COPEPODA	Copepoda								
COPEPODA	Cylcopoida								x
COPEPODA	Dactylopoda								x
COPEPODA	Diosaccidae								
COPEPODA	Ectinosomatidae								
COPEPODA	Enhydrosoma							x	
COPEPODA	Harpacticoida							x	x
COPEPODA	Harpacticus	x							x
COPEPODA	Nannopus							x	
COPEPODA	Paranannopus		x						x
COPEPODA	Psammis	x	x						
COPEPODA	Typhanlampopos typhlops		x					x	x
CUMACEA	Campylaspis	x	x						x
CUMACEA	Campylaspis canaliculata								x
CUMACEA	Campylaspis rubicunda					x	x		
CUMACEA	Campylaspis rubromaculata		x		x				x
CUMACEA	Cumacea								x
CUMACEA	Cummella	x				x	x	x	x
CUMACEA	Cummella vulgaris		x		x			x	
CUMACEA	Diastylidae							x	
CUMACEA	Diastylis		x			x	x	x	x
CUMACEA	Diastylis alaskensis			x		x			
CUMACEA	Diastylis aspera							x	
CUMACEA	Diastylis bidentata							x	
CUMACEA	Diastylis dalli							x	
CUMACEA	Diastylis hirsuta								
CUMACEA	Diastylis parasinulosa		x						
CUMACEA	Diastylis pellucida							x	
CUMACEA	Diastylis spinulosa							x	
CUMACEA	Diastylis umatellensis						x		
CUMACEA	Diastylopsis dawsoni	x							x
CUMACEA	Diastylopsis tenuis		x					x	x
CUMACEA	Eudorella								x
CUMACEA	Eudorella emarginata							x	
CUMACEA	Eudorella pacifica			x			x		x

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
CUMACEA	Eudorellopsis biplicata		x						x
CUMACEA	Hemilampropos californiensis	x						x	
CUMACEA	Hemilampropos gracilis								x
CUMACEA	Lamprops quadriplicata		x						
CUMACEA	Lamprops triserrata				x				
CUMACEA	Leptostylis								x
CUMACEA	Leptostylis macrura							x	
CUMACEA	Leucon								
CUMACEA	Leucon nasica								x
CUMACEA	Leucon subnasica		x					x	
CUMACEA	Leuconidae	x	x			x	x		
CUMACEA	Pentalosarsia declivis		x						
DECAPODA	Argis alaskensis								x
DECAPODA	Brachyura		x		x				
DECAPODA	Brachyuridae		x					x	
DECAPODA	Callianassa		x		x	x	x	x	x
DECAPODA	Cancer		x		x				x
DECAPODA	Cancer gracilis								x
DECAPODA	Cancer magister	x			x	x		x	x
DECAPODA	Cancer productus							x	
DECAPODA	Crangon alaskensis		x	x					x
DECAPODA	Crangon alba		x			x			
DECAPODA	Crangon stylirostris							x	
DECAPODA	Crangonidae							x	
DECAPODA	Decapoda		x						x
DECAPODA	Eualus avinus							x	
DECAPODA	Eualus berkeleyorum		x		x			x	
DECAPODA	Eualus lineatus								x
DECAPODA	Eualus pusiolus				x				
DECAPODA	Heptacarpus				x			x	x
DECAPODA	Heptacarpus decorus								x
DECAPODA	Lissocrangon stylirostris							x	
DECAPODA	Majidae		x				x	x	
DECAPODA	Metacrangon munita	x	x			x	x		x
DECAPODA	Metacrangon spinosissima							x	
DECAPODA	Nebaleacea								
DECAPODA	Oregonia gracilis		x						
DECAPODA	Paguridae				x				
DECAPODA	Paguristes turgidus								x
DECAPODA	Pagurus								x
DECAPODA	Pagurus armatus		x					x	
DECAPODA	Pandalus jordani							x	x
DECAPODA	Pandalus platyceros	x			x			x	
DECAPODA	Pandalus stenolepis								
DECAPODA	Pasiphaea pacifica						x		
DECAPODA	Pinnixa								x
DECAPODA	Pinnixa eburna		x		x				x
DECAPODA	Pinnixa occidentalis								

Appendix 4. (continued)

CLASS	GENUS, SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
DECAPODA	Pinnixa schmitti			x					
DECAPODA	Pugettia richi		x						
DECAPODA	Spirontocaris		x		x	x	x	x	x
DECAPODA	Spirontocaris arcuata		x						
DECAPODA	Spirontocaris lamellicornis		x						
DECAPODA	Spirontocaris ochotensis	x				x			
DECAPODA	Spirontocaris truncata		x					x	x
DEMOSPONGI	Microciona primitiva		x						x
DEMOSPONGI	Myxilla incrustans				x	x			x
DEMOSPONGI	Poecilosel	x						x	
ECHINOIDEA	Allocentrotus fragilis	x							
ECHINOIDEA	Brisaster latifrons							x	x
ECHINOIDEA	Dendraster excentricus				x				
ECHINOIDEA	Echinodea	x	x		x	x	x	x	
ECHINOIDEA	Eupentacta							x	
ECHINOIDEA	Strongylocentrotus pallidus	x	x						
ECHIURIDA	Echiurida							x	
ECHIURIDA	Echiurus echiurus								x
ENOPLA	Emplectonema gracile								
ENOPLA	Hoplonemertea								
EUPHAUSIAC	Euphaiidae							x	
EUPHAUSIAC	Euphausia pacifica							x	
EUPHAUSIAC	Euphausiacea								x
EUPHAUSIAC	Thysanoessa spinifera							x	
GASTROPODA	Acmaeidae					x			
GASTROPODA	Admete gracilior	x							
GASTROPODA	Alvania	x						x	x
GASTROPODA	Alvania compacta			x		x	x		x
GASTROPODA	Alvania rosana								
GASTROPODA	Amphissa bicolor					x	x	x	x
GASTROPODA	Amphissa columbiana		x						
GASTROPODA	Amphissa versicolor	x	x	x	x			x	x
GASTROPODA	Antiplanes voyi							x	
GASTROPODA	Balcis	x	x		x	x	x	x	x
GASTROPODA	Bathybembix cidaris							x	
GASTROPODA	Bittium							x	
GASTROPODA	Bittium attenuatum				x				
GASTROPODA	Bittium munitum		x	x				x	x
GASTROPODA	Bittium vancouverensis		x						
GASTROPODA	Boreotrophon dalli		x			x	x		
GASTROPODA	Buccinum glaciale		x				x	x	x
GASTROPODA	Caecum crebricinctum								
GASTROPODA	Calyptraea fastigata								x
GASTROPODA	Calyptraeidae					x		x	x
GASTROPODA	Cephalaspida								x
GASTROPODA	Columbellidae								
GASTROPODA	Colus halli	x	x		x			x	x
GASTROPODA	Crepidula adunca		x	x	x				

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
GASTROPODA	Crepidula dorsata		x		x				
GASTROPODA	Cryptogemma adrastia					x			
GASTROPODA	Cyclostrema							x	
GASTROPODA	Cylichna alba		x		x			x	x
GASTROPODA	Cylichna attonsa						x	x	
GASTROPODA	Cylichnella culcitella								
GASTROPODA	Cylichnidae				x			x	
GASTROPODA	Eulima rutila							x	
GASTROPODA	Gastropoda							x	
GASTROPODA	Gastropteron pacificum							x	
GASTROPODA	Haminoea vesicula							x	
GASTROPODA	Lacuna carinata			x					
GASTROPODA	Lacuna porrecta								x
GASTROPODA	Leptogyra alaskana		x					x	x
GASTROPODA	Limacina helicina					x	x		
GASTROPODA	Lirularia lirulata	x				x	x		
GASTROPODA	Mangelia	x	x						x
GASTROPODA	Margarites helicinus							x	
GASTROPODA	Margarites pupillus	x							x
GASTROPODA	Mitrella carinata							x	
GASTROPODA	Mitrella gausapata			x				x	
GASTROPODA	Mitrella tuberosa			x					
GASTROPODA	Mohnia frielei	x	x					x	
GASTROPODA	Nassarius fossatus		x		x				
GASTROPODA	Nassarius mendicus			x				x	
GASTROPODA	Natica clausa		x					x	x
GASTROPODA	Neptunea lyrata		x						
GASTROPODA	Neptunidae								x
GASTROPODA	Nitidiscala catalinae							x	
GASTROPODA	Nitidiscala indianorum							x	
GASTROPODA	Nitidiscala sawinae		x						x
GASTROPODA	Oenebra interfossa						x		
GASTROPODA	Odostomia				x			x	
GASTROPODA	Odostomia avellana							x	
GASTROPODA	Odostomia barkleyensis							x	
GASTROPODA	Odostomia columbiana			x					
GASTROPODA	Odostomia cypria							x	
GASTROPODA	Odostomia oregonensis					x			
GASTROPODA	Odostomia quadrae			x					
GASTROPODA	Odostomia vancouverensis			x					
GASTROPODA	Oenopota elegans								
GASTROPODA	Oenopota harpa	x							
GASTROPODA	Olivella baetica		x			x	x	x	x
GASTROPODA	Ophiodermella cancellata	x							
GASTROPODA	Ophiodermella inermis	x							x
GASTROPODA	Philine polaris			x			x	x	
GASTROPODA	Plicifusus brunneus	x	x		x	x	x	x	x
GASTROPODA	Polinices lewisi	x	x					x	x

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelt
GASTROPODA	Polinices pallidus		x		x		x	x	x
GASTROPODA	Punctarella galeata							x	
GASTROPODA	Rectiplanes piona								x
GASTROPODA	Rictaxis punctocoelatus			x				x	
GASTROPODA	Rissoina newcombei								x
GASTROPODA	Solariella obscura			x				x	
GASTROPODA	Solariella peramabilis	x							
GASTROPODA	Thaisidae					x	x		
GASTROPODA	Trichotropis borealis								x
GASTROPODA	Trichotropis cancellata							x	x
GASTROPODA	Trochidae	x							
GASTROPODA	Trophonopsis orpheus			x					
GASTROPODA	Turbonilla	x	x		x	x	x	x	x
GASTROPODA	Turbonilla aurantia							x	
GASTROPODA	Turbonilla lyalli		x	x	x				
GASTROPODA	Turbonilla newcombei		x					x	x
GASTROPODA	Turbonilla pedroana	x							
GASTROPODA	Turbonilla pugetensis				x				
GASTROPODA	Turbonilla vancouverensis			x					
GASTROPODA	Turridae					x			
GASTROPODA	Urosalpinx cinerea	x	x			x	x		x
GASTROPODA	Vitrinella		x						
GASTROPODA	Vitrinella columbiana						x	x	
GASTROPODA	Volvulella cylindrica		x						
HEXACTINEL	Rossellidae		x		x			x	x
HOLOTHUROI	Chiridota albatrossi	x	x		x		x	x	x
HOLOTHUROI	Chiridota nanaimensis							x	
HOLOTHUROI	Cucumaridae							x	
HOLOTHUROI	Dendrochirotida	x	x		x			x	
HOLOTHUROI	Havelockia benti							x	
HOLOTHUROI	Holothuroidea				x				
HOLOTHUROI	Leptosynapta roxtana		x						
HOLOTHUROI	Leptosynapta transgressor		x			x	x		
HOLOTHUROI	Molpadia intermedia	x	x		x	x	x		x
HOLOTHUROI	Molpadiidae				x				
HOLOTHUROI	Parastichopus		x		x				
HOLOTHUROI	Pentamera							x	
HOLOTHUROI	Pentamera populifera	x							
HOLOTHUROI	Pentamera pseudocalcigera		x						
HOLOTHUROI	Psolus squamata								
HYDROZOA	Campanulariidae		x						x
HYDROZOA	Halecium	x				x	x		
HYDROZOA	Lafoea dumosa		x						x
HYDROZOA	Sertularella				x			x	x
HYDROZOA	Velella velella							x	
ISOPODA	Cryptoniscidae	x	x		x			x	x
ISOPODA	Eugerda		x					x	
ISOPODA	Gnathia	x	x		x			x	x

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
ISOPODA	Gnathia hirsuta	x							x
ISOPODA	Gnathia trilobata								x
ISOPODA	Gnorimosphaeroma oregonensis	x							x
ISOPODA	Idotea								x
ISOPODA	Idotea resecata	x	x						x
ISOPODA	Idoteidae	x	x		x	x	x	x	x
ISOPODA	Isopoda							x	
ISOPODA	Jaeropsis dubia							x	
ISOPODA	Janiralata solasteri		x		x			x	
ISOPODA	Limnoria	x							
ISOPODA	Limnoria lignorum								x
ISOPODA	Munna fernaldi		x						x
ISOPODA	Munna stephenseni								
ISOPODA	Munna ubiquita		x	x					
ISOPODA	Munnogonium tillerae							x	x
ISOPODA	Munnopsurus	x		x					x
ISOPODA	Pleurogonium							x	
ISOPODA	Pleurogonium californiense		x						
ISOPODA	Pleurogonium inerme	x	x					x	
ISOPODA	Pleurogonium rubicundum				x				x
ISOPODA	Rocinela angustata								
ISOPODA	Rocinela belliceps		x						x
ISOPODA	Synidotea								x
ISOPODA	Synidotea angulata								x
ISOPODA	Synidotea media	x							
ISOPODA	Synidotea nebulosa							x	
ISOPODA	Synidotea nodulosa								x
ISOPODA	Synidotea picta		x						
KINORHYNCHA	Kinorhynchus cataphractus								
KINORHYNCHA	Kinorhynchus ilyocryptus	x	x					x	
KINORHYNCHA	Pycnophyes sanjuanensis		x						
LEPTOSTRAC	Nebalia pugettensis				x				
LEPTOSTRAC	Nebaliidae					x			
MEROSTOMATA	Halacaridae		x						
MYSIDACEA	Archaeomys grebnitzkii								x
MYSIDACEA	Disacanthomysis dybowskii								x
MYSIDACEA	Holmesiella anomala		x						
MYSIDACEA	Inusitatom insolita							x	
MYSIDACEA	Meterythrops robusta		x						
MYSIDACEA	Mysidacea								
MYSIDACEA	Neomysis kadiakensis			x					x
MYSIDACEA	Pacificanthomysis nephrophthalma		x		x				x
MYSIDACEA	Pseudomma truncatum								x
MYSIDACEA	Stilomysis grandis	x							
N/A	Chaetagnatha								x
N/A	Cnidaria							x	
N/A	Echiura					x	x		
N/A	Nematoda								x

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
N/A	Nemertea				x	x	x	x	x
N/A	Nemertinea								
N/A	Phascolosoma		x		x			x	
N/A	Pogonophora		x						
OLIGOCHAET	Aktedrilus knoellneri								x
OLIGOCHAET	Aktedrilus labeosus		x						
OLIGOCHAET	Aktedrilus locyi					x	x		
OLIGOCHAET	Enchytraeidae							x	
OLIGOCHAET	Grania								
OLIGOCHAET	Isochaetid columbiensis								x
OLIGOCHAET	Limnodriloides		x						
OLIGOCHAET	Limnodriloides monotheca							x	
OLIGOCHAET	Limnodriloides victoriensis	x				x	x		x
OLIGOCHAET	Monopylephorus cuticulatus	x				x			
OLIGOCHAET	Monopylephorus rubroniveus		x					x	x
OLIGOCHAET	Naididae	x							
OLIGOCHAET	Oligochata								x
OLIGOCHAET	Paranais frici				x			x	x
OLIGOCHAET	Paranais litoralis								
OLIGOCHAET	Rhizodrilus pacificus							x	
OLIGOCHAET	Tectidrilus diversus		x						
OLIGOCHAET	Tectidrilus verrucosus				x				
OLIGOCHAET	Tubificidae								x
OLIGOCHAET	Tubificoides bakeri							x	
OLIGOCHAET	Tubificoides benedii		x						x
OLIGOCHAET	Tubificoides brevicoleus		x						
OLIGOCHAET	Tubificoides brownae						x		x
OLIGOCHAET	Tubificoides crenacoleus		x					x	x
OLIGOCHAET	Tubificoides cuspisetosus		x						
OLIGOCHAET	Tubificoides diazi		x						
OLIGOCHAET	Tubificoides fraseri	x			x	x	x	x	
OLIGOCHAET	Tubificoides imajimai	x							
OLIGOCHAET	Tubificoides motei	x							
OLIGOCHAET	Tubificoides palacoleus				x				
OLIGOCHAET	Tubificoides parapectinatus					x	x		
OLIGOCHAET	Tubificoides postcapillatus						x	x	
OLIGOCHAET	Tubificoides pseudogaster							x	
OLIGOCHAET	Tubificoides wasselli	x							
OPHIUROIDE	Amphiodia					x	x	x	
OPHIUROIDE	Amphiodia periercta								x
OPHIUROIDE	Amphiodia urtica			x					
OPHIUROIDE	Amphiopholus pugetana								
OPHIUROIDE	Amphiopholus squamata	x		x					
OPHIUROIDE	Amphioplus							x	
OPHIUROIDE	Amphioplus macraspis							x	
OPHIUROIDE	Amphioplus strongyloplax							x	
OPHIUROIDE	Gorgonocephalus eucnemus	x				x	x		
OPHIUROIDE	Ophiura leptoctenia	x			x		x	x	x

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
OPHIUROIDE	Ophiura leutkeni							x	
OPHIUROIDE	Ophiura sarsi	x	x		x	x	x	x	x
OPHIUROIDE	Ophiuridae							x	
OSTRACODA	Alacia alata minor	x						x	
OSTRACODA	Bathyleberis							x	
OSTRACODA	Bythocypris				x	x	x	x	
OSTRACODA	Cletocythe noblissimus					x	x		
OSTRACODA	Cypridina								
OSTRACODA	Cytheropteron							x	
OSTRACODA	Euphilomedes				x			x	
OSTRACODA	Euphilomedes carcharodonta	x		x		x			
OSTRACODA	Euphilomedes producta			x				x	
OSTRACODA	Krite sawanensis				x				
OSTRACODA	Leprocythere		x					x	
OSTRACODA	Macrocypris		x			x	x	x	
OSTRACODA	Munsiella								x
OSTRACODA	Myodocopoida	x	x						
OSTRACODA	Ostracoda							x	
OSTRACODA	Palmenella californicus	x				x	x		
OSTRACODA	Paracypri		x			x	x	x	x
OSTRACODA	Pectocyth re clavata				x				
OSTRACODA	Philomedinae	x							x
OSTRACODA	Rutiderma lomae						x	x	
OSTRACODA	Sclerocoucha trituberculatus	x							
PHORONIDA	Phoronopsis harmeri	x	x		x			x	
POLYCHAETA	Acesta catherinae						x		
POLYCHAETA	Acesta lopezi			x	x	x	x		
POLYCHAETA	Acesta neosuecica	x						x	x
POLYCHAETA	Aglaophamus							x	x
POLYCHAETA	Aglaophamus malmgreni		x						
POLYCHAETA	Aglaophamus rubella anops					x	x		x
POLYCHAETA	Allia quadrilobata				x				
POLYCHAETA	Amage anops			x					
POLYCHAETA	Ampharete							x	
POLYCHAETA	Ampharete acutifrons			x				x	
POLYCHAETA	Ampharete finmarchica			x			x		x
POLYCHAETA	Ampharete labrops		x	x				x	x
POLYCHAETA	Ampharetidae		x						
POLYCHAETA	Amphicteis							x	
POLYCHAETA	Amphicteis glabra			x					
POLYCHAETA	Amphicteis mucronata								
POLYCHAETA	Amphicteis scaphobranchiata	x	x	x	x	x	x	x	x
POLYCHAETA	Amphictene moorei			x	x		x	x	
POLYCHAETA	Amphinomidae				x			x	x
POLYCHAETA	Amphitrite				x			x	
POLYCHAETA	Anaitides citrina								x
POLYCHAETA	Anaitides groenlandica	x		x		x	x	x	x
POLYCHAETA	Anaitides hartmani		x	x					

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
POLYCHAETA	Anaitides mucosa							x	
POLYCHAETA	Ancistrosyllis		x			x	x	x	
POLYCHAETA	Ancistrosyllis groenlandica					x	x		
POLYCHAETA	Anobothrus gracilis				x	x		x	x
POLYCHAETA	Antinoella sarsi					x	x		x
POLYCHAETA	Aonides								
POLYCHAFTA	Aphrodita							x	
POLYCHAETA	Aphrodita japonica								
POLYCHAETA	Aphroditidae								x
POLYCHAETA	Apistobranchus ornatus								x
POLYCHAETA	Apistobranchus tullbergi								x
POLYCHAETA	Apri-tobranchidae								x
POLYCHAETA	Arabellidae								-
POLYCHAETA	Araphura brevimana								x
POLYCHAETA	Arcteobia spinelytris			x					
POLYCHAETA	Arctonoe pulchra								x
POLYCHAETA	Arctonoe vittata								x
POLYCHAETA	Aricidea								x
POLYCHAETA	Aricidea cerruti							x	
POLYCHAETA	Aricidea minuta								x
POLYCHAETA	Armandia brevis	x		x	x				x
POLYCHAETA	Artacama coniferi		x		x				x
POLYCHAETA	Artacamella hancocki	x						x	x
POLYCHAETA	Asabellides lineata					x	x		
POLYCHAETA	Asabellides sibirica							x	
POLYCHAETA	Asclerocheilus beringianus					x	x		x
POLYCHAETA	Asychis	x							
POLYCHAETA	Asychis disparidentata							x	
POLYCHAETA	Asychis similis					x			
POLYCHAETA	Autolytus		x		x	x	x		x
POLYCHAETA	Axiothella rubrocincta								x
POLYCHAETA	Barentolla americana			x					
POLYCHAETA	Boccardia pugettensis								x
POLYCHAETA	Brada sachalina						x		
POLYCHAETA	Brada villosa	x					x		x
POLYCHAETA	Byglides macrolepida							x	x
POLYCHAETA	Capitella capitata			x			x	x	
POLYCHAETA	Capitellidae				x				
POLYCHAETA	Caulleriella	x							
POLYCHAETA	Caulleriella bioculata		x					x	
POLYCHAFTA	Caulleriella hamata		x						
POLYCHAETA	Caulleriella oculata							x	
POLYCHAETA	Chaetopteridae							x	
POLYCHAETA	Chaetopterus variopedatus								x
POLYCHAETA	Chaetozone acuta		x						
POLYCHAETA	Chaetozone spinosa			x			x	x	
POLYCHAETA	Chone		x						
POLYCHAETA	Chone duneri			x				x	x

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
POLYCHAETA	Chone ecaudata							x	
POLYCHAETA	Chrysopetadae		x					x	
POLYCHAETA	Cirratulidae		x		x			x	
POLYCHAETA	Cirratulus cirratus		x	x					
POLYCHAETA	Cistenides granulata			x					
POLYCHAETA	Clymenura columbiana							x	
POLYCHAETA	Cossura								
POLYCHAETA	Cossura longocirrata	x		x			x		x
POLYCHAETA	Cossura modica								
POLYCHAETA	Cossura soyeri					x	x		
POLYCHAETA	Cossuridae							x	
POLYCHAETA	Crucigera irregularis				x				
POLYCHAETA	Crucigera zygophora								x
POLYCHAETA	Decamastus							x	x
POLYCHAETA	Decamastus gracilis							x	
POLYCHAETA	Demonax media							x	
POLYCHAETA	Diop a ornata				x				x
POLYCHAETA	Dorvi ea pseudorubrovittata		x						
POLYCHAETA	Dorvillea rudolphi			x					
POLYCHAETA	Drilonereis falcataminor	x							
POLYCHAETA	Drilonereis longa							x	
POLYCHAETA	Drilonerles falcata							x	
POLYCHAETA	Eteone								
POLYCHAETA	Eteone columbiensis				x				
POLYCHAETA	Eteone longa			x					
POLYCHAETA	Etionides coineaui				x	x	x		
POLYCHAETA	Etionides coineauidificilis				x			x	x
POLYCHAETA	Euchone arenae				x				
POLYCHAETA	Euchone hancocki				x				
POLYCHAETA	Euchone incolor			x				x	
POLYCHAETA	Euclymene								
POLYCHAETA	Euclymene geralis							x	
POLYCHAETA	Euclymene zonalis		x	x	x	x	x	x	x
POLYCHAETA	Eulalia		x					x	
POLYCHAETA	Eulalia bilineata			x				x	
POLYCHAETA	Eulalia levicornuta								
POLYCHAETA	Eulalia sanguinea			x					
POLYCHAETA	Eulalia viridis			x				x	
POLYCHAETA	Eunoe								x
POLYCHAETA	Eunoe depressa							x	
POLYCHAETA	Eunoe senta		x			x	x	x	
POLYCHAETA	Eunoe uniseriata							x	
POLYCHAETA	Eusyllis assimilis							x	
POLYCHAETA	Eusyllis blomstrandi								
POLYCHAETA	Eusyllis magnifica	x	x						
POLYCHAETA	Exogone lourei	x							
POLYCHAETA	Exogone molesta				x			x	x
POLYCHAETA	Exogone verugera				x	x	x		

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Vanl	Van2	Bound	AA82	AA3-9	Hec	Shelf
POLYCHAETA	Flabelligera affinis						x	x	
POLYCHAETA	Flabelligeridae								
POLYCHAETA	Galathowenia oculata			x			x	x	
POLYCHAETA	Gattyana ciliata							x	x
POLYCHAETA	Gattyana cirrosa		x						
POLYCHAETA	Gattyana treadwelli			x	x				
POLYCHAETA	Glycera							x	
POLYCHAETA	Glycera americana					x			
POLYCHAETA	Glycera capitata			x					
POLYCHAETA	Glycera oxychephala	x				x	x		
POLYCHAETA	Glyceridae							x	
POLYCHAETA	Glycinde							x	
POLYCHAETA	Glycinde armigera			x			x	x	
POLYCHAETA	Glycinde picta	x	x	x		x	x	x	x
POLYCHAETA	Glyphanostomum pallescens								
POLYCHAETA	Goniada								x
POLYCHAETA	Goniada annulata			x			x		
POLYCHAETA	Goniada brunnea							x	
POLYCHAETA	Goniada maculata							x	
POLYCHAETA	Goniadidae								
POLYCHAETA	Gyptis								
POLYCHAETA	Harmothoe extenuata		x						
POLYCHAETA	Harmothoe imbricata			x			x		
POLYCHAETA	Harmothoe lunulata			x				x	
POLYCHAETA	Hemipodus borealis				x				
POLYCHAETA	Hesionidae								x
POLYCHAETA	Heteromastus							x	
POLYCHAETA	Heteromastus abiseta		x						
POLYCHAETA	Heteromastus filiformis				x				
POLYCHAETA	Heteromastus filobranchus			x	x		x		
POLYCHAETA	Idanthyrsus armatus	x			x				x
POLYCHAETA	Idanthyrsus ornamentatus			x	x				
POLYCHAETA	Isocirrus longiceps		x						
POLYCHAETA	Jasmineira pacifica				x				
POLYCHAETA	Kefersteinia cirrata	x				x	x		
POLYCHAETA	Lanassa venustavenusta			x				x	
POLYCHAETA	Laonice cirrata	x		x					
POLYCHAETA	Leitoscoloplos pugettensis			x			x		x
POLYCHAETA	Lepidasthenia berkeleyae		x						
POLYCHAETA	Lepidasthenia longicirrata		x						
POLYCHAETA	Lepidonotus squamatus			x		x	x		
POLYCHAETA	Levinsenia gracilis					x	x	x	
POLYCHAETA	Lumbrineridae				x			x	x
POLYCHAETA	Lumbrineris					x	x		x
POLYCHAETA	Lumbrineris acuta					x			
POLYCHAETA	Lumbrineris bicirrata		x	x					
POLYCHAETA	Lumbrineris cruzensis		x						
POLYCHAETA	Lumbrineris lagunae		x						

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
POLYCHAETA	Lumbrineris latreilli						x		
POLYCHAETA	Lumbrineris limicola	x			x	x	x		x
POLYCHAETA	Lumbrineris luti	x					x	x	x
POLYCHAETA	Lumbrineris zonata								x
POLYCHAETA	Lysippe labiata								x
POLYCHAETA	Macroclymene		x						
POLYCHAETA	Macrocylindrus	x							
POLYCHAETA	Magelona hobsonae		x						x
POLYCHAETA	Magelona longicornis		x						
POLYCHAETA	Magelona sacculata		x						x
POLYCHAETA	Magelonidae							x	
POLYCHAETA	Maldane glebifex						x		x
POLYCHAETA	Maldanella harai								x
POLYCHAETA	Maldanidae	x							
POLYCHAETA	Mediomastus	x							
POLYCHAETA	Mediomastus ambiseta	x							
POLYCHAETA	Mediomastus californiensis	x		x			x		
POLYCHAETA	Mediomastus capensis								x
POLYCHAETA	Megalomma splendida	x	x			x	x	x	x
POLYCHAETA	Melodorvillea minuta	x	x						
POLYCHAETA	Melinna cristata	x							
POLYCHAETA	Melinna elisabethae							x	
POLYCHAETA	Mesochaetopterus taylori	x							x
POLYCHAETA	Micromaldane ornithochaeta							x	
POLYCHAETA	Micropodarke dubia	x		x					
POLYCHAETA	Mystides borealis								x
POLYCHAETA	Naineris quadripclicata			x					
POLYCHAETA	Neoamphitrites edwardsi		x						
POLYCHAETA	Neoamphitrites robusta							x	x
POLYCHAETA	Nephtyidae	x						x	x
POLYCHAETA	Nephtys							x	
POLYCHAETA	Nephtys assignis								x
POLYCHAETA	Nephtys caeca							x	x
POLYCHAETA	Nephtys californiensis		x			x	x		
POLYCHAETA	Nephtys ciliata							x	
POLYCHAETA	Nephtys cornutacornuta						x	x	
POLYCHAETA	Nephtys cornutafranciscanum			x				x	
POLYCHAETA	Nephtys ferruginea			x				x	
POLYCHAETA	Nephtys longosetosa	x							
POLYCHAETA	Nephtys punctata	x	x		x	x	x	x	x
POLYCHAETA	Nephtys rickettsi							x	
POLYCHAETA	Nereidae							x	
POLYCHAETA	Nereis	x							
POLYCHAETA	Nereis brandti			x					
POLYCHAETA	Nereis procera							x	
POLYCHAETA	Nereis zonata			x					
POLYCHAETA	Nicolea zostericola			x	x				
POLYCHAETA	Nicomache		x		x				

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3 9	Hec	Shw 1
POLYCHAETA	Nicomache lumbricalis							x	
POLYCHAETA	Nicomache personata								x
POLYCHAETA	Ninoe gemmea							x	
POLYCHAETA	Nothria elegans					x			
POLYCHAETA	Nothria geophilliformis		x			x	x		x
POLYCHAETA	Notomastus lineatus							x	
POLYCHAETA	Notomastus tenuis								x
POLYCHAETA	Notoproctus pacificus								x
POLYCHAETA	Odontosyllis phosphorea								x
POLYCHAETA	Onuphidae								x
POLYCHAETA	Onuphis								x
POLYCHAETA	Onuphis conchylega		x						x
POLYCHAETA	Ophelia limacina							x	
POLYCHAETA	Opheliidae								x
POLYCHAETA	Ophelina acuminata	x	x	x		x	x		x
POLYCHAETA	Ophelina breviata				x				
POLYCHAETA	Ophiodromus pugettensis			x					x
POLYCHAETA	Ophryotrocha				x				
POLYCHAETA	Ophryotrocha pugettensis		x			x			
POLYCHAETA	Orbiniidae								x
POLYCHAETA	Owenia fusiformis								
POLYCHAETA	Oweniidae				x				
POLYCHAETA	Paleanotus bellis			x					
POLYCHAETA	Parandalia fauveli			x					
POLYCHAETA	Paraninoe simpta						x		
POLYCHAETA	Paraonidae							x	
POLYCHAETA	Paraprionospio pinnata			x					
POLYCHAETA	Pectinaria					x	x		
POLYCHAETA	Pectinaria californiensis			x					
POLYCHAETA	Petaloproctus tenuisborealis								
POLYCHAETA	Petaloproctus tenuistentis				x				
POLYCHAETA	Pherusa negligens								x
POLYCHAETA	Pherusa plumosa						x	x	
POLYCHAETA	Pholoe minuta	x		x			x		
POLYCHAETA	Pholoides aspera			x				x	
POLYCHAETA	Pholoididae		x						
POLYCHAETA	Phyllochaetopterus							x	
POLYCHAETA	Phyllodoce							x	
POLYCHAETA	Phyllodoce castanea							x	
POLYCHAETA	Phyllodoce papillosa			x					
POLYCHAETA	Phyllodoce polynoides	x	x			x	x		
POLYCHAETA	Phyllodocidae					x	x	x	x
POLYCHAETA	Phyllo felix	x							
POLYCHAETA	Pilargiidae							x	
POLYCHAETA	Pilargis berkeleyi				x				
POLYCHAETA	Pionosyllis uraga	x		x	x	x	x	x	
POLYCHAETA	Pisione remota							x	
POLYCHAETA	Pisionidae								x

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
POLYCHAETA	Pista		x						
POLYCHAETA	Pista brevibranchiata							x	
POLYCHAETA	Pista cristata								
POLYCHAETA	Pista elongata							x	
POLYCHAETA	Pista moorei		x	x					
POLYCHAETA	Pista pacifica				x				x
POLYCHAETA	Platynereis bicanaliculata			x				x	
POLYCHAETA	Podarkeopsis brevipalpa		x	x			x		
POLYCHAETA	Polychaeta				x				
POLYCHAETA	Polyeirrus								
POLYCHAETA	Polydora							x	
POLYCHAETA	Polydora brachycephala			x				x	
POLYCHAETA	Polydora cardalia		x	x	x				x
POLYCHAETA	Polydora giardi			x				x	
POLYCHAETA	Polydora socialis			x					
POLYCHAETA	Polynoe canadensis		x					x	
POLYCHAETA	Polynoidae								x
POLYCHAETA	Potamilla intermedia				x			x	
POLYCHAETA	Praxillella		x						
POLYCHAETA	Praxillella affinisaffinis	x			x				x
POLYCHAETA	Praxillella gracilis								x
POLYCHAETA	Praxillella pratermissa		x						
POLYCHAETA	Praxillells affinispacifica							x	
POLYCHAETA	Prionospio		x		x			x	
POLYCHAETA	Prionospio lighti			x	x				
POLYCHAETA	Prionospio multibranchiata				x				x
POLYCHAETA	Prionospio steenstrupi	x		x			x	x	
POLYCHAETA	Proclea graffi	x	x		x			x	
POLYCHAETA	Protodorvillea gracilis			x					x
POLYCHAETA	Pseudochitinopoma occidentalis			x				x	
POLYCHAETA	Pseudopolydora kempi	x	x			x	x	x	x
POLYCHAETA	Pygospio elegans		x	x		x	x	x	x
POLYCHAETA	Rhodine bitorquata	x			x				x
POLYCHAETA	Rhynchospio		x						
POLYCHAETA	Rhynchospio glutaea							x	
POLYCHAETA	Sabella pacifica		x		x			x	x
POLYCHAETA	Sabellaria cementarium		x	x	x				x
POLYCHAETA	Sabellariidae							x	
POLYCHAETA	Sabellidae					x	x		
POLYCHAETA	Samytha californiensis	x							
POLYCHAETA	Scalibregma inflatum							x	
POLYCHAETA	Scalibregmidae		x		x			x	
POLYCHAETA	Schistocomus hiltoni							x	x
POLYCHAETA	Schistomeringos annulata				x				x
POLYCHAETA	Schistomeringos caeca	x							
POLYCHAETA	Schizobranchia insignus					x			x
POLYCHAETA	Scionella estevanica			x		x			
POLYCHAETA	Scionella japonica	x	x		x	x	x		

Appendix 4. (continued)

CLASS	GENUS,SPECIES	Fjo1	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelt
POLYCHAETA	Scolelepis								x
POLYCHAETA	Scolelepis foliosa		x						
POLYCHAETA	Scolelepis squamata				x	x			
POLYCHAETA	Scoloplos		x						
POLYCHAETA	Scoloplos acmeceps			x	x				x
POLYCHAETA	Scoloplos armiger				x				
POLYCHAETA	Serpulidae	x	x			x	x		
POLYCHAETA	Sigalion				x				
POLYCHAETA	Sigalionidae					x	x		
POLYCHAETA	Sigambra tentaculata								
POLYCHAETA	Sosanopsis hesslei								x
POLYCHAETA	Sphaerodoridae		x		x				
POLYCHAETA	Sphaerodoropsis minuta		x						
POLYCHAETA	Sphaerodoropsis sphaerulifer			x		x	x		
POLYCHAETA	Sphaerosyllis brandhorsti		x	x					
POLYCHAETA	Sphaerosyllis pirifera					x			x
POLYCHAETA	Spio butleri		x						
POLYCHAETA	Spio cirrifera			x				x	
POLYCHAETA	Spio filicornis							x	
POLYCHAETA	Spiochaetopterus costarum								
POLYCHAETA	Spionidae							x	
POLYCHAETA	Spiophanes berkeleyorum			x					
POLYCHAETA	Spiophanes kroyeri						x	x	
POLYCHAETA	Spiorbidae		x						
POLYCHAETA	Sternaspidae					x	x		
POLYCHAETA	Sternaspis scutata			x			x		
POLYCHAETA	Sthenelais tertiaglabra		x						
POLYCHAETA	Streblosoma bairdi		x		x			x	
POLYCHAETA	Streblospio benedicti					x	x		
POLYCHAETA	Streptosyllis					x	x		x
POLYCHAETA	Syllidae								x
POLYCHAETA	Syllides longocirrata		x						
POLYCHAETA	Syllis								
POLYCHAETA	Syllis alternata		x						
POLYCHAETA	Syllis elongata			x					x
POLYCHAETA	Syllis harti				x			x	
POLYCHAETA	Syllis heterochaeta			x	x				
POLYCHAETA	Syllis hyalina	x	x		x	x	x	x	x
POLYCHAETA	Tenonia kitsapensis		x						
POLYCHAETA	Tenonia priops			x					
POLYCHAETA	Terebellidae					x			
POLYCHAETA	Terebellides californica		x						
POLYCHAETA	Terebellides stroemi			x			x	x	
POLYCHAETA	Thalenessa					x			
POLYCHAETA	Tharyx								
POLYCHAETA	Tharyx multifilis			x			x	x	
POLYCHAETA	Tharyx secundus			x					x
POLYCHAETA	Tharyx tessalata		x			x		x	x

Appendix 4. (continued)

CLASS	GENUS,SPECIES	rjol	Van1	Van2	Bound	AA82	AA3-9	Hec	Shelf
POLYCHAETA	Thelepus cincinnatus		x			x	x	x	x
POLYCHAETA	Thelepus japonicus								
POLYCHAETA	Thelepus setosus							x	
POLYCHAETA	Travisia		x						
POLYCHAETA	Travisia brevis							x	
POLYCHAETA	Travisia pupa								
POLYCHAETA	Trichobranchidae								
POLYCHAETA	Trichobranchus glacialis								x
POLYCHAETA	Trochochaeta multisetosa			x					x
POLYCHAETA	Trochochaetidae		x						
POLYCHAETA	Trypanosyllis							x	
POLYPLACOP	Lepidochitona flectens								
POLYPLACOP	Lepidochitonidae							x	
POLYPLACOP	Lepidozona mertenzii								
POLYPLACOP	Polyplacophora		x						
PYCNOGONIDA	Achelia alaskensis								x
PYCNOGONIDA	Achelia nudiuscula							x	
PYCNOGONIDA	Phoxichilidium femoratum							x	
SCAPHOPODA	Cadulidae								x
SCAPHOPODA	Cadulus	x						x	
SCAPHOPODA	Cadulus aberrans		x				x		x
SCAPHOPODA	Cadulus hepburni		x						
SCAPHOPODA	Cadulus tolmiei				x			x	
SCAPHOPODA	Dentaliidae					x			
SCAPHOPODA	Dentalium agassizii	x							
SCAPHOPODA	Dentalium pretiosum						x	x	
SCAPHOPODA	Leavidentalium dalli	x							
SCAPHOPODA	Polyschides californicus		x						
SCAPHOPODA	Rhabdus rectius						x	x	
SCAPHOPODA	Scaphopoda				x			x	x
SIPUNCULA	Golfingia				x	x	x		
SIPUNCULA	Golfingia margaritacea							x	
SIPUNCULA	Golfingia minuta							x	
SIPUNCULA	Golfingia vulgaris							x	
SIPUNCULA	Sipunculus		x						
STENOLAEMA	Ascophora							x	
TANAIDACEA	Leptochelia dubia			x					x
TANAIDACEA	Leptognathia brevimanus							x	
TANAIDACEA	Leptognathia gracilis	x					x		
TANAIDACEA	Neotanaidae						x		
TANAIDACEA	Pseudotanais								
TANAIDACEA	Stenotholdae				x			x	
TANAIDACEA	Typhlotanais								x
TURBELLARI	Polycladida		x						
TURBELLARI	Turbellaria				x	x	x	x	
TURBELLARI	Turbellaria				x	x	x		