

AN ABSTRACT OF THE THESIS OF

Robert Spencer Carney for the degree of Doctor of Philosophy
in Oceanography presented on September 14, 1976
Title: PATTERNS OF ABUNDANCE AND RELATIVE ABUNDANCE OF BENTHIC HOLO-
THURIANS (ECHINODERMATA:HOLOTHURIOIDEA) ON CASCADIA BASIN AND TUFT'S
ABYSSAL PLAIN IN THE NORTHEAST PACIFIC OCEAN

Abstract approved: *Redacted for Privacy*
Dr. Andrew G. Carey, Jr.

Cascadia Basin and the deeper Tuft's Abyssal Plain are inhabited by a common set of holothuroid species but differ markedly in proportional composition and apparent abundance. Seventy-six trawl samples were collected in a grid on Cascadia Basin. Depth appeared to be the major factor affecting the proportional composition of the dominant species. The fauna became progressively more uniform as the depth gradient decreased. The region adjacent to the base of the slope was distinct in its low diversity and low proportions of small specimens of the most common holothuroid species. These features might be due to increased competition and predation in that region. Sixteen trawl samples were examined from Tuft's Plain. Again the fauna appeared to be affected primarily by depth. While the abundance of holothuroids remained uniform across the flat Cascadia Basin, it appeared to decrease exponentially with depth across Tuft's Plain.

The uniformity of proportional composition and abundance of the holothurian fauna across the floor of Cascadia Basin is in marked contrast with previously reported patterns of infaunal organisms. It

is suggested that the differences reflect basic differences in the ecologies of the infauna and the motile epifauna, and that the size distribution of food material from overlying water may be of importance in determining the benthic fauna composition.

A geometric representation of the analyses used is given. Concepts of deep-sea benthic ecology are reviewed, and current diversity hypotheses are reviewed relative to the findings of the study.

The Patterns of Abundance and Relative Abundance
of Benthic Holothurians (Echinodermata:Holothurioidea)
on Cascadia Basin and Tuft's Abyssal Plain in the
Northeast Pacific Ocean.

by

Robert Spencer Carney

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

June 1977

APPROVED:

Redacted for Privacy

Associate Professor of Oceanography
in charge of major

Redacted for Privacy

Acting Dean of the School of Oceanography

Redacted for Privacy

Dean of the Graduate School

Date thesis is presented September 14, 1976

Typed by Rebecca Rakish for Robert Spencer Carney

ACKNOWLEDGEMENTS

The research reported in this thesis was undertaken because of an interest in marine life that began twenty years ago on Sanibel Island off the west coast of Florida. Since that beginning I have been most fortunate to have had several people make a contribution to the process by which a childhood fascination turns into directed scientific inquiry. Through their encouragement, teaching, and direction, each has directly contributed to the completion of this thesis.

I am indebted to Dr. Andrew Carey for serving as my major professor and freeing me from worries about funding and facilities. By introducing me to the fascinating aspects of quantitative ecology, Dr. Scott Overton significantly improved my ability to recognize, phrase, and answer ecological questions. Dr. Charles Miller provided excellent company during my varied attempts to both learn and to teach numerical techniques. In addition, the thoughtful criticism he provided on very short notice greatly improved this thesis. Dr. William Percy and Dr. Vern Kulm both helped me to see the importance of my study in a larger ecological context.

Although not serving on my graduate committee, several persons contributed to the thinking behind this thesis by sharing their own ideas and being tolerant of mine. In chronological order these include: Mrs. Francis Wild, Dr. D.A. Livingstone, Dr. Gilbert Rowe, Dr. Willis Pequegnat, Dr. David Pawson, Miss Maureen Downey, Dr. Peter Dawson, Dr. John Wiens, Dr. Author Boucot, and Dr. Jorn Theide.

The production of this thesis was greatly facilitated by the help and advice of many people. Pat Tester frequently provided editorial assistance, and Rebecca Rakish was quite tolerant of my many revisions. I would especially like to thank Dr. Charles Shluts for providing a needed bit of peace of mind, and the Oregon State Sea Grant Program (grant number 4-5-158-2) for partial financial support. Computer use was funded through a grant from the Oregon State University Computer Center.

Of all the thanks that I owe, that due to my family is the greatest. They have continued to be my greatest source of encouragement since the days of gallon jar aquaria and ghost crabs on the warm beaches of Sanibel Island.

TABLE OF CONTENTS

	Page
I. INTRODUCTION	1
General Considerations	1
General Approach	2
Evaluation of the Importance of Depth and Distance	3
II. REVIEW OF CONCEPTS	5
III. BIOLOGY OF THE HOLOTHURIOIDEA	16
IV. THE ENVIRONMENT SAMPLED	20
V. SAMPLING	33
Evaluation of the Beam Trawl	37
Attempt to Determine Area Sampled	37
Sampling Efficiency	40
VI. ANALYSES	46
General Considerations	46
Vector Representation of a Sample	48
Vector Lengths-Distances	49
Angles Between Vectors - SIMI	51
Restraining Surfaces	54
AIDN Analysis of Variation on the Proportion-Surface	57
Computation Form of the AIDN Analysis of Variance	60
Reducing the Dimensionality of a SIMI matrix	62
Analysis of Size Relationships	64
VII. RESULTS	66
Vertical Zonation	66
Holothurian Catch vs. Total Invertebrates	69
Abundance of Holothurians	71
Within Sample Relative Abundance	79
AIDN Analyses of Variance	79
Inter-area Similarities	88
CABFAC Vector Analysis	91
Diversity Patterns	97
Distribution of Species	104
Abundance vs. Occurrence	114
Body Sizes	119
Dependence of Small:Large Upon Region Sampled	123
Summary of Results	127
VIII. DISCUSSION	130
Depth Controlled Species Composition	130
Distribution of Size Classes	132

	Page
Holothuroid Size and Diversity Hypotheses	136
Infauna-Holothuroid Comparisons	139
Suggested Importance of Food Grain Size	145
IX. CONCLUSIONS	150
BIBLIOGRAPHY	153
APPENDIX I	162
Station data for beam trawl samples.	
APPENDIX II	166
Faunal lists for beam trawl samples.	

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Vertical ranges of holothuroid species off Oregon.	67
2	The average, maximum, and minimum catch of Holothuroids per trawl at each sampling area.	77
3	AIDN analysis of variance for Cascadia Basin series of samples.	85
4	Separate AIDN analyses of variance for each offshore series.	86
5	AIDN analysis of variance for Tuft's Plain series of samples.	87
6	Matrix of inter-area SIMI's, similarity index.	89
7	Unrotated CABFAC factor scores.	92
8	Three measures of diversity at each sample area.	103
9	Proportion of each species at each pooled sample area.	105
10	Contingency tables for large and small specimens of six species across the basin and plain.	124
11	Comparison of SIMI matrices for holothurians and for infaunal polychaetes along the CP-E series of samples	141

LIST OF FIGURES

Figure		Page
1	Major physiographic features off Oregon.	24
2	Gradation of percent clay in surface sediments of Astoria Fan and adjacent areas of Cascadia Basin.	26
3	Decrease in terrestrially derived detrital grains in the surface sediments of Cascadia Basin.	27
4	Gradation of percent of terrigenous plant fragments in the coarse fraction of surface sediments of Cascadia Basin.	28
5	Distribution of postglacial clay mineral facies.	29
6a	Location of beam trawl samples taken in Cascadia Basin and Tuft's Plain.	34
b	Identifying codes for the sample grid.	35
7	Scatter plot of number of holothurians collected per trawl versus area of bottom sampled according to the odometers.	39
8	Effect of selection ogive upon the fauna sampled.	42
9	The cumulative size frequency histogram for 11,320 specimen lengths taken from seven species.	44
10a	Samples 1 and 2 modeled as two points in three dimensioned species space.	50
b	Three distance, vector length, measures.	50
c	Comparing two samples by the angular separation of two vectors.	52
d	Comparing two sample points by the angular separation between the two SD vectors,	52
e	The angle Rho when looking from the center-line of space towards the origin.	53
f	Insertion of the proportion surface.	53
g	Distance measures and the angle Rho on the proportion surface.	56
h	The right tetrahedron of diversity, equitability, and similarity.	56
i	Insertion of the unit sphere restraining surface.	63
j	Position of new, orthogonal axes (factors) relative to the old axes and sample vectors.	63
11	Plot of the number of holothuroid specimens per trawl versus the number of invertebrates.	70

Figure		Page
12	The rank of abundance of the first and second most abundant holothuroids per trawl when all invertebrates are ranked.	72
13	The number of holothuroids per trawl versus the depth of collection.	75
14	Plot of holothurians per trawl versus position seaward.	76
15	Change in abundance of the four major species on Tuft's Plain.	80
16	Change in abundance of three major species at CP-1 with accompanying changes in Simpson's D squared.	81
17	Change in abundance of three major species at CP-2 with accompanying changes in Simpson's D squared.	82
18	Change in abundance of three major species at CP-3 with accompanying changes in Simpson's D squared.	83
19a	Cosine of angle between each sample vector and the first reference axis.	94
b	Cosine of angle between each sample vector and the second reference axis.	95
c	Cosine of angle between each sample vector and the third reference axis.	96
20	The number of holothurian species per trawl against the log of both number of holothurian specimens and total invertebrates on Cascadia Basin.	99
21	The number of holothuroid species per trawl against the log of both number of holothurian specimens and total invertebrates on Tuft's Plain.	100
22	The rank-abundance diagrams for the pooled samples of Tuft's Plain and Cascadia Basin showing the similarity of form.	101
23	The rank of abundance diagrams for holothurians in the pooled samples from each Cascadia Basin offshore series.	102
24a	Abundance versus occurrence for the three major species on Cascadia Basin.	116
b	Abundance versus occurrence for the minor species on Cascadia Basin.	116

24c	Abundance versus occurrence for the major species on Tuft's Plain.	117
d	Abundance versus occurrence for the minor species on Tuft's Plain.	117
e	Abundance versus occurrence for <u>Psychropodes longicaudata</u> .	118
25	Size frequency histograms of body lengths for the seven most abundant holothuroid species.	120
26	Wet weight and estimated density of infauna across the CP-E series and out onto Tuft's Plain.	142

PATTERNS OF ABUNDANCE AND RELATIVE ABUNDANCE OF BENTHIC HOLOTHURIANS
(ECHINODERMATA:HOLOTHURIOIDEA) ON CASCADIA BASIN AND TUFT'S ABYSSAL
PLAIN IN THE NORTHEAST PACIFIC OCEAN

I. INTRODUCTION

General Considerations

Most samples of the deep-sea benthos have been collected along transects where both distance to land and water depth increased together. Thus it has been difficult to determine the relative importance of depth-related and distance-related factors in causing the observed variations in faunal composition and abundance. Depth primarily affects hydrographic parameters that are of physiological importance (see Kinne, 1970). However, depth may also determine sediment composition through dissolution of calcium carbonate and affect the amount of surface productivity reaching the bottom. Distance to land is of primary importance in determining the amount of terrestrial sediment in the bottom, the flux of near-shore production to the benthos, and the level of productivity in the overlying surface water.

This present study is directed at describing the distribution of the fauna on Cascadia Basin and Tuft's Abyssal Plain. The relative importance of depth and distance was assessed by comparison of transects in which depth varied but distance from land had a relatively fixed value. Cascadia Basin is a southward tilting plain lying at approximately 2800 m depth off the coast of Oregon, U.S.A. For much of the world ocean this depth occurs on the relatively steep face of the continental slope and rise. The sampled portion of Tuft's Plain tilts westward so that depth increases from 3354 m to 3900 m seaward.

The echinoderm class Holothurioidea, sea cucumbers, is the faunal component studied in detail. With few exceptions the deep-sea species feed by ingestion of surface sediments and any associated organic material. Because of the uniformity of feeding type the holothurians may be studied both as a functional ecological unit and as a taxonomic unit. The class is strictly marine, but otherwise cosmopolitan and eurybathic. They are one of the most abundant taxa collected in trawls below 2000 m and may be numerically dominant in hadal trenches (Belyaev, 1972, and Hansen, 1975). The distribution of sediment feeding reported by Sokolova (1959) was primarily reflective of the distribution of holothuroids more than any other taxa.

General Approach

Examination of Distribution Patterns

Distribution patterns were examined in hierarchical fashion, alternately treating the region sampled as a whole and then as subunits. Similarly all holothurians specimens were first treated together as a whole, separately as species, and then individual size classes within each species. My intent in performing this hierarchical examination was to let the findings of each step provide a framework for interpretation of the next more detailed examination.

1. The holothuroid specimens from Tuft's Plain, Cascadia Basin, the continental slope and continental shelf were identified. This placed the faunas of the two principal sites into a larger regional and bathymetric context.

2. The holothuroids were related to the rest of the invertebrates collected in the same trawls. This placed the holothuroids into a larger faunal context and indicated the extent to which my conclusions might predict findings based on the entire invertebrate fauna.
3. The relative abundance and statistics based upon relative abundance such as diversity, were examined for pattern across the basin and plain.
4. The pattern of absolute abundance, as reflected by catch size, for total holothurians was examined and then patterns of absolute abundance of individual species.
5. The abundant species were divided into two size classes in order to seek possible size specific variation in distribution across the region sampled.

Evaluation of the Importance of Depth and Distance

A multivariate factorial analysis of variance (Section VI) was used to evaluate the relative importance of depth-related and distance-related environmental parameters upon the proportional composition of the holothurian fauna. This analysis was possible due to the bathymetry of Cascadia Basin (Section IV) and the grid system of samples (Section V). Depth increased from north to south along each uniform distance from land transect.

1. The total variation of the proportions of holothuroids was computed.
2. The total variation was partitioned into that due to position in the sampled region and that due to the trawl samples.

3. The variation due to position was then partitioned into its distance component and its north-south component which corresponded with depth.

4. The variation among the individual trawls was the residual variation by which the significance of other sources of variation was tested.

II. REVIEW OF CONCEPTS

Curiosity as to the changes undergone by the fauna of the ocean bottom as it slopes downward beyond the reach of the early dredges provided the scientific impetus for deep-sea studies in the nineteenth century. In the eighteenth century it had been established that the coastal bottom fauna could be classified into bathymetric zones. These zones had sufficient regularity in their similarity to one another that some workers even predicted the type of faunal changes that might be found in deeper unsampled areas. Good reviews of the ideas concerning the biology of the ocean bottom prior to and after the voyage of H. M. S. Challenger have been given by T. H. Huxley (1873) and Sir John Murray (1895). Two major postulations stand out in these reviews. Edward Forbes had extrapolated from his Adriatic sampling that the deep oceans were devoid of life below a depth of approximately 600 meters, and Sir Wyville-Thompson had extrapolated from the occurrence of Crinoids at deep continental shelf depths that the abyss would be populated by an archaic fauna. The Darwin-Wallace theory of natural selection had only recently been proposed, so there was considerable general scientific interest in the relationships between organisms and extreme environmental conditions. Forbes was primarily concerned with the extreme conditions of pressure and darkness, while Wyville-Thompson was concerned with extremely low environmental fluctuation rather than absolute values of environmental parameters. If natural selection proceeded in response to a fluctuating environment, then a relatively constant deep-sea must be filled with animals that had changed little since

entering the abyss. So certain was A. Agassiz that the deep-sea fauna would prove to be archaic that he announced this very conclusion on the basis of both the Challenger and his own expeditions, even though detailed studies had not been completed (A. Agassiz cited in Anon., 1877). Unlike the English workers, he considered this to be contrary to the predictions based upon natural selection theory, rather than supportive of them.

Although the initial deep-sea sampling programs were organized around specific objectives that were based upon current biological concepts, they contributed surprisingly little to the body of knowledge that gave rise to the field of ecology (Hedgpeth, 1957). The major naturalists associated with these expeditions did, however, develop general opinions on what we could now call deep-sea benthic ecology. Unfortunately, these overviews are generally overlooked although they are often strikingly similar to conclusions being drawn anew today. The most extensive account is that of Murray (1895), but the published lectures on the subject by Mosely (1880) and Jeffreys (1881) are also informative. It was well noted by all three that the deep-sea had a fauna that was both far more numerous and diverse than had been anticipated. Murray devoted several pages of his summary to a careful documentation of the fact that sample for sample the deep-sea contained more species and less dominance by a single species than was encountered in temperate shallow seas. The abyss was acknowledged not to contain a fossil fauna, although some distinctly primitive animals were taken there. It was also noted that there was monotony in the fauna over large areas of the oceans, but that samples from far apart were more

dissimilar than samples taken close together. Having found an unexpectedly diverse and abundant fauna it was suggested that the sinking of dead organisms from the overlying water column was the primary source of nutrition supplemented by nutrient material discharged from land. Moseley reported that the sinking rate of dead salps was so great that they could sink to 2000 fathoms in as little as four days. He concluded that this fast rate was partial confirmation that the deep-sea bottom fauna relied upon the productivity of the overlying water, and that investigation of the fauna to be found between producer surface and consumer bottom was the major area of research in the deep-sea.

That the above ecological conclusions were meager for such grand expeditions as the Challenger is obvious in the contemporary criticism of Anton Stuxburg (1883). He charged that the collection and classification of specimens was inadequate to assess anything of the synecological nature of the fauna in each area. Stuxburg listed the type of data that must be obtained and analyzed to gain an understanding of those factors which give rise to the observed distribution of animals upon the seafloor. In addition to the obvious environmental parameters Stuxburg required that the relative "plurality" of all species sampled in each trawl be compiled, and that only through the examination of such data could any understanding of the "laws" governing distributions be gained. This present study is thus the extension of the type of taxonomic studies demanded by Stuxburg. I have combined the study of holothurians as items of considerable taxonomic interest with the study of their patterns of relative plurality, or abundance.

The holothurians collected from the deep-sea by the Challenger expedition were so abundant and distinct from shallow water forms that they resulted in a two-volume monograph containing considerable revision (Theel, 1882, 1886). Most major deep-sea expeditions have produced at least a single work devoted to the identity and taxonomic relationships of the numerous holothurian specimens, but very little concerning possible ecological relations of this obviously abundant component of the deep-sea benthic fauna.

Just as English benthic studies of the deep-sea during the Challenger era were an out-growth of the great interest in animal-environment relations inspired by the theory of natural selection, a large portion of modern American studies are conducted within the conceptual framework of current ecological thought. In the nineteenth century notions of the effect of severe environments lead to the inaccurate prediction that the deep-sea would be devoid of life. In this second half of the twentieth century a prediction drawn from modern niche theory (Hutchinson, 1953) that a uniform environment, such as the deep-sea benthos is assumed to be, must be dominated by a few competitively superior species has been found to be incorrect. As indicated earlier in this section the discovery of high diversity in samples from the deep-sea is a published conclusion of the Challenger expedition, however, the levels of species richness and equitability found by Sanders and Hessler (summarized in Hessler and Sanders, 1967) off the northeast coast of the United States exceeds even that found by the Challenger. Additionally, these contemporary workers were the first to discuss this unexpected diversity in the context of niche theory.

Interestingly there have been several explanations as to why the deep-sea benthos has not been taken over by a few competitively superior species, but none have entertained the simple explanation that the competitive exclusion hypothesis is simply wrong, and that similar species utilizing similar environmental resources can indeed co-exist. The proposed explanations, usually put forward as hypotheses, each deny or admit certain assumptions about the deep-sea environment. The most basic assumption that the benthic environment is so physically uniform as to provide no boundaries or refuges from competition has been rejected by Gray (1974). His contention is that the very high diversities in the deep-sea are associated with sediments which have the highest variability of composition. Diversity in the deep-sea is explained by environmental heterogeneity and no special mechanism is required to allow for the high faunal diversities. The Stability-Time hypothesis formalized for the deep-sea by Slobodkin and Sanders (1969) and the Cropper hypothesis proposed by Dayton and Hessler (1972) can be considered opposing views, yet they are quite similar in that both assume the deep-sea benthos to be a vast, homogenous environment. The two hypotheses differ only in the suggested mechanisms which prevent competitive exclusion in a structurally simple environment. The Stability-Time hypothesis proposes that in a physically uniform environment natural selection has been due more to biological interactions than physical stress. Evolution under these conditions of selection should give rise to a community of species that are "biologically accommodated" to one another. The accommodation would manifest itself in the form of reduced competition for the limited

resources available. The Cropper hypothesis also assumes a biological control acting to reduce competition, but rather than slow coadaptive evolution involving many species, intense nonselective predation is invoked. The envisioned predation must be so intense as to keep all potentially competing species below the carrying capacity of the environment and thus prevent exclusion through monopolization of the common resources.

As Menzies et al. (1973) pointed out the Stability-Time hypothesis is similar to a number of hypotheses put forward to explain the high diversities found in the terrestrial tropics. All are firmly based upon the old idea that the tropics have remained climatically unchanged over millions of years. Therefore all of these hypotheses have been greatly weakened by the increasing body of paleontological evidence indicating that there was considerable environmental variation during the Quaternary in what is today the tropics (Livingstone, 1975). Eventually determinations of paleotemperature from benthic foraminifera collected at abyssal depths may also cause revision of the Stability-Time hypotheses. However, even now it has been suggested that the deep-sea has not been a stable environment over a geological time span (Benson, 1975). The diversity of fossil faunas does not increase in vertical sections assumed to represent millions of years of relatively unchanged climatic conditions (Boucot, 1975). Between environments which differ mainly by the variation in physical parameters, high diversity is not seen in the more stable environment (Abele, 1976).

The Cropper hypothesis is an admitted extension of concepts obtained from the study of inter-tidal rock epifauna in Puget Sound,

Washington, U. S. A. Similar predator-control of diversity have been suggested for the tropics (Jansen, 1970). The two most effective attacks on this hypothesis have come from Van Valen (1974) and Grassle and Sanders (1973). Both demonstrate that random predation will not prevent competing prey organisms from outcompeting one another. However, as admitted by these latter authors, the randomness of the predation is only implicit in the Cropper hypothesis and not actually specifically claimed by Dayton and Hessler. It is a simple task to envision predation which would act more strongly against a prey species which was beginning to dominate the environment and thus maintain diversity by reducing the dominance of that one prey species. This may have been what Dayton and Hessler had in mind. Alternately, they could have intended a model such as that proposed by Levin and Paine (1975) in which a "patch" of resource cleared by a random disturbance is re-populated by a sussesional sequence. In this disturbed environment there would be a mosaic of successional stages contributing to an overall high diversity.

The Stability-Time and Cropper hypotheses may be classed as homogenous environment explanations of high diversity as opposed to Grey's explanation of diversity simply reflective of a heterogenous environment. However, the latter two are quite different from the Stability-Time hypothesis in that they include a relatively nonselective biological control of diversity. Grey suggests that one component of the variability in the deep-sea benthic community may be due to the action of sediment burrowing and ingesting animals such as holothurians. Unfortunately, the genus Psolus which he chose to cite as an example

is a sedentary suspension feeder; nevertheless there are numerous other species which might fill the role. In the Cropper hypothesis holothurians are among the large epifaunal animals suggested as the source of the needed high intensity, nonselective predation. In both hypotheses the sediment feeding behavior of holothurians is seen as a possible biological control allowing for the maintenance of a high infaunal diversity.

Studies of the zonation of the deep-sea fauna are one of the main descriptive activities in deep-sea research. Unlike diversity studies which are largely dominated by Americans working with the meiofauna and macrofauna, zonation studies are more universal in both scope and nationality. Summary works such as that of Ekman (1953) recognized that the fauna was vertically zoned on the continental slopes, but appeared dispersed at random with the abyssal plains. Le Danois (1948) compiled the results of trawling in the eastern Atlantic and found a distinctly zoned fauna down to 2500 meters. Beyond this depth the distinctive zonation with depth disappeared. Since the holothurians collected in the cruises in the eastern Atlantic had received careful taxonomic study, they were an important portion of the fauna considered by LeDanois. As Rowe (1968) has noted, samples collected to specifically study vertical zonation have usually been restricted to a narrow transect. The faunal changes seen along a narrow transect into deeper water will appear to be depth dependent even though there may be great horizontal changes at any one isobath. Such horizontal change was Rowe's (1968) finding. The densities of mega-epifauna seen in bottom photographs taken off the coast of North Carolina, U. S. A. were

found to vary considerably along any horizon, presumably due to effects of deep currents. To the contrary, Sanders et al. (1965) found that the infaunal species collected by dredge do show very strict circumscribed depth zonation in the Atlantic. Obviously, there are those species which do show a considerable variation in depth and those that do not. As to whether the deep-sea is to be typified as strictly zoned or not, depends mostly upon what animals are considered. The possibility exists that the difference in findings between people like Rowe (1968) who worked with the motile mega-epifauna and those like Sanders and associates who worked with potentially less motile, smaller infauna illustrates a real, basic dissimilarity in the ecologies of these two general categories of benthic animals. A much fuller review of zonation schemes along with a few new suggestions is to be found in Menzies, George, and Rowe (1973). More recently, photogrammetric surveys have been utilizing the deep submersible Alvin (Grassle et al. 1975). This present study stands out as the most extensive trawl survey of relatively level bottom fauna at lower bathyal and abyssal depths.

Soviet zonation studies have been of particular interest in that their sampling has been done at the deepest of hadal depths and also over wide areas of the central oceans. Zenkevitch (1963) presents a summary of the zonation studies done primarily by Vinogradova. Belyaev (1972) similarly summarizes studies in the hadal depths. A beam trawl is a standard piece of collecting gear on Soviet expeditions, therefore, holothurians are a major component of the collections. Belyaev (1972, English translation, p. 85) characterizes the hadal environment

as the "kingdom of the holothurian". In a series of papers Sokalova (see 1972, for a full list of references) has modeled the areal distribution of the abyssal fauna of the central abyssal plains in terms of trophic level. At the continental margins she claims that motile sediment ingesters such as holothurians abound and are predominant due to the high productivity of the overlying water. This high food input from above is coupled with a high sedimentation rate which serves to bury and preserve the food raining down. In the central areas of the ocean with low productivity and low sedimentation rate sediment feeders cannot be successful because the low input is not preserved by sediments, thus suspension feeders predominate. Hessler and Jumars (1974) working with polychaetes did not confirm Sokolova's findings of a suspension feeder fauna in these areas.

Since the Challenger expedition deep-sea holothurians have received greater interest as items of taxonomic study than of ecology. The published taxonomic works reflect the pattern of sampling, with greatest information coming from the Atlantic Ocean. Early information specifically on the holothurian fauna of the Pacific Ocean came mainly from the Pacific stations of the H. M. S. Challenger and the U. S. F. S. steamer Albatross. This latter vessel sampled with a trawl along the Pacific Rim from Peru to Northern Japan. The holothurian specimens have been studied by many workers and described piece meal by six authorities so far (Ludwig, 1894; Oshima, 1915; Fisher, 1907; Edwards, 1907; H. L. Clark, 1920; and Mitsukuri, 1912). More recently the results of Soviet sampling in hadal trenches of the northwestern Pacific

(Belyaev, 1970, 1971) and the results of the Galathea expedition which included Eastern Pacific samples (Hansen, 1975) have been published.

Hansen's recent monograph on the order Elasipoda, that taxon most restricted to the deep-sea, is the most comprehensive account currently available. In addition to the taxonomic work, Hansen has begun a lengthy synthesis which will ultimately allow the placing of the holothurians in a larger ecological context. However, at the present a summary of their known or presumed ecological significance can be brief.

III. BIOLOGY OF THE HOLOTHURIOIDEA

Holothuroids, sea cucumbers, are one of the five living classes of echinoderms. The approximately 1100 species (Hansen, 1975) have the pentaradial symmetry of most echinoderms but are usually elongated orally-aborally and have assumed varying degrees of bilateral symmetry. Historically the holothurians have received less study than other echinoderms. Thus, only a few comprehensive biologies have been compiled (Cuenot, 1948; Deichmann, 1930; Frizzel and Exline, 1966; Hyman, 1955; and Pawson, 1969). Although the general biology of holothurians has been learned from the study of shallow water forms, the increased deep-sea sampling of the past few decades has resulted in increased interest in the biology of the abundant deep-sea forms. As has been pointed out by Pawson (in press) the striking differences in morphology between the shallow and deep forms are suggestive of major ecological differences that have yet to be studied.

The current taxonomy of holothurians is in flux, but the system proposed by Pawson and Fell (1965) provides an adequate framework for revision. There are six orders which are distinguished both by morphology and ecology. The order Dendrochirotida Grube 1940, has bushy oral tentacles with which it feeds upon material suspended in the water. In the deep-sea only two genera of this order are found, Psolus and Abyssocucumis. The order Dactylochirotida Pawson and Fell, 1965, is similar to Dendrochirotida, but the oral tentacles are reduced to short digits. These animals are restricted to the deep-sea and appear to be infaunal forms feeding from the sediment surface.

Only the genus Ypsiolothuria of this order has been collected off Oregon. Most species of deep-sea holothurians are members of either the order Aspidochirota Grube, 1840, or Elasipoda Theel, 1882. Both of these orders are motile sediment ingesters. The order Aspidochirotida is most typical of the shallow water trophics where the families Holothuridae and Stichopidae may achieve very high densities. The order is represented in the deep-sea by the family Synallactidae which shows considerable morphological variation. The order Elasipoda is considered the most typically deep-sea of all holothurian orders. The genera of this order are distinct in that most have elaborate development of the dorsal podia. Hansen (1975) has produced a very complete monograph on the order Elasipoda. It was Hansen's finding that variations in tentacle structure and gut size indicated some feeding specializations within the order. This is excellently seen in three common elasipodes off Oregon, Peniagone cf. dubia, Scotoplanes globosa, and Psychropodes longicaudata. While Peniagone has relatively long, bushy tentacles and a narrow gut with very large mesentral blood sinuses, Scotoplanes and Psychropodes have shorter, simpler tentacles and very large mud-filled intestines. The significance of these distinctions, however, is not known.

The artificial order Apodida Brandt, 1835, and Molpadida Haeckel, 1896, are the most worm-like of holothurians with virtually no podia along the sides of the body. The molpadids are clearly infaunal sediments feeders in shallow water while the apodes have a wide variety of ecologies. Examples of both orders were taken in the collection off Oregon.

While shallow water holothurians are relatively sedentary animals, it appears that as many of the deep-sea forms of both the order Aspidochirotida and Elasipodita are morphologically adapted to perform some swimming off the bottom. The early evidence for off-bottom swimming of abyssal holothurians has been reviewed by Hansen and Madsen (1956). More recently Pawson (in press) has collected information gained from observation in deep submersibles and observation of 80,000 deep-sea bottom photographs. Of the species collected off Oregon both the genus Paelopatides and Psychropodes have been known to swim. The other common genera Scotoplanes and Peniagone, to the contrary, have never been observed to swim when disturbed by submersibles.

From the examination of bottom photos it would appear that holothurians in the deep-sea often form dense aggregations possibly in response to feeding conditions. On the basis of bottom photographs from baited cameras there is some evidence that holothurians can detect and respond to the bait (Pawson, *ibid*, and Hessler, 1972). There is, however, no evidence that holothurians ever eat anything other than ingested sediment, nor that they are capable of consuming larger organisms. Early speculation by Hansen (1956) that the deep-sea molpadid Ceroplectana might be carnivorous was not confirmed by examination of specimens in this study.

Extremely little is known about the mode or periodicity of reproduction in the deep-sea holothurians. As Hansen (1975) has noted, even the smallest ova found in the elasipoda are large by comparison to those of other echinoderms. The ova from specimens of Psychropodes

are the largest ever recorded for any echinoderm, measuring over 4 mm in diameter. This preponderance of large ova is suggestive of a lecitotrophic development.

IV. THE ENVIRONMENT SAMPLED

The only portions of the vast deep-sea bottom that have been subjected to extensive faunal surveys are the small areas within a few days cruising of oceanographic research facilities. Even though the usual goal of such surveys is to gain a general understanding of the whole deep-sea ecosystem, some of the findings must reflect strictly local phenomena. While the vastness and monotony of the ocean's surface encourages a tendency towards making general statements from localized observations, it is extremely important that unique aspects of each locality be considered during the planning, actual collection, and final analysis of data. The greatest understanding of ecosystems under study will be obtained through the examination of the faunal differences that may be found along gradients of environmental change.

Without attention to unique environmental conditions, the presence of very important physical gradients might be overlooked in the rush to draw conclusions with wide application. The area of this present study must then be considered both as representative of the rest of the deep-sea benthos and distinctive from it. The following discussion will establish that in many, if not most regards, Cascadia Basin is a unique deep-sea environment.

The continental borders of the Pacific Ocean are distinct in that there is almost a continuous hadal trench extending around the Pacific Rim. These trenches are of possible ecological importance because they are the deepest marine environments and may serve as

traps preventing the seaward transport of terrigenous material. Unlike the rest of the Pacific Rim, from Central America to the Aleutian chain there is no distinctive deep trench. The holothurian specimens discussed in this present study were collected within this atypical region.

The northeastern Pacific border has a slope composed of basins and ridges that have been extensively studied geologically (Emery, 1960) and biologically (Hartmann, 1955) particularly off California. Menard (1955) classed this continental margin as a ridge and trough province, noting that Cascadia Basin off Oregon, Washington, and British Columbia is by far the largest of the basins. This large basin covers 170,000 square kilometers and is walled to the north and east by the North American continental slope, to the south-southwest by the Gorda Ridge, and to the west-northwest by the Juan deFuca Ridge. The general reference on the bathymetry of the Basin is MacManus (1964) who arbitrarily placed the upper boundary of the basin at the 2400 m contour.

Cascadia Basin may be a recent feature no older than Miocene. This age is inferred from magnetic anomalies associated with the Blanco Fracture Zone and the Juan deFuca Ridge (Atwater, 1970). Some workers interpret these structures to be part of the East Pacific Rise which disappears into the North American Continent off Lower California. In this interpretation the Gorda and Juan deFuca Ridges represent a sea floor spreading region much like that associated with the Mid-Atlantic Ridge (Wilson, 1965). Ewing, et al. (1968) and more recently Kulm and Fowler (1974) have stated that a hadal

trench may have existed along the coasts of Oregon and Washington similar to other sections of the Pacific Rim. The rate of terrigenous sedimentation into this trench must have been greater than the rate at which sediments were subducted under the continental margin by the spreading sea floor. As a result the former trench is now completely filled with sediments.

The bathymetry of Cascadia Basin is unique. The Basin extends from the arbitrary upper isobath at 2400 m to approximately 3000 m at its deepest corners. Unlike most of the ocean bottom at these depths, Cascadia Basin slopes to the south parallel to the continent. It is mostly a level plain from one wall seaward to the other. It is thus a large area with the depths and hydrographic conditions usually associated with a narrow zone on the steep continental margin. Menard (1955) has characterized Cascadia Basin and Tuft's Plains as, "A smooth plain communicating with a deeper smooth plain, separated by a ridge and trough province." There are two gaps in the seaward walls of the basin through which it communicates with deeper areas; the Blanco Gap to the south at the base of the continental slope and Cascadia Gap at the southwestern corner. Because these gaps coincide with the areas of the basin's maximal depth the walls do not form a continuous sill. The Basin can exchange both bottom water and possibly fauna with the deeper water to the south and west rather than being faunally and hydrographically isolated. The Juan deFuca Ridge is actually not a bathymetrically marked structure except around the associated seamounts. At its shallowest points it rises only about 400 m above the floor of the adjacent Cascadia Basin.

The sedimentary features within Cascadia Basin and Tuft's Abyssal Plain are of interest because they both determine depth of the present environment and reflect terrestrial influence through geological time (Figure 1). Extending into the basin from the continental shelf adjacent to the mouth of the Columbia River is the Astoria Submarine Fan studied by Nelson (1968) and Duncan (1968). Two deep-sea channels are associated with this fan. The presently inactive Astoria Fan Channel (Carlson, 1968) runs across the face of Astoria Fan then due south along the base of the slope exiting Cascadia Basin through the Blanco Gap. The Willapa Channel passes between Astoria Fan and Nitinat Fan to the north. At the base of the fans it merges with the larger Cascadia Sea Channel. The Cascadia Channel is the major feature of the central portion of the basin. Menard (1955) has classed this channel system as one of the world's longest. The channel is a major route for the transportation of terrigenous material across the basin (Griggs and Kulm, 1970). Structurally and sedimentologically the Cascadia Channel represents a physical environment distinct from the adjacent sea floor. The densities and biomass estimates taken from within the channel also suggest that its fauna may be dissimilar from that surrounding it (Griggs, Carey, and Kulm, 1969). Tuft's Plain lies seaward of Cascadia Basin, and is not as extensively studied. It is crossed by several sea channels that originate on the North American continental slope. The largest is Cascadia Channel which links the plain with Cascadia Basin.

In the surface sediments of Cascadia Basin there is a progressive decrease in terrigenous sediment (silt and sand layers) and increase

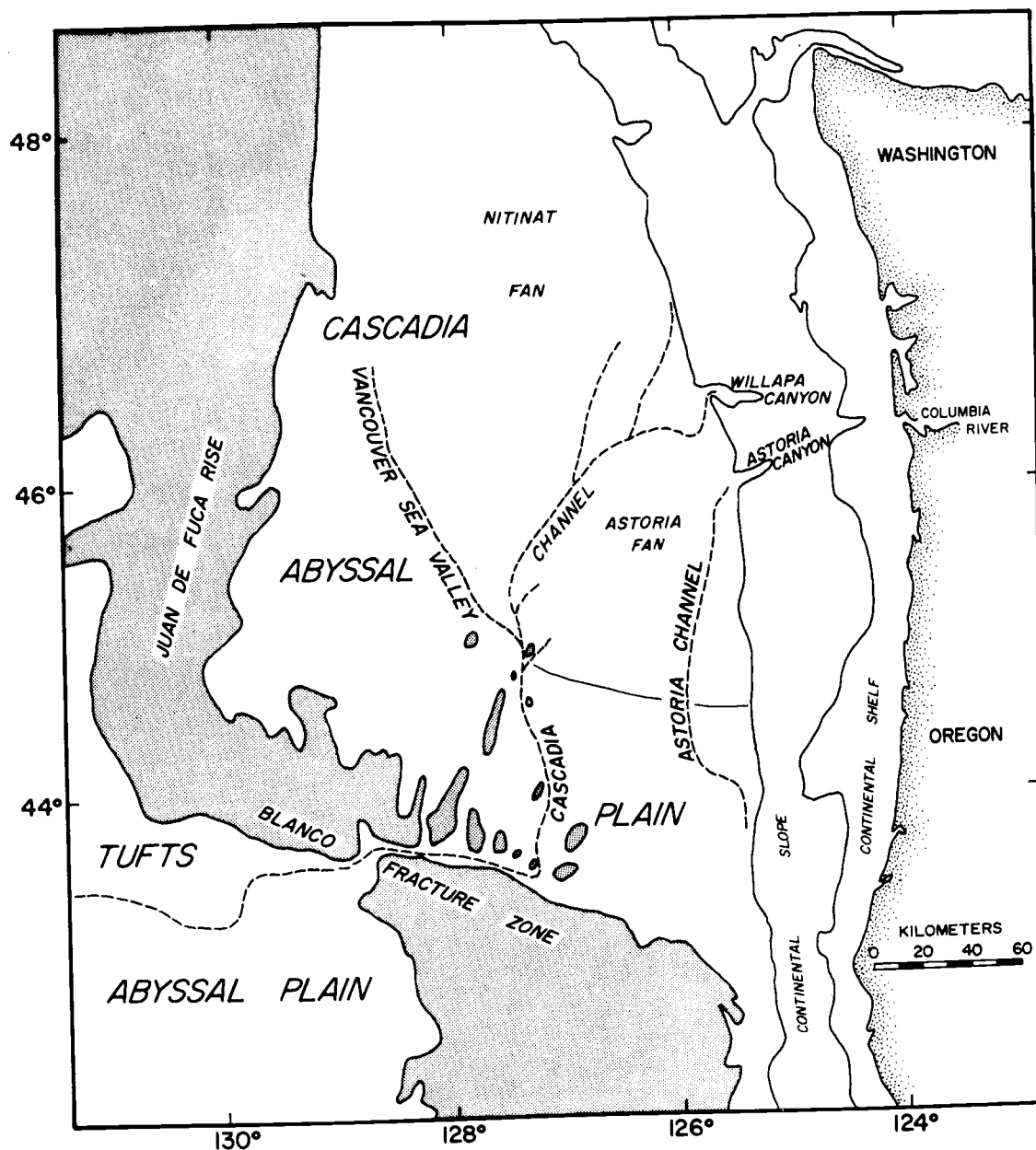


Figure 1. Major physiographic features off the coast of Oregon. Taken from Duncan and Kulm (1970).

in pelagic-hemipelagic sediments progressing seaward. The detailed distribution of surface sediment facies is the result of processes which may be only about 12,500 years old. At the end of the last glaciation (about 12,500 BP) terrigenous sedimentation into the ocean basins was greatly altered by the rising sea level. The sediment load of rivers was increasingly restricted to estuarine systems and the continental shelf. At the present the terrigenous sediments of Cascadia Basin are derived from two sources. The Columbia River discharge acts as a point source radiating seaward. Other coastal rivers and coastal erosion deposit sediment on the continental shelf. This material is resuspended, sorted, and transported across the shelf in turbid flows to serve as the second source of terrigenous input (Kulm, et al., 1975).

The general input of terrigenous sediments from along the entire coast has caused the terrigenous component of Cascadia Basin sediments to be zoned parallel to the coast (Figure 2-4). It is only at the base of the slope that there is a large terrigenous component (Nelson, 1968), and differences between the holothurian fauna in this area and elsewhere on Cascadia Basin may reflect the sedimentological difference. The Holocene influence of the Columbia River discharge is seen in the distribution of clay minerals rather than in the coarse fraction which easily identifies the shelf derived input. The clay mineral facies delineated by Duncan et al. (1970) (Figure 5) are concentrically arrayed about the mouth of the Columbia River rather than parallel to the coast. Although the Cascadia Channel serves as an avenue of transport across the basin, very little terrigenously derived

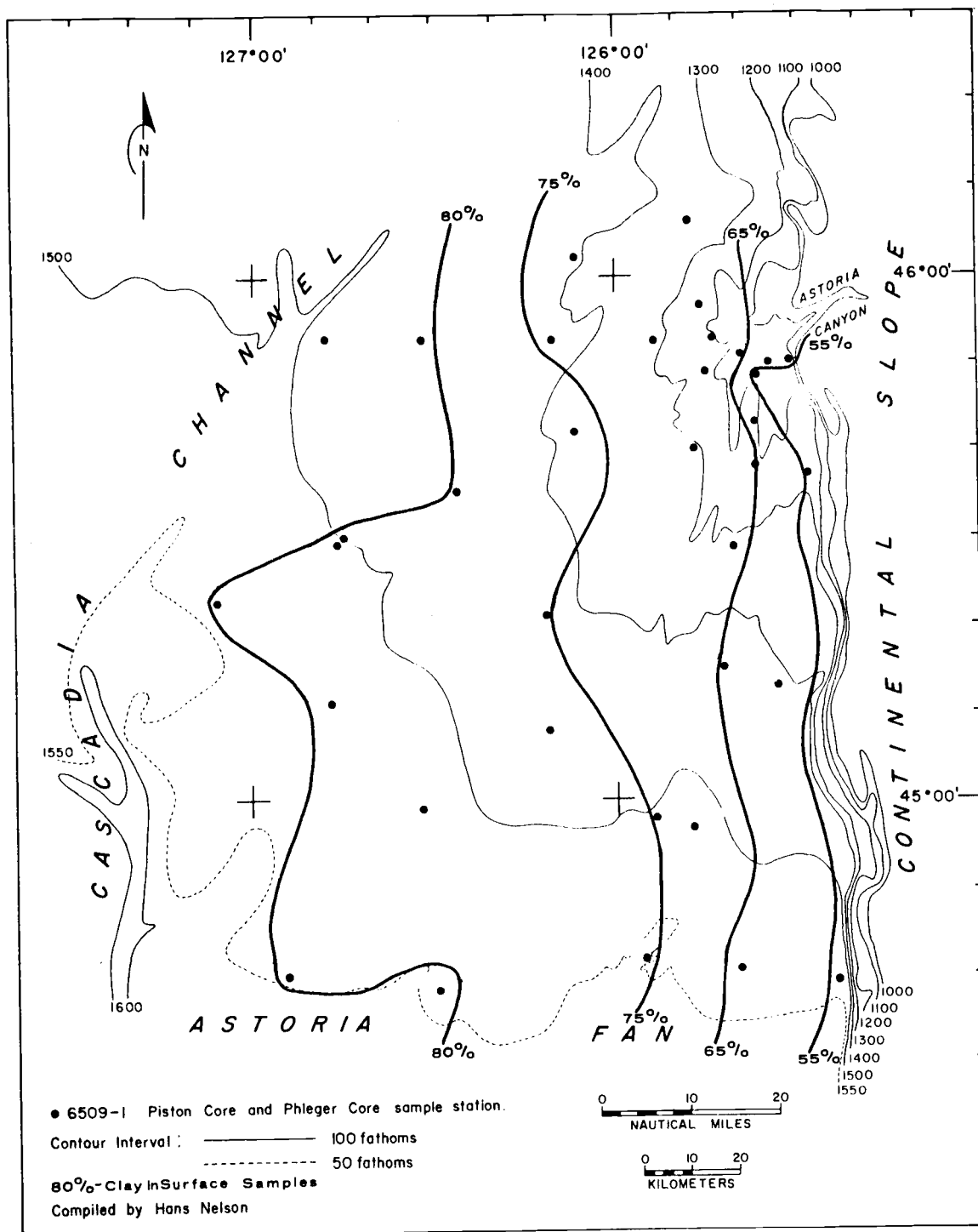


Figure 2. The gradation of the percent of clay in surface sediments of Astoria Fan and adjacent areas of Cascadia Basin, taken from Nelson (1968).

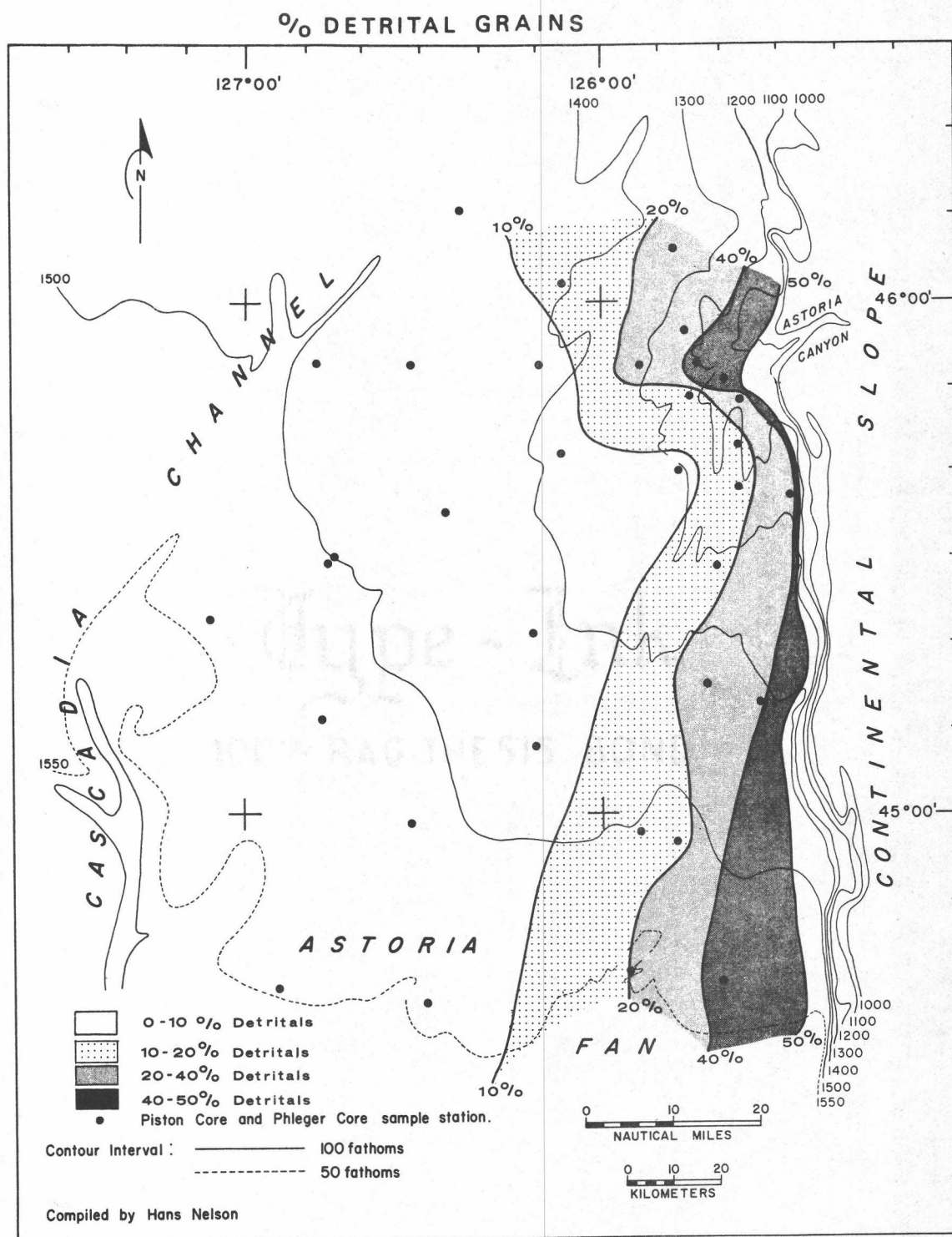


Figure 3. Decrease in terrestrially derived detrital grains in the surface sediments of Astoria Fan and Cascadia Basin taken from Nelson (1969).

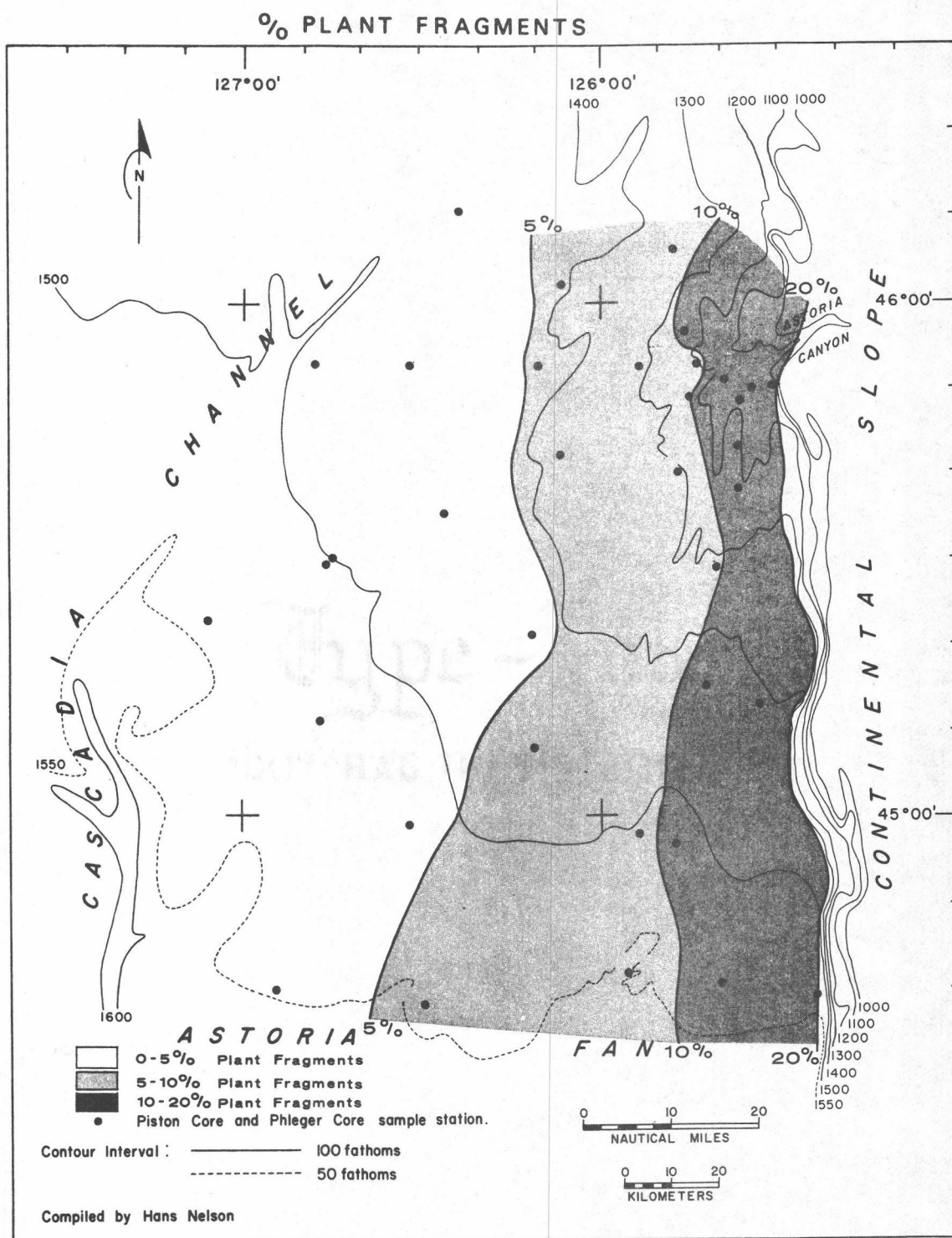


Figure 4. Gradation of the percent of terrigenous plant fragments in the coarse fraction of Cascadia Basin surface sediment, taken from Nelson (1968).

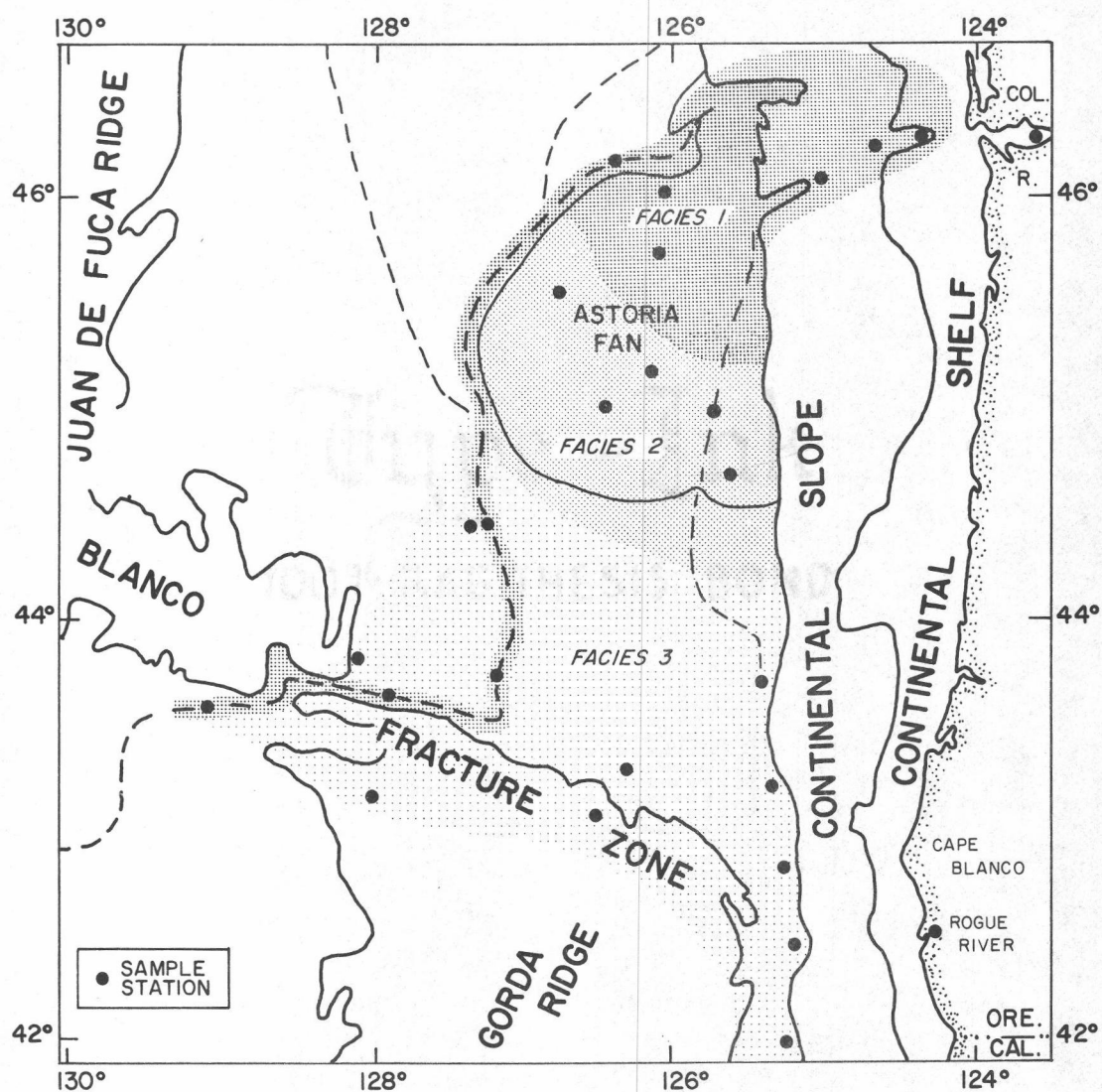


Figure 5. Distribution of postglacial clay mineral facies. The concentric zonation about the mouth of the Columbia River indicates different contribution of river borne fine sediments to the bottom, taken from Duncan et al. (1970).

sediment reaches Cascadia Basin west of the channel or large areas of Tuft's Plain.

During the Pleistocene the sedimentary environment on Cascadia Basin was considerably different from that now present. Sea level lowering exposed large portions of the shelf to erosion and decreased the amount of river deposition on the shelf. Terrigenous material was transported across the narrowed shelf, deposited upon the slope, and carried into the basin by frequent turbidity currents. As a result areas of the Cascadia Basin now covered with fine pelagic sediments were then covered by terrigenous silt and sand (Duncan and Kulm, 1970). While the processes of sedimentation may have completed a transition from Pleistocene to Holocene, the surface sediments of some portions of Cascadia Basin may still reflect Pleistocene conditions. On the basis of sedimentation rates estimated by Duncan (1968) it may be suggested that on the western half of Cascadia Basin Pleistocene sediments may easily have been mixed into the 10 or 20 cm thick Holocene surface layer. Thus sedimentary environment of Cascadia Basin and Tuft's Plain has undergone a major change in textures in the last few thousand years. This implies that the holothurian fauna now inhabiting these areas may thus represent species which have relatively recently arrived.

The pattern of productivity in the surface above Cascadia Basin is strongly influenced by coastal upwelling of nutrient-rich water. These upwelling events are the subject of continuing study; the most recently published description is that of Mooers, Collins, and Smith (1976). The seaward extent of the biological influence of the upwelling

has not been firmly established. Anderson (1964) traced a subsurface chlorophyll maximum, presumably produced in upwelled water, farther than 200 kilometers seaward. Pearcy (1976) placed the limit of effects upon higher trophic level standing stocks at about 100 km from land. Cushing (1971) placed the influence farthest seaward when he concluded that productive upwelled water off S. California could be traced as far as 500 km seaward. The variance in findings of seaward extent and the localized nature of upwelling events suggests that food input to the benthos from upwelling production may be quite variable in time and space. The bottom nearest to the upwelling may receive greatest input, although there is no evidence to support such a conjecture.

The water overlying Cascadia Basin is a mixture of Subarctic Pacific Water transported south by the California Current System and water transported north by the Davidson Current and abyssal circulation (Rosenburg, 1972). Subarctic Water is the major component to a depth of about 1000 m. In the sampled region Equatorial Pacific Water is the major component of the bottom water. Beyond 1400 km seaward the surface Subarctic Water grades into Eastern North Pacific Water. Near-shore there is a coastal water mass extending to a depth of about 400 m. It is greatly affected by seasonal weather patterns. In spring and summer the same wind reversal that causes upwelling deflects the Columbia River plume south and westward over the eastern half of Cascadia Basin (see Barnes et al., 1972, for a full review). Small and Cross (1972) found that the plume did alter the distribution of at least two species of copepods. In addition to whatever alterations

in near surface ecology are caused by the seaward extension of the plume, it is the agent for transport of clay minerals from the Columbia River. Gross (1972) concluded from radionuclide studies that sedimentation from the plume water was the major ecological impact of the Columbia River on the floor of the Basin.

The trawl samples examined in this study come from portions of Cascadia Basin and Tuft's Plain that must differ in the input of particulate material from terrestrial and surface water sources. Along the base of the continental slope terrigenous sediment input and input from upwelling productivity are probably greater than elsewhere in the sampled region. Progressively seaward terrestrial and coastal influences must decrease while depth remains fairly uniform. Samples taken near the mouth of the Columbia River or under its summer plume may reflect the influence of the bottom sediments or the altered surface ecology.

V. SAMPLING

Larger epifauna of Cascadia Basin and Tuft's Abyssal Plain is being sampled through an ongoing program of deep-sea trawling. In the present study detailed analyses are restricted to the holothurian contents of 95 beam trawl samples collected from 19 areas on the basin and plain. The Cascadia Basin samples are arrayed in a grid pattern which parallels lines of latitude and longitude and is thus parallel and perpendicular to the coast (Figures 6a and 6b). The planned grid has not been fully sampled, but the Cascadia Basin portion is largely complete. On the basin all but one sample area has been trawled, (3-B). An extra (1-X) area was added to the series (CP-1) along the base of the continental slope. Generally each area has been visited on two separate cruises. Details as to location, depth, and date may be found in Appendix I, Table 1. Additional holothurian specimens were collected in 298 otter and beam trawl hauls which were not a portion of the grid system. These specimens were examined to determine the vertical ranges of species present in the grid samples.

The grid pattern of trawl locations allows the variation in sampled fauna to be analyzed with a two factor analysis of variance explained in the next section. Fauna collected from the three completed offshore series, CP-1, CP-2, and CP-3 may reflect the influence of environmental factors which change with distance from shore. Fauna collected along the cross basin series CP-A, CP-B, CP-C, CP-D, and CP-E may reflect environmental factors that vary north to south over

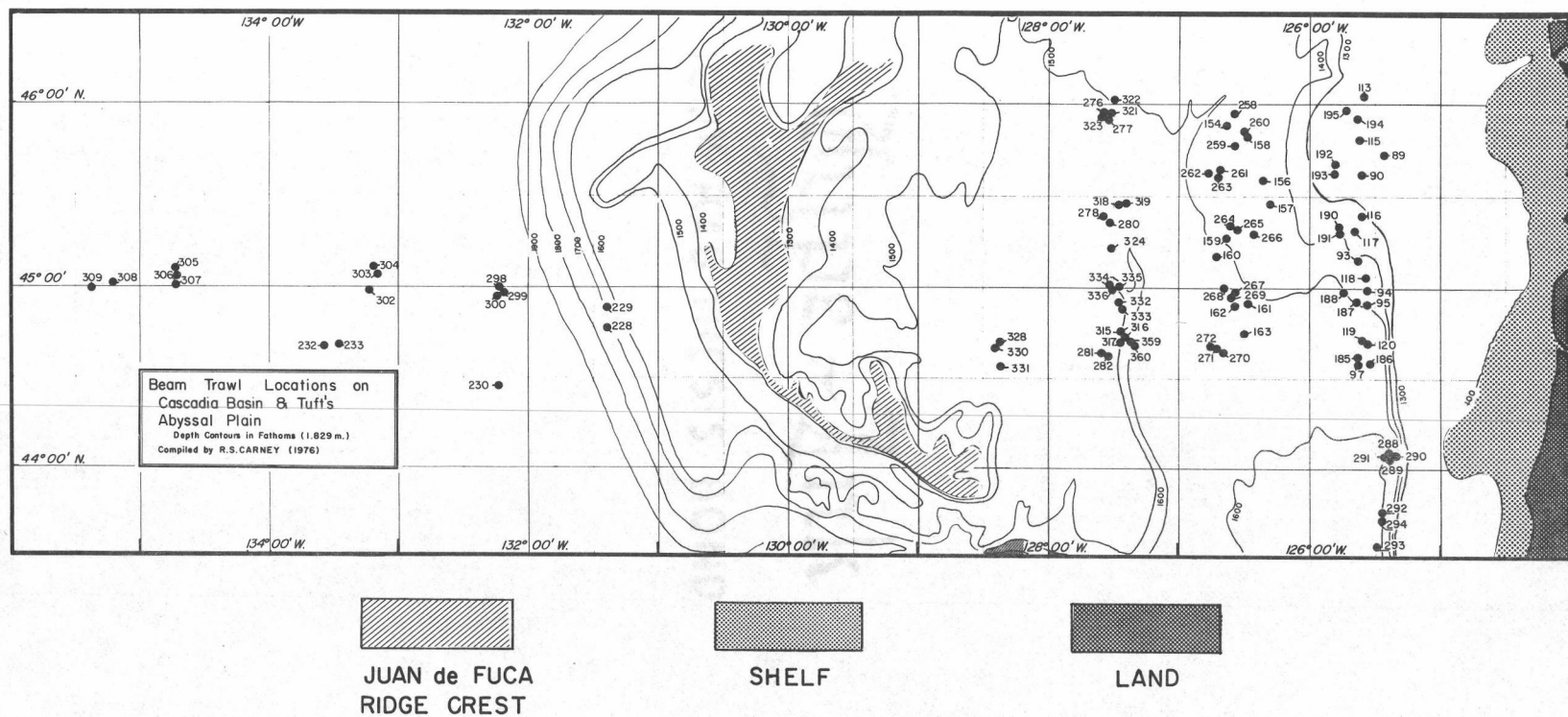


Figure 6a. Location and identification of beam trawl samples taken on Cascadia Basin and Tuft's Plain. Dark Stipple - Land; Light Stipple - continental shelf; Hatched - Juan de Fuca Ridge.

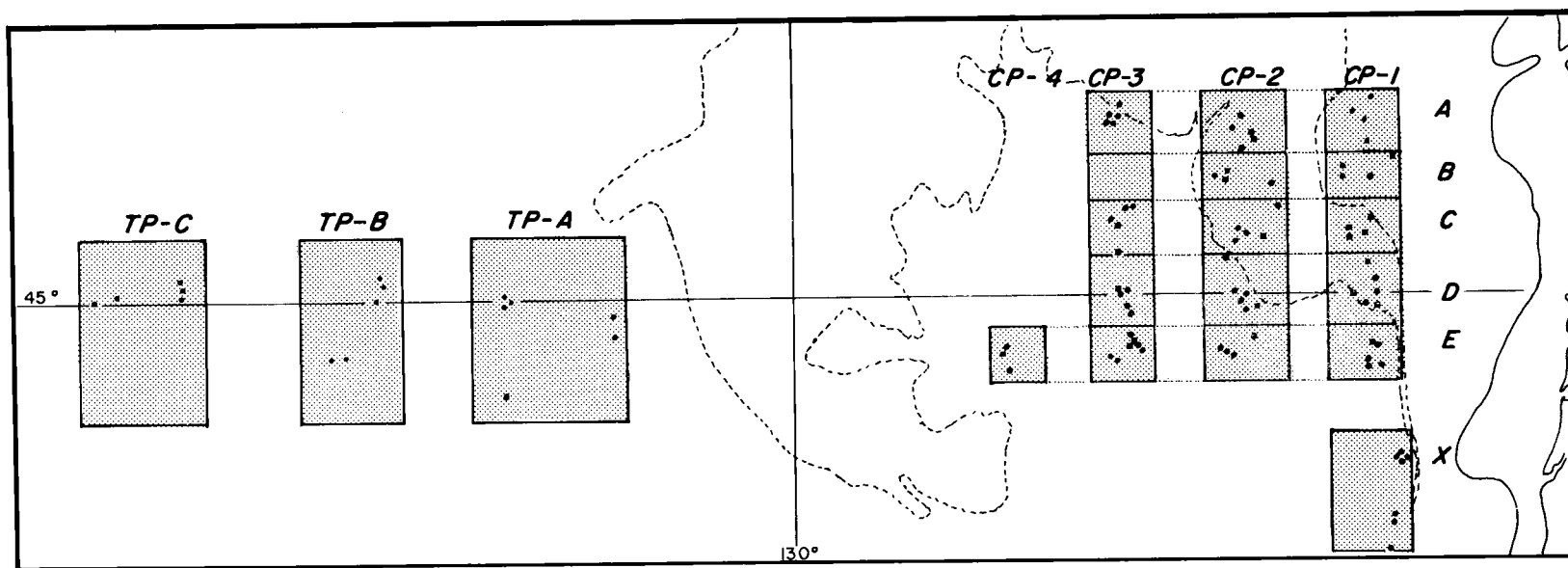


Figure 6b. Identifying codes for the sample grid on Cascadia Basin and three sampled regions on Tuft's Plain.

the basin. However, I have pointed out in the previous section that depth, sediment type, and Columbia River influence do not vary parallel to either latitude or longitude. Most conspicuous is the southward tilt of the basin floor which causes both sets of grid lines to contain a depth gradient.

The beam trawl consists of a hollow aluminum beam bolted across the top of two net-lined steel skids with an otter trawl net fastened to the trailing edges of the skids and beam (Carey and Heyomoto, 1972). This design is little different than that used for bottom fishing as early as the sixteenth century (Davis, 1958) except that it is smaller and constructed of more modern materials. Earlier bicycle rim odometer wheels have been replaced by heavier, spiked aluminum disks which do not turn in the water and resist damage during launch and recovery. The axle of each wheel is coupled to a hub odometer, Veeder Root model 54-794962 (Veeder Root Corp., Hartford, Connecticut). The beam trawl net was 4.1 cm stretch mesh lined with 1.3 cm mesh netting to improve retention of smaller organisms. The otter trawl design was a semi-balloon Gulf of Mexico shrimp trawl equipped with hydro-flow doors. The net used on the otter trawl varied with the specific project but was commonly 4.1 cm stretch mesh sometimes including a full or partial 1.3 cm liner.

Both nets were played out underway to prevent overturning and fouling of the net on the cable. Playing out while underway causes bottom contact to occur so far behind the vessel that detection of bottom contact is difficult. Since bottom contact could not be positively determined, a wire out versus depth table was used (Carey and

Heyomoto, Table 18.1, 1972). The trawls were considered to be on bottom once the appropriate amount of wire was played out, and were then towed with that amount of wire for two hours.

Upon retrieval the specimens were preserved in 10% buffered formalin until sorting. The total trawl contents were hand sorted, counted, and weighed by species when possible. All holothurian specimens not destroyed by other analyses were re-examined by myself to validate or determine identity. If not badly damaged the specimens were measured and appropriate morphological features noted.

Evaluation of the Beam Trawl

The towing of beam or otter trawls over several hundred square meters of ocean bottom is the only practical means of collecting large epifaunal organisms such as holothurians and asteroids. Unfortunately trawls are considered to be non-quantitative samplers unfit for the estimation of faunal densities (Holme, 1971 and McIntyre, 1971). It was hoped that the beam trawl used to collect the material examined in this thesis might provide quantitative data. Because the trawl mouth had a fixed aperture of 3.00 m or 2.72 m and carried odometers to measure distance trawled it might be possible to determine the area sampled.

Attempt to Determine Area Sampled

The effectiveness of using odometers to determine the distance the beam trawl was on bottom has been examined in a separate study

(Carney and Carey, in preparation). In summary, it was found that the wheels were positively correlated with other estimates of the distance trawled. However, when several measures of catch size were compared with the indicated area no convincing positive correlations could be found. Subsequent photographic evaluation of the trawl on the bottom has shown that the foot chain, sampling edge, is often clear of the bottom while the odometer wheels are tending the sediment. Although the attached photographic gear may have aggravated this design defect, the lifting of the lead line while trawling without the cameras is fully consistent with the lack of correlation between wheel counts and the trawl catch. The wheels have been measuring the distance traversed and not the area sampled. Lack of knowledge concerning the percent of time the lead line is on bottom prevents conversion of the wheel counts into area sampled. Figure 7 shows the scatter when total holothurians per trawl is plotted against the odometer estimates of the area.

On only seventeen deep-sea tows a time depth recorder was mounted to the trawl in order to compare the assumed two hours on bottom with actual time on bottom. On the average the trawl was on bottom 23 minutes longer than the assumed two hours. The time on bottom ranged from as much as 75 minutes shorter to 65 minutes longer than the two hours decided from wire out tables. Comparison of catch size is thus made cautiously because the duration of tow might differ by a factor of three, one hour versus three hours.

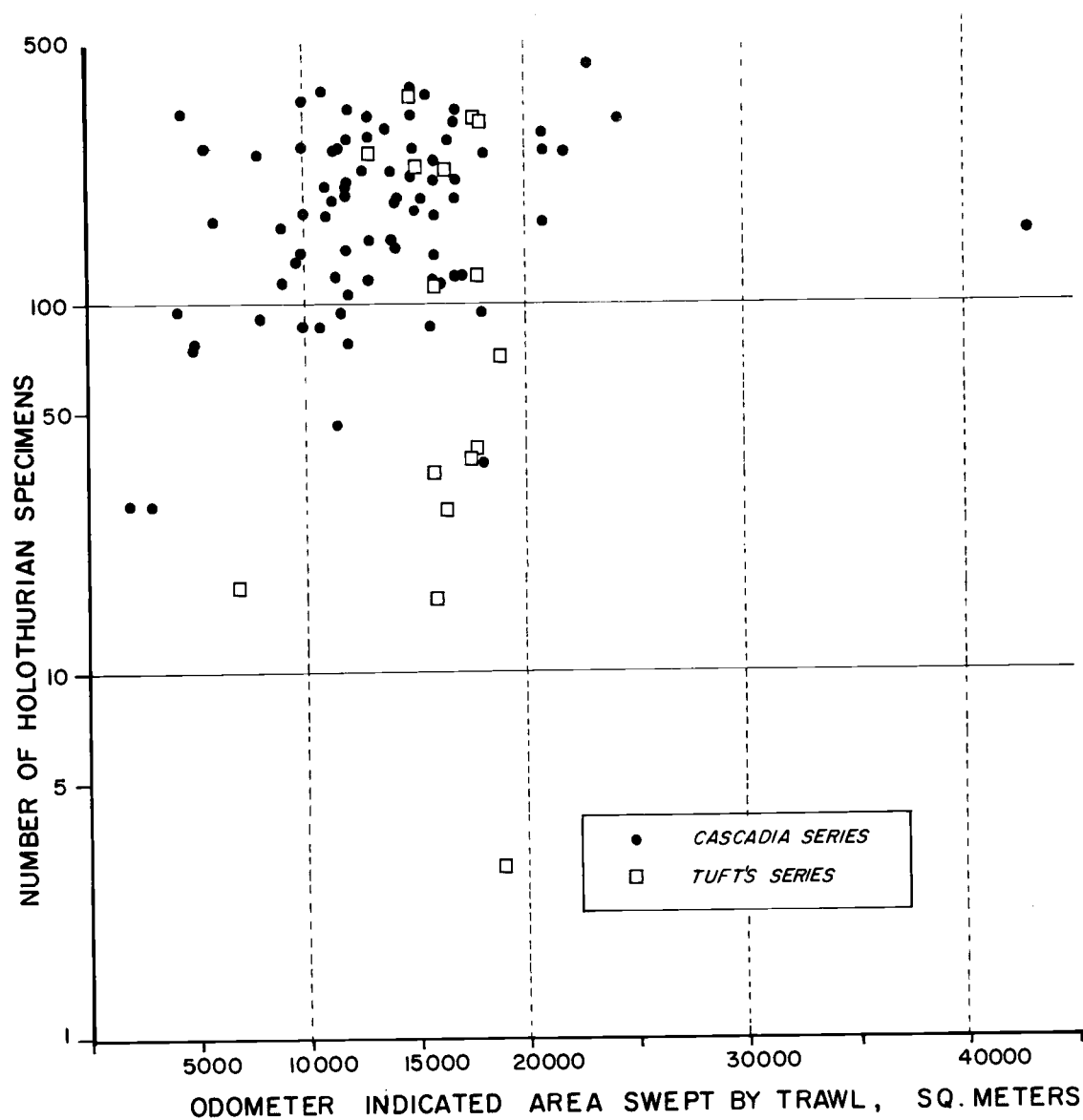


Figure 7. Scatter plot of the number of holothurian specimens collected per trawl versus the area of ocean bottom sampled according to the odometers. Log scales were used to reduce dimensions.

Sampling Efficiency

The selectivity of a trawl as it moves over bottom encountering organisms has been the object of study due to its obvious application in net fisheries. An excellent, thoughtful, discussion of this selectivity can be found in Beverton and Holt (1957). The probability that an animal encountered by the trawl will be included in the catch can be estimated by the proportion encountered which are caught. This probability can be partitioned into components such as escapement, avoidance and net selectivity that may be evaluated through experimental design as done by Kuipers (1975) on flat fish. Although some holothurian species are capable of swimming off of the bottom, they can be considered sedentary relative to fishes and not likely to avoid or escape from the net. Being lightweight in water they may be blown from in front of the trawl by the preceeding wire, and small specimens may slip through the mesh or pass under the lead line.

Size selectivity, as expressed by the probability that an animal of a certain size will be included in the catch, generally takes the shape of a sigmoid curve similar in shape to a cumulative normal distribution (Beverton and Holt, 1957 and Stander, 1970). Such a curve, or ogive, indicates that below a certain small size the probability of capture and the proportion captured is exceedingly small. Once some larger size is encountered, the proportion captured rapidly increases until further size increase no longer improves probability of capture. As the size of the encountered organism gets even larger it will eventually become so big relative to the aperture

of the samples that there will be a decreasing probability that it can even fit into the sampler. The holothurians encountered here, however, are so small relative to the large mouth of the beam trawl that the simpler sigmoid selection ogive is a reasonable model of possible selection by the trawl.

The number of holothurians collected by the beam trawl will often be treated as if all species have the same probability of capture. I assume the selection ogive for each species is about the same, and more importantly that the sizes encountered at each site are about equally vulnerable to being captured by the trawl. Figure 8 illustrates what might happen if this were not the case. Assume there is a species, A, which has a very marked distribution pattern with respect to the size of specimens occupying different areas of the bottom; very small individuals in one place and very large in another. In both areas species A is distinctly the dominant species on the bottom, but the selection probability for the large specimens is at its maximum with the net, while the small specimens have a very low probability of capture. Following collection and specimen counts we would conclude that in one area species A is clearly the dominant animal while in the other it is represented by only a few small specimens. Since the size distribution in the net is the product of the actual on bottom sizes and the selection ogive of that particular net, it is of great importance that we gain some feeling of where the specimens collected fall on the selection ogive even if we do not know the exact probability values. Otherwise, we will end up interpreting areal patterns in population size structure as areal patterns in species dominance.

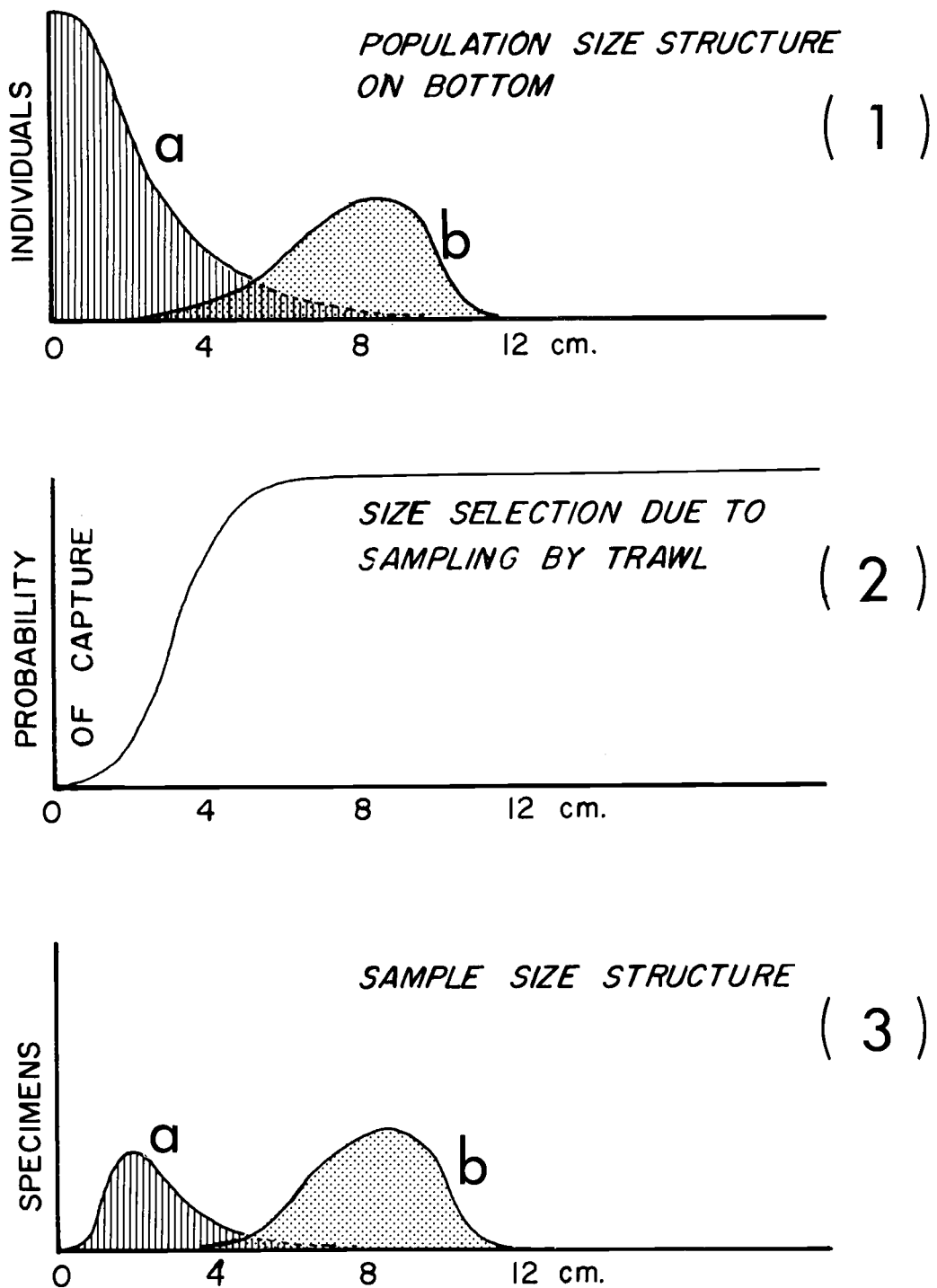


Figure 8. Effect of selection ogive upon the fauna sampled. A two species assemblage (1), sampled by a trawl with a selection ogive (2) would produce a sample (3) in which species "B" appears to be dominant.

It is obviously desirable that future trawl surveys include an evaluation of trawl selectivity in their design by that method suggested by Stander (1970) or by simultaneous photographic inventory. A simple examination of the sizes of holothurians caught, is, nevertheless, quite informative. From the size frequency histograms, seen in Figures 28a to 28g a conspicuous feature of most of the histograms is a marked central peakedness. Assuming that these lengths are reflective of the dimensions with which the trawl selects encountered specimens, it can be easily seen that no species collected has a maxima in the 0 to 3 cm long range, although literally thousands of specimens have been collected at sizes greater than this. Generally, the specimens in the 0 to 3 cm range would be less than a centimeter in cross section and quite prone to slipping through the mesh of the net. It is reasonable to assume as a first estimate that this 0 to 3 cm range falls on the low probability portion of the selective ogive and that very few of the encountered specimens are actually retained in the catch (Figure 9).

Of special interest is that both Peniagone cf. dubia and Scotoplanes globosa are taken in large numbers in the 4 cm size class, a size next to the apparently low probability of capture 3 cm size. The possibility must then be considered that a 4 cm animal has a probability of capture considerably less than a 5 or 6 cm specimen. If a poorly sampled size class is caught in abundance it suggests that on the bottom these two species may be far more abundant than indicated by the trawl contents.

In summary, I have no information concerning the actual selectivity ogive of the trawl other than knowing the size of the mesh employed

Cumulative Size Frequency Histogram for
11,320 Measured Specimens

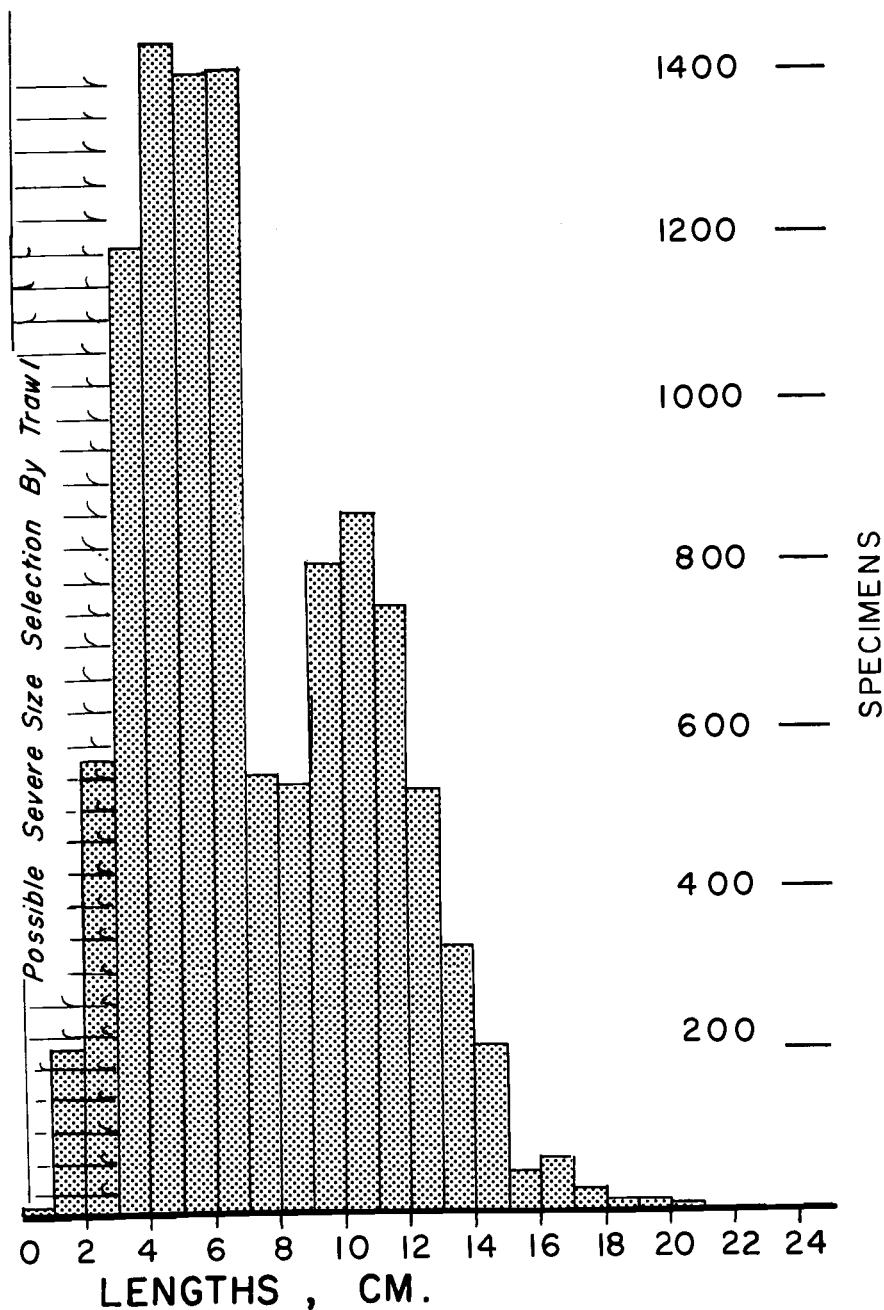


Figure 9. The cumulative size frequency histogram for 11,320 specimen lengths taken from seven species. Specimens three cm long or less may be poorly sampled by trawl.

and knowing the size of specimens collected. In general, the sizes collected tend to agree with the selection one might expect due to the mesh; specimens 0 to 3 cm long may have been poorly retained. Two important species were taken in the size class immediately adjacent to these apparently poorly sampled sizes. The possibility does then exist that these two species were even more abundant on the bottom than indicated by the net and that size selection may have distorted the patterns of relative abundance. With the information at hand it is not possible to assess the extent of any such distortion.

VI. ANALYSES

General Considerations

The basic process by which spatial patterns are recognized involves the determination of the inter-location similarities across the area being examined. Therefore, a method of assessing similarity must be adopted before spatial patterns in the faunal composition can be sought and described. If a sample can be characterized by a single scalar quantity, then similarity is easily represented as the differences between the values taken by that scalar measure over the sampled region. It is informative simply to map these values and visually inspect for patterns. In this study maps were prepared of the total holothuroid catch per trawl, the number of species per trawl, the number of each separate species, and Simpson's D^2 diversity index (SDSQ).

A more versatile and comprehensive method is to consider the entire sample as a multivariate entity characterized by a column vector of species counts or proportions. In this study I have been primarily concerned with the proportional composition of the holothurian fauna, and thus have used a column vector of within sample proportions. Since no single value characterizes a sample, it is impractical to look for spatial patterns by mapping. However, a matrix of inter-sample similarities can be computed between all pairs of sample vectors. The great versatility of this method lies in the manipulations that may be performed upon certain similarity and related matrices. The matrix may be partitioned to construct analyses of variance or to reduce the dimensionality of the data.

The multivariate analyses in this study were all based upon basic manipulations of a matrix of inter-sample similarities. The basic index used was an index of proportional similarity termed SIMI in a program for the Analysis of Information and Diversity over N samples (AIDN) developed by Dr. Scott Overton of Oregon State University. A factorial analysis of variance was performed by techniques described below with the assistance of AIDN to test the significance of any effect due to location, distance from shore, and north-south position upon the faunal composition of Cascadia Basin. Then, to graphically present the areal patterns in similarity, the SIMI matrix was reduced in dimension to three principal axes and the SIMI's between each sample and the axes were mapped out. Principal axes were fitted by a portion of the Calgary-Brown Factor Analysis (CABFAC) program (Klovan and Imbrie, 1971). AIDN and CABFAC are complimentary in that the first evaluates the significance of factors included in the experimental design, while the second separates orthogonal factors latent in the SIMI matrix (Imbrie and Van Andel, 1964). Both CABFAC and AIDN are available on the OS3-CDC3300 computer system of Oregon State at the time of writing. AIDN is on public file as *AIDNEX.

SDSQ, SIMI, and related indices were selected because they derive from a common geometric model in which each sample is represented by a vector in euclidean species space. Because of the simplicity of the model, the indices are readily interpretable, and the investigator can use a large body of preexisting analytical tools. A full development of the statistical properties of the model is beyond the scope of this thesis. However, there is no clear exposition in the

literature of the technique, so a full intuitive development for a three-dimensional case is presented. Stander (1970) has presented an excellent discussion of most of the indices, concentrating on the relationship between sample and population parameters. The present discussion will extend Stander's work and give a description of the factorial analysis of variance. Some general background can be obtained from books by Sneath and Sokal (1973), Clifford and Stephenson (1975), Cooley and Lohnes (1971). Zelinsky's (1968) linear algebra text is extremely helpful because he consistently explains linear algebra through its geometric representation.

Vector Representation of a Sample

A sample containing some measure of abundance for each of S species can be represented as a column vector \vec{x} (eq. 1). In this study the raw data consisted of specimen counts for each of i ($1 \leq i \leq S$) species.

$$\vec{x}_j = \begin{bmatrix} x_{1j} \\ x_{2j} \\ \vdots \\ x_{sj} \end{bmatrix} \quad 1$$

Geometrically each value x_{ij} is a coordinate of the head of the \vec{x}_j vector in S -dimensioned euclidean space. The tail of the vector lies at the origin. In Figure 10a two samples are plotted as points 1 and 2 in three dimensional species space. Each point is the head of a sample vector, \vec{x}_1 and \vec{x}_2 . In this way samples which contain a long list of species may be compared and characterized by use of the simple geometric concepts of distance between points and angles between vectors.

Vector Lengths - Distances

Two distances, that is vector lengths, are commonly used to characterize a sample and one distance used to compare samples in multidimensional space. A sample point may be characterized by determining the distance between the point and the origin or the point and a hypothetical point E . E contains the same number of specimens as the sample, but equal proportions of all species (Figure 10b). The \vec{E}_j for each \vec{x}_j is obtained from equation 2. E is a point representing the within sample mean. The distance from E_j to the corresponding sample point (D_{Ej} , eq. 3) is a measure of the equitability of the sample. The distance from the origin (D_{Oj} , eq. 4) is the square root of the within sample uncorrected sums of squares, the length of \vec{x}_j .

$$\text{if } \vec{x}_j = \begin{bmatrix} x_{1j} \\ x_{2j} \\ \vdots \\ x_{ij} \\ \vdots \\ x_{Sj} \end{bmatrix} \quad \text{then } \vec{E}_j = \begin{bmatrix} \sum_{i=1}^S x_{ij} \\ \vdots \\ \sum_{i=1}^S x_{ij} \end{bmatrix} \times \frac{1}{S} = \begin{bmatrix} \bar{x}_j \\ \bar{x}_j \\ \vdots \\ \bar{x}_j \end{bmatrix} \quad 2$$

The inter-sample distance (D_{12} , eq. 5) is the euclidean distance measure of similarity commonly used to compare two samples (see Sneath and Sokal, 1973).

$$D_{Ej} = \left(\sum_{i=1}^S (x_{ij} - \bar{x}_j)^2 \right)^{1/2} = [(\vec{x}_j - \vec{E}_j)' (\vec{x}_j - \vec{E}_j)]^{1/2} \quad 3$$

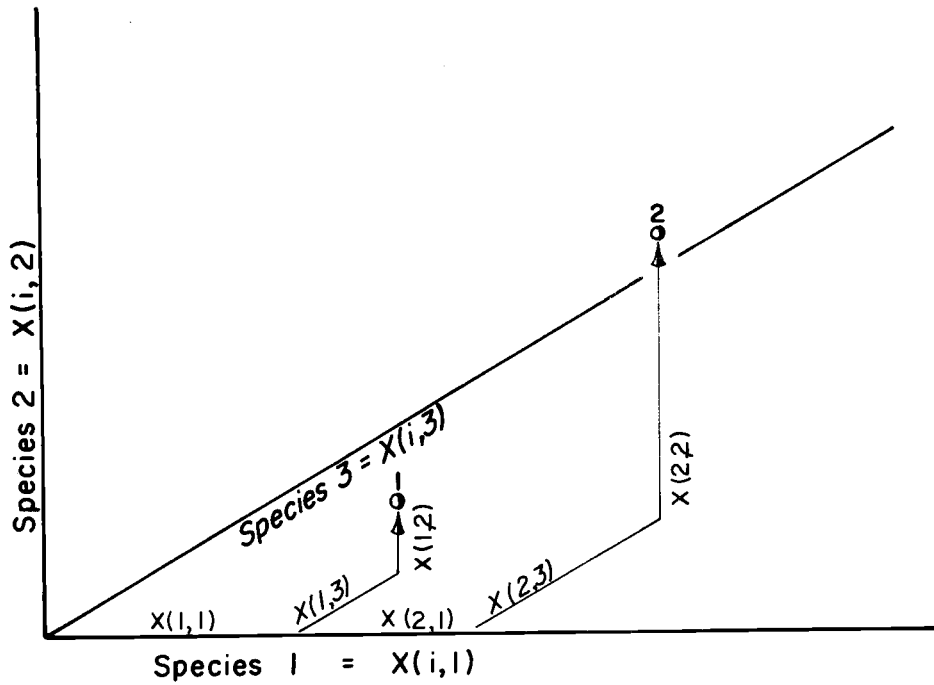


Figure 10a. Samples 1 and 2 modeled as two points in three dimensional species space.

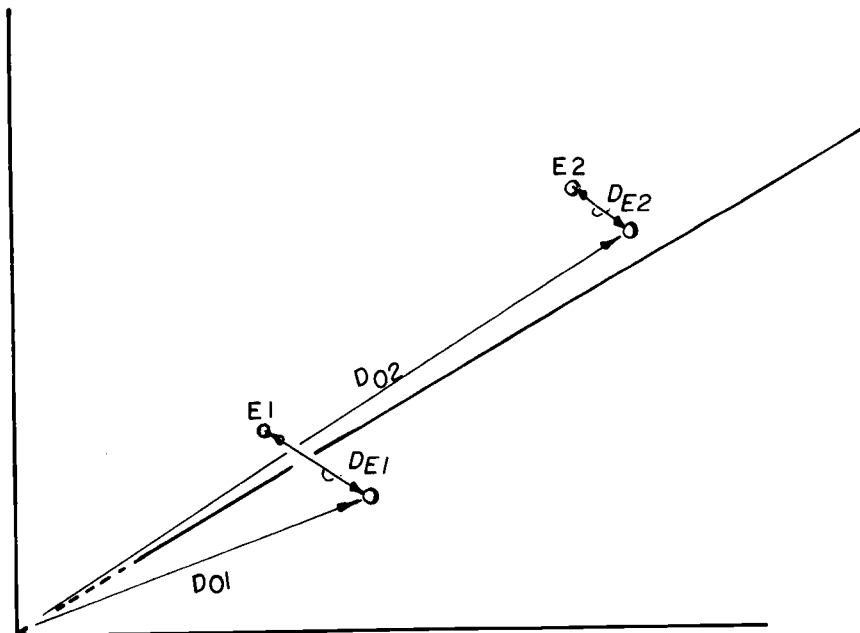


Figure 10b. Three distance, vector length, measures. See text for explanation.

$$D_{0j} = \left(\sum_{i=1}^S (x_{ij} - 0)^2 \right)^{\frac{1}{2}} = (\vec{x}_j, \vec{x}_j)^{\frac{1}{2}} = \|\vec{x}_j\| \quad 4$$

$$D_{12} = \left(\sum_{i=1}^S (x_{i1} - x_{i2})^2 \right)^{\frac{1}{2}} = [(\vec{x}_1 - \vec{x}_2), (\vec{x}_1 - \vec{x}_2)]^{\frac{1}{2}} \quad 5$$

Angles Between Vectors - SIMI

The cosine of the angle Theta between any pair of sample vectors is the similarity index SIMI (Figure 10c). It is easily computed from the trigonometric identity of the cosine of an angle in a triangle (eq. 6). In this present study SIMI is preferable to intersample distance as a measure of similarity. If a sample vector were multiplied by a constant, all of the above distance measures would be altered. The vector would change in length, but not in direction. Thus SIMI is unaffected by changes in vector length that are due to variation in the number of specimens caught caused by the unknown variation in size of the area sampled by each trawl.

$$SIMI_{12} = \frac{D_{01}^2 + D_{02}^2 - D_{12}^2}{2 \sqrt{D_{01}^2 \times D_{02}^2}} = \frac{\vec{x}_1, \vec{x}_2}{\|\vec{x}_1\| \times \|\vec{x}_2\|} \quad 6$$

Just as with distances, angles may be measured from different points in species space. The cosine of the angle Rho (Figure 10d and e) is analogous to the product moment correlation coefficient used to compare two variables. Conceptually, Rho is the angle of rotation between the two sample points, about the central vector that contains

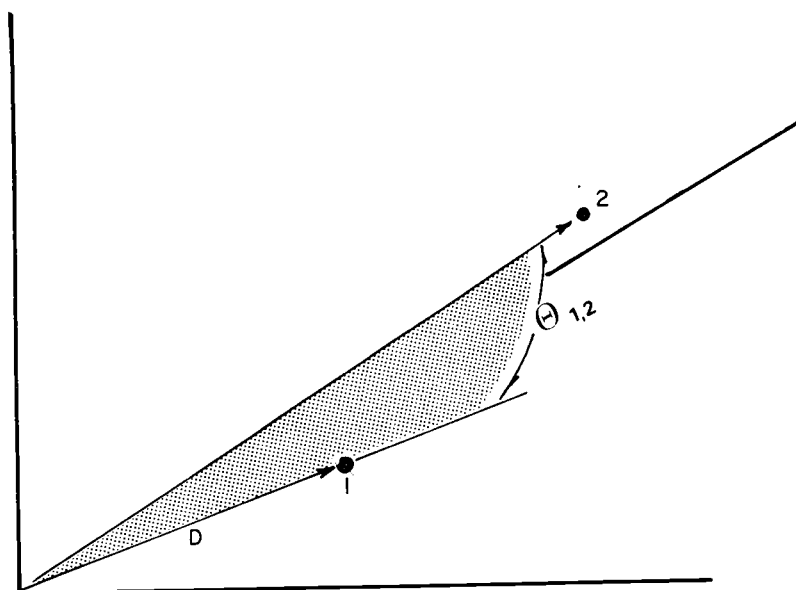


Figure 10c. Comparing two sample points by the angular separation Theta between the two \vec{x} vectors.

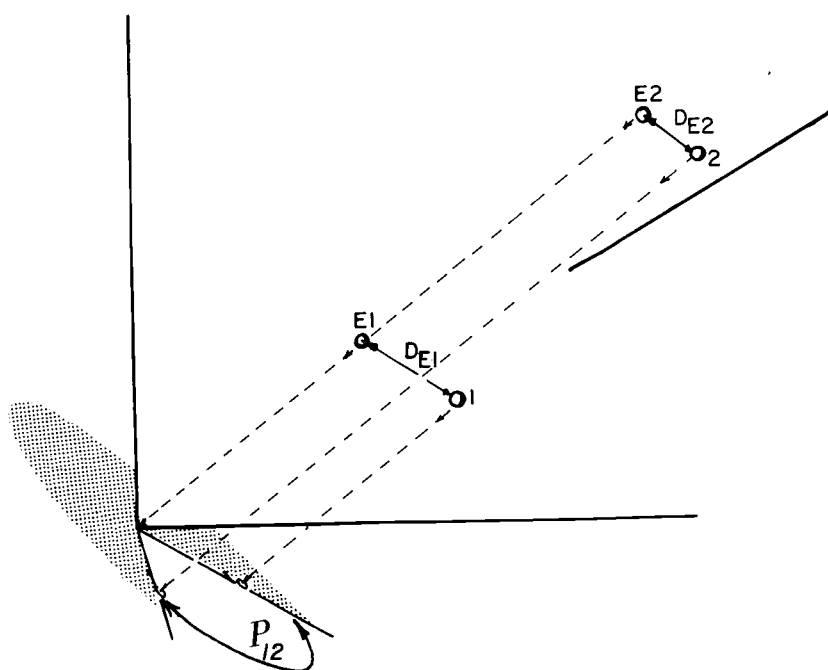


Figure 10d. Comparing two sample points by the angular separation Rho between the two translated D_{Ej} vectors.

all E_j points. Computationally, the two sample points are translated to a plane containing the origin and perpendicular to the vector containing all E_j 's. Following this translation the cosine of Rho is obtained from the same trigonometric identity as SIMI (eq. 7).

$$\cos \rho_{12} = \frac{D_{E1}^2 + D_{E2}^2 - D_{12}^2}{2 \sqrt{D_{E1}^2 \times D_{E2}^2}} = \frac{\vec{x}_1 \cdot \vec{x}_2}{\|\vec{x}_1 - \vec{E}_1\| \times \|\vec{x}_2 - \vec{E}_2\|} \quad 7$$

The cosine of Rho is of little use when the data set contains a large number of zero's. By inspection of equations 6 and 7 it can be seen that the cosine of Rho will approach SIMI as the number of zero's within each sample vector causes the values in the \vec{E}_j vectors to become small. In this present study approximately 4/5ths. of the data matrix contained zero's, and the values of cosine of Rho were very similar to SIMI.

Restraining Surfaces

Although SIMI is conceptually simple and insensitive to variation in abundance and to numerous zero's, it cannot directly be used in an analysis of variance because angles cannot be partitioned. Lengths are partitioned by projecting a vector onto orthogonal axes; an angle becomes 0 if projected onto a single axis. However, the distances generated by sample vectors intersecting a restraining surface can be partitioned. The proportion-surface is inserted into species space simply by converting each sample vector \vec{x}_j into a within-sample, proportion vector \vec{p}_j (eq. 8). This insertion is shown in Figures 10f and g.

$$\vec{p}_j = \vec{x}_j / \sum_{i=1}^S x_{ij} = \begin{bmatrix} x_{1j} \\ x_{2j} \\ \vdots \\ x_{Sj} \end{bmatrix} \left(\sum_{i=1}^S x_{ij} \right)^{-1} = \begin{bmatrix} p_{1j} \\ p_{2j} \\ \vdots \\ p_{Sj} \end{bmatrix} \quad 8$$

Since the transformation to within sample proportions involves nothing more than multiplication of each sample vector by a scalar, SIMI and Cosine Rho are not altered. Distances are no longer measured to the actual sample point, but to the transformed point on the proportion-surface, at the head of the \vec{p}_j vector. The distance from the origin is the \vec{p}_j vector length, or $\text{SDSQ}_j^{\frac{1}{2}}$. Simpson (1949) proposed this length as an index of diversity because of its probabilistic interpretation. As computed by AIDN (eq. 9) it is a biased estimator of the population parameter (Simpson, 1949). The distance between points on the proportion-surface, DIST_{12} , is simply euclidean distance computed from proportions (eq. 10). Equitability may be measured as distance from the center (E) of the proportion-surface to a sample point on that surface. A geometric summary of the indices that may be determined for any pair of points on the proportion surface is given in Figure 10h.

$$\text{SDSQ}_j = \vec{p}_j' \vec{p}_j = (\|\vec{p}_j\|)^2 \quad 9$$

$$\text{DIST}_{12} = [(\vec{p}_1 - \vec{p}_2)' (\vec{p}_1 - \vec{p}_2)]^{\frac{1}{2}} = \|\vec{p}_1 - \vec{p}_2\| \quad 10$$

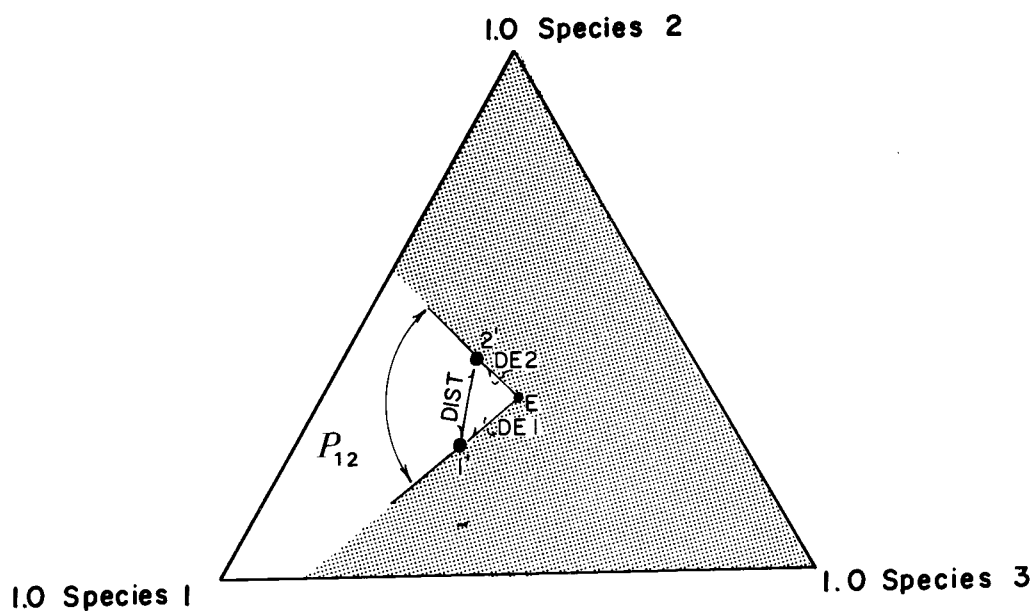


Figure 10g. Distance measures and the angle Rho on the proportion surface. See text for explanation.

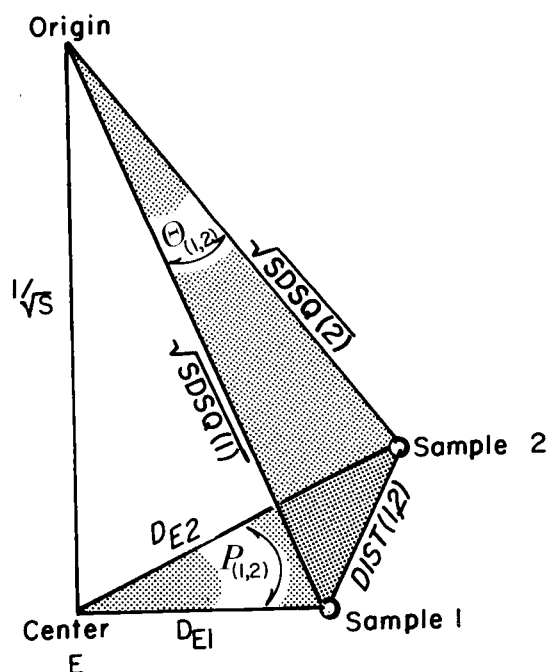


Figure 10h. The right tetrahedron of diversity, equitability, and similarity. See text for explanation.

AIDN Analysis of Variation on the Proportion-Surface

To this point I have only considered determination of similarity between two \vec{p}_j vectors. It is my desire, however, to evaluate the effect of sample position upon the data set as a whole. While trellis diagrams or clustering techniques may be informative, they do not readily allow evaluation of the relative importance of factors that were the basis of the design of the sampling program. Therefore, a factorial analysis of variance will be used for analyzing the data collected from the two-factor grid of samples on Cascadia Basin. Conceptually, the analysis contained in AIDN is identical to a univariate factorial analysis of variance (see Snedecor and Cochran 1967, Chapter 12). Total variability is first computed. This is then partitioned into the component due to treatment blocks and that due to error. The treatment blocks variability may then be partitioned into the variability due to the separate factors and that due to interaction of these factors. F ratio's are then computed between appropriate mean squares to test the significance of any factor or interaction.

Each \vec{p}_j vector in the data set is identified by three subscripts, \vec{p}_{jkm} . The number of the trawl is given by j ; k gives the level of the first factor, and m the level of the second. In this study the first factor is the offshore series, and the second factor is the north-south series. The data set is represented by the rectangular $S \times N$ (species x samples) matrix $[P]$ (eq. 11).

$$[P] = \begin{bmatrix} p_{11km} & p_{12km} & \dots & p_{1Nkm} \\ p_{21km} & p_{22km} & \dots & p_{2Nkm} \\ \vdots & \vdots & & \vdots \\ p_{S1km} & p_{S2km} & \dots & p_{SNkm} \end{bmatrix} = [\vec{p}_{1km}, \vec{p}_{2km}, \dots, \vec{p}_{Nkm}] \quad 11$$

If this data matrix were to be analyzed in the usual manner of a multivariate analysis of variance (see Cooley and Lohnes, 1971), the determinate of the variance-covariance matrix computed from $[P]$ would be used as the estimate of total dispersion. The variance-covariance matrix is obtained by equation 12. Note that the \vec{a} vector is a column vector of within species average proportions. This vector represents a centroid sample derived from all samples. Because the columns of $[P]$ sum to 1.0, $[V]$ is a singular

$$\vec{a} = \begin{bmatrix} \sum_{j=1}^N p_{1j} \\ \vdots \\ \sum_{j=1}^N p_{Sj} \end{bmatrix} \times \frac{1}{N}, \quad [V] = \frac{1}{N} ([P] - \vec{a}) ([P] - \vec{a})' \quad 12$$

matrix with a determinate of 0.0. Thus the determinate cannot be used as an estimate of total dispersion of proportional data.

The estimate of total dispersion used by Overton in the AIDN analysis of variance is the average square of the distance from the centroid sample \vec{a} to all \vec{p}_{jkm} vector heads. The squares of the distances from each \vec{p}_{jkm} to the centroid are the diagonal elements of the square array $[Q]$ (eq. 13). Note that $[Q]$ is obtained simply by

reversing the order of multiplication used to compute [V]. Thus the trace of [V] (written $\text{tr}[V]$) is equal to the trace of [Q] divided by N (eq. 14). The corrected sum of squares summed over all S species is equal to the sum of squared distances from the centroid to all sample points on the proportion-surface. The primary difference between the AIDN factorial analysis of variance and regular multivariate analysis lies in the use of the trace of the variance-covariance matrix rather than the determinate.

$$[Q] = ([P] - \vec{a})'([P] - \vec{a}) \quad 13$$

$$\text{tr}[V] = \text{tr}[Q] \frac{1}{N} \quad 14$$

The remainder of the analysis is fairly straight-forward. The columns of [P] are replaced by columns of within-species mean proportions for each treatment block. In this study the blocks are the 15 positions on Cascadia Basin around which trawls were located. The overall mean vector \vec{a} is subtracted, the resulting deviation matrix postmultiplied by its transpose, and the trace of the variance-covariance matrix obtained. Subsequently a matrix of columns of mean proportions for each level of factor 0 is similarly converted to a variance-covariance matrix. The same is done for all levels of factor Two. The sums of squares for error and for interactions are obtained by subtraction. The procedure is almost identical to that used in a univariate factorial analysis of variance.

Once the total sum of squares has been partitioned into an error component and a position (treatment blocks) components, the significance of position on the proportional composition of the

fauna can be tested by an F ratio. Then the sums-of-squares due to position can be partitioned into the components due to each factor and to factor interaction. The significance of these components are also tested against the error term by an F ratio.

At this time the AIDN analysis of variance is still undergoing development. Rather surprisingly, the statistical properties of distances on the proportion-surface for many dimensions have not been evaluated (Webb, 1974). Since the trace of a variance-covariance matrix is the sum of variances, the ratio of traces should have an F distribution. However, until the actual distributions of distances on a proportion surface have been evaluated through Monte Carlo techniques, the appropriate degrees of freedom for testing significance of a given F ratio remains unknown. Until these evaluations are made, the degrees of freedom are approximated by multiplying the degrees of freedom appropriate for a univariate analysis of variance by $S-1$. Thus if there are a total of 76 trawls, 15 locations, 3 levels of factor one, and 5 levels of factor two, there will be $75(S-1)$, $14(S-1)$, $2(S-1)$ degrees of freedom respectively for evaluation of total variation, location effects, and factor effects.

Computational Form of the AIDN Analysis of Variance

In the preceeding presentation of the AIDN analysis of variance, vector and matrix notation were used to facilitate comparison with other forms of multivariate analysis of variance. However, as the AIDN analysis uses only the trace of the variance-covariance matrix

as a dispersion estimate it is pointless to compute the entire matrix. The total corrected sums of squares for any species is given by equation 15. The trace of the variance-covariance matrix [V] is the sum of all corrected sums of squares divided by N (eq. 16).

$$\text{SUMSQ}_i = \sum_{j=1}^N \left(p_{ijk} - \left(\sum_{j=1}^N p_{ijk} \right) / N \right)^2 \quad 15$$

$$\text{tr}[V] = \frac{1}{N} \sum_{i=1}^S \sum_{j=1}^N \left(p_{ijk} - \left(\sum_{j=1}^N p_{ijk} \right) / N \right)^2 \quad 16$$

Equation 16 can be expanded and rearranged into equation 17 which is equivalent to equation 18. Thus total corrected sums of squares is easily computed from the SDSQ values of samples and pooled samples.

SDSQ_a is the diversity of the pooled centroid sample.

$$\text{tr}[V] = \frac{1}{N} \left(\sum_{j=1}^N \sum_{i=1}^S p_{ijk}^2 - N \sum_{i=1}^S \left(\frac{1}{N} \sum_{j=1}^N p_{ijk} \right)^2 \right) \quad 17$$

$$\text{tr}[V] = \frac{1}{N} \left(\sum_{j=1}^N \text{SDSQ}_j - N \times \text{SDSQ}_a \right) \quad 18$$

Computation of the corrected sums of squares for treatment blocks and factors is done in a similar manner. [P] is replaced with a matrix of within-species mean proportions for each level of the appropriate factor. The SDSQ for each of these pooled vectors is computed. Each SDSQ is weighted by the number of sample vectors contributing to it, and then $N \times \text{SDSQ}_a$ is subtracted to obtain the corrected sums of squares due to that factor.

Reducing the Dimensionality of a SIMI Matrix

A matrix of inter-sample SIMI's may be conveniently computed from the [P] matrix if each \vec{p}_j is first divided by its own length (eq. 19). Where as [P] gives the position of each vector head as a list of S coordinates, [SIMI] gives the direction of each vector as a list of cosines of the angles between that vector and all other sample vectors.

$$[SIMI] = [T]'[T] \quad \text{where} \quad [T] = \begin{bmatrix} \vec{p}_1 & \vec{p}_2 & \dots & \vec{p}_N \\ \|\vec{p}_1\| & \|\vec{p}_2\| & \dots & \|\vec{p}_N\| \end{bmatrix} \quad 19$$

The task of finding patterns of inter-sample similarity within a [SIMI] is greatly simplified if a few reference vectors are selected. Then sample vectors may be compared with one another by their similarities with the common reference vectors. One method of providing reference vectors is to insert a set of orthogonal axes into species space using a principal component technique. CABFAC was intended as a Q-mode factor analysis. However, as with other factor analyses, it determines the number of factors present by first performing a Q-mode principal component analysis.

CABFAC computes [SIMI] as shown above in equation 19. Geometrically this transformation sets all sample vector lengths to unity (Figure 10i), but does not alter the [SIMI] matrix. CABFAC then proceeds to fit orthogonal axes such that each succeeding axis is a decreasing component of the total length of sample vectors (Figure 10j). Since all vectors are unit length, the total length is equal to N. The new reference axes, termed "principal factors" in CABFAC,

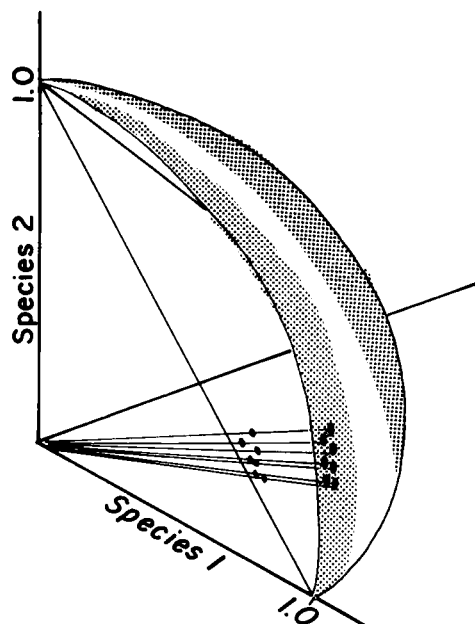


Figure 10i. Insertion of the unit sphere restraining surface upon sample vectors.

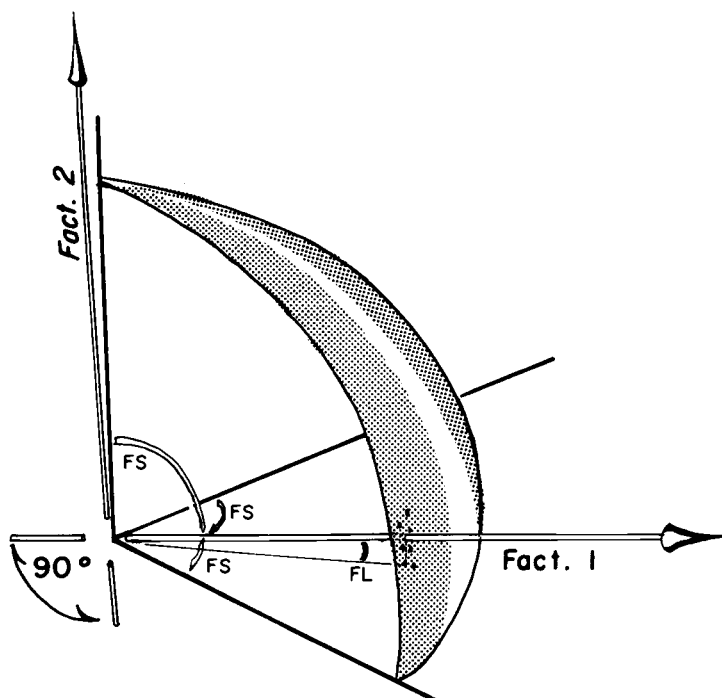


Figure 10j. Position of new, orthogonal axes (factors) relative to old axes and sample vectors.

can be considered wholly dissimilar ($SIMI = 0.0$) faunal assemblages that mix to form the assemblages in the data. In CABFAC a factor score, FS, serves to locate the new principal factor axis relative to the original species axes. A factor loading, FL, locates the sample vectors relative to the principal factor axis. Although both FS's and FL's are usually the lengths of vector projections, both loadings and scores are equal to the SIMI between vectors, since all vectors in CABFAC are unity.

Once a limited number of principal axes are extracted to serve as reference vectors, the factor loadings of each sample onto each principal axis may be separately mapped. These maps may then be visually examined for pattern.

Analysis of Size Relationships

While identifying holothurian specimens from Cascadia Basin it became apparent that small specimens of several species were generally collected in bunches. They were either missing in a sample or were relatively numerous. Assuming that the small individuals represented young specimens, an analysis was needed to test the hypothesis that young specimens might be non-randomly distributed over the area occupied by the whole species. Since holothurians depend upon hydrostatic pressure and elastic gels to maintain support, dead specimens are so flabby and mucoid that they are uninviting to an advocate of meristic studies. Nevertheless length to the nearest centimeter was selected as the measurement of size because it is easily

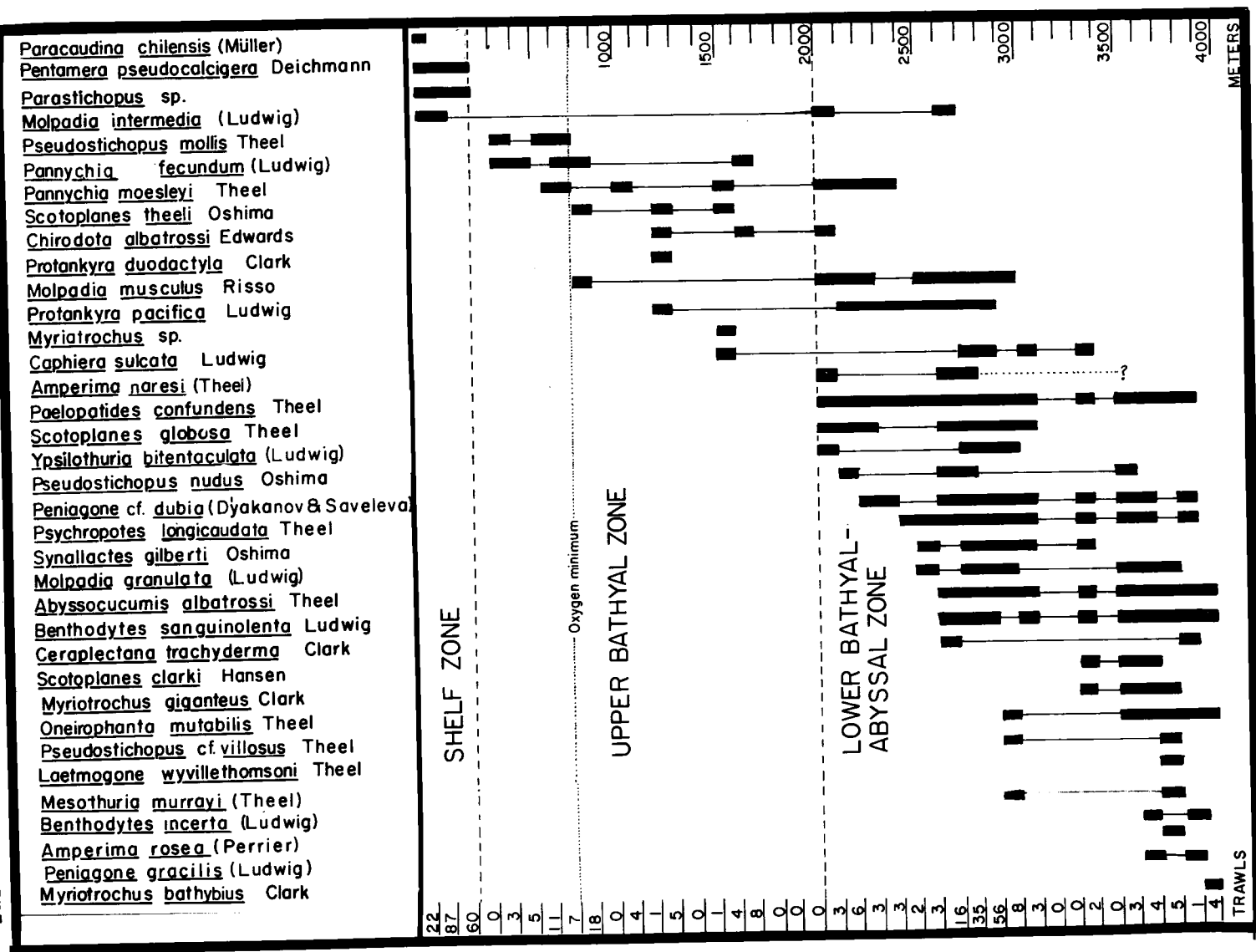
taken and reflects the overall body size of the animal. For all species length was measured from the center of the mouth to the center of the anus. Anterior brims and posterior appendages were thus excluded. Distorted specimens were pressed flat to facilitate measurement. Only samples which were well preserved were included in the compilation and are identified in Appendix II.

The lengths for each species were compiled into a histogram that was used to define "small" and "large" specimens (Figure 26a-26g). The "small" size class generally was below the modal size and corresponded with an inflection in the histogram. Once a small and a large size category are established, body length can be modelled as a binomial attribute. The hypothesis that the proportion of small specimens is independent of the region sampled is easily tested by constructing contingency tables (see Snedecor and Cochran, 1967).

VII. RESULTS

Vertical Zonation

More than 15,000 specimens of holothurians have been collected in the 393 beam and otter trawl samples that were surveyed in this study. At least thirty-five species were collected and all orders of holothurians. Excluding two species of the genus Psolus which inhabits hard substrates, the vertical ranges of these species suggest three bathymetric zones (Table 1). Above the 300 meter isobath is the Shelf Zone. Infaunal sediment eaters such as Molpadia intermedia and Paracaudina chilensis probably are numerically dominant in this zone but much more poorly sampled than the larger epifaunal Parastichopus sp. Of these shelf species only Molpadia intermedia has ever been recorded from the basin floor, and then only sporadically near the base of the slope. Between 300 meters and 2000 meters is the poorly sampled Upper Bathyal Zone which is poor in holothurians above about 800 meters. This area of few holothurian species and specimens generally corresponds to the zone of lowest oxygen concentration and the change from surface hydrographic conditions to those of the deep-sea. In the deeper portion of the Upper Bathyal Zone three species are sometimes taken in large numbers, Pannychia fecundum, Scotoplanes theeli, and Pannychia moesleyi. Only this last mentioned common slope species is found on the basin floor. It is very similar to Pannychia fecundum in morphological features, but is generally found deeper. Similarly, Scotoplanes



globosa, which is abundant on the floor of the basin, is very similar to Scotoplanes theeli but may be distinguished by the podial arrangement. The transition to the Lower Bathyal-Abyssal Zone is marked by the first appearance at 2000 meters by five species. Above 3000 meters Paelopatides confundens, Peniagone cf. dubia, and Scotoplanes globosa are very distinctly the most abundant holothurians. Below 3000 meters these species are still often collected, but Abyssocucumis albatrossi, Benthodytes sanguinolenta, and Onierophanta mutabilis have become numerically dominant.

Simply on the basis of presence or absence the lower bathyal-abyssal zone which spans both Cascadia Basin and Tuft's Plain can not be divided into two sections. Only 7 species have been collected only on Tuft's Plain. Of these Myriotrochus bathybius, Myriotrochus giganteus, and Scotoplanes clarki may prove to be conspecific with Cascadia Basin species.

It must be noted that the two boundaries I have drawn coincide with intervals of zero samples (400 m and 2000 m). As such they may ultimately prove to be arbitrary lines drawn across a relatively uniform gradient of faunal change with depth. However, it is not my purpose by establishing these zones to indicate that any zone is absolutely dissimilar from another. I simply wish to stress the dissimilarities which can be seen, and to simplify the pattern of changing holothurian species so that segments of the gradient may be isolated for further examination. In general the holothurians collected in the Lower Bathyal-Abyssal Zone are different species than those collected on either the continental slopes or the continental shelf and the proposed zones simply reflect this fact.

Holothurian Catch vs. Total Invertebrates

Holothurians were consistently collected in all trawl samples taken on Cascadia Basin and Tuft's Plain. Above 2000 m on the continental slope and the shelf they were frequently absent from samples. Across the basin they comprised a highly variable proportion of the total catch of invertebrates (Figure 11). The pattern of proportion is apparent when all the proportions for series CP-1, CP-2, CP-3, and TP A-C are tallied as the percent of total catch:

	Average	Median	Minimum	Maximum	No. Trawls
CP-1	7.137	5.468	1.345	25.649	24
CP-2	6.082	5.312	.300	19.618	30
CP-3&4	7.166	5.952	1.247	30.692	25
Tuft's	2.114	.927	.063	7.362	16

On Cascadia Basin the proportion varies about a common median but then decreases markedly across the width of Tuft's Plain. On the eastern side of the plain, sample area TP-A, the proportion is similar to those seen on Cascadia Basin. The minimum proportion is seen at the far from land and deepest sample area TP-C.

Holothurians are not only a relatively consistent percent of the total invertebrates catch on Cascadia Basin, they also occupy a relatively consistent position in the species rank-abundance diagrams.

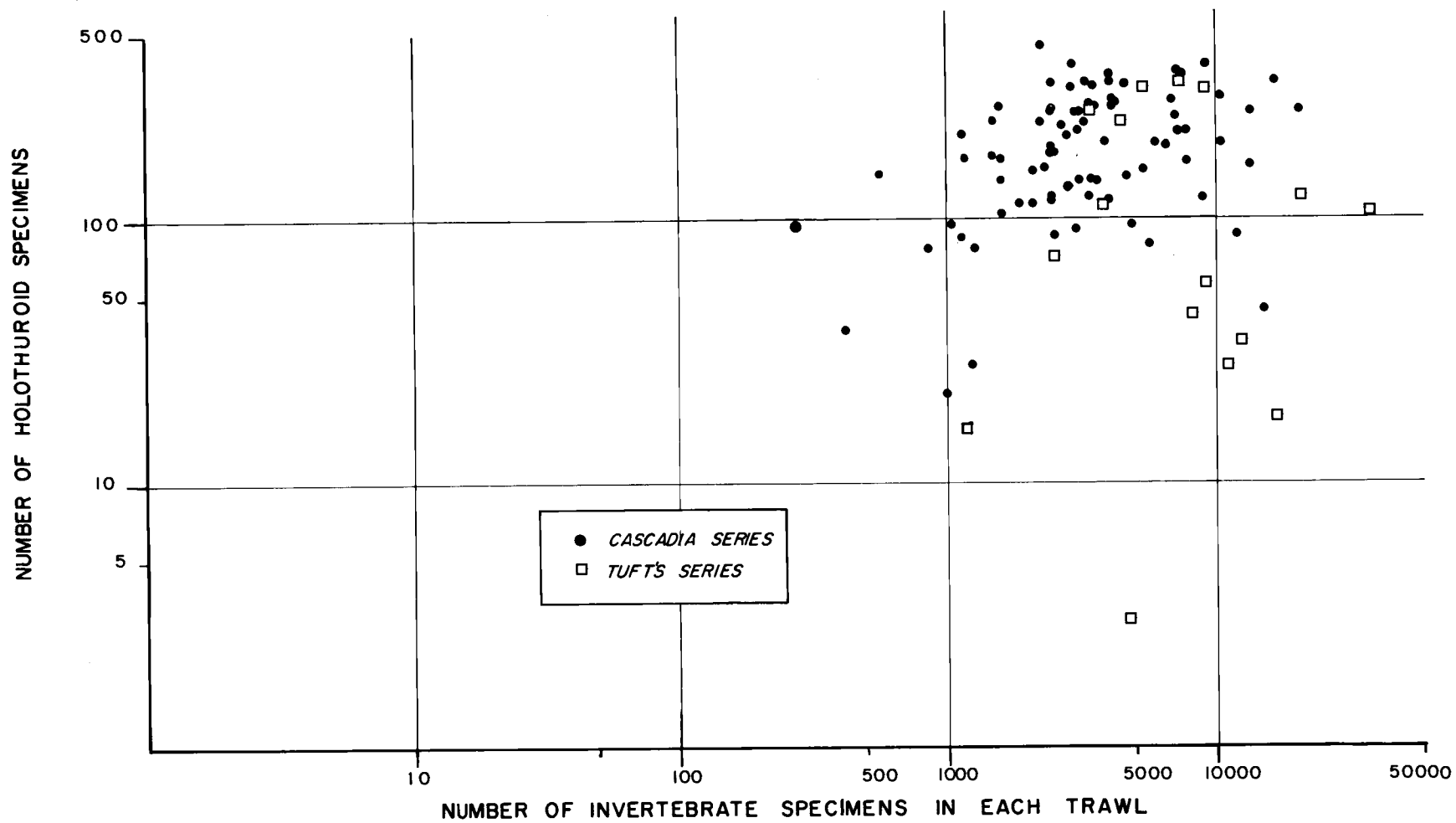


Figure 11. Plot of the number of holothurian specimens collected per trawl versus the number of invertebrates collected. Log scales were used to reduce size.

When the rank of the first and second most abundant holothurian in each trawl sample are compiled (Figure 12) they have adjacent modes at the seventh and eighth most abundant species in the total contents. The exact species in these positions change across the sampled area, but the two or three most abundant holothurians usually are found in adjacent rank classes.

With very few exceptions the 6 or fewer species more abundant in a sample than holothurians are ophiuroids, brittle starfish. On Cascadia Basin the most abundant holothurians is usually Paelopatides confundens or Peniagone cf. dubia, which are surpassed in abundance by the ophiuroid species Ophiocten pacificum, Ophiura leptoctenia, Amphiura koreae, Amphilepis platytata, Pandelia carchara, and Ophiacantha bathybia. On Tuft's Plain the most abundant holothurians are Benthodytes sanguinolenta and Abyssocucumis albatrossi, which are generally preceded in rank by the ophiuroid species Ophiura bathybia and a variety of other fauna. The number of ophiuroids in a sample may be one or two orders of magnitudes greater than the number of holothuroids.

Abundance of Holothurians

The number of animals living in a given area at any moment in time can be considered the end product of a myriad of processes involving a host of biological and physical factors. This number must ultimately bear some relationship to the food available for conversion into tissue and offspring. It is this single

FIRST MOST ABUNDANT
HOLOTHUROID'S RANK

SECOND MOST ABUNDANT
HOLOTHUROID'S RANK

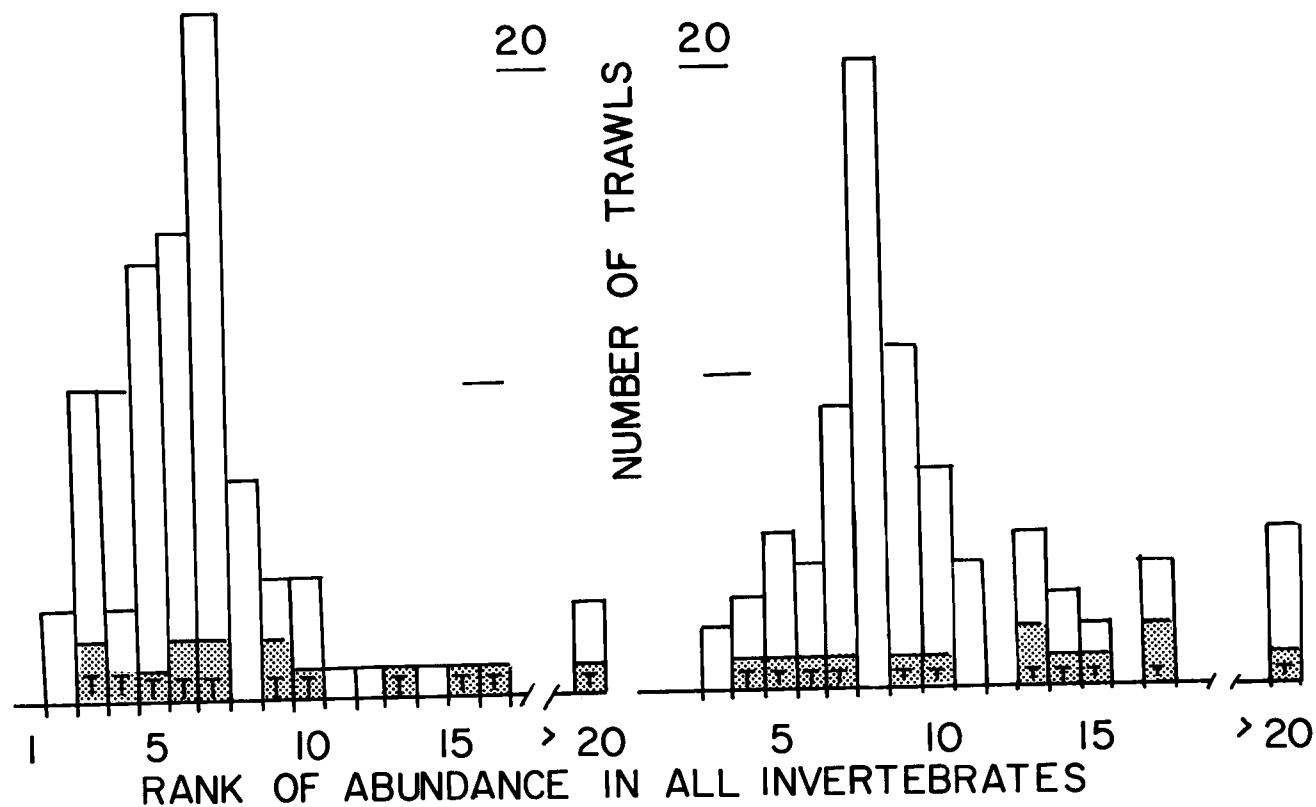


Figure 12. The rank of abundance of the first and second most abundant holothuroids per trawl when the entire invertebrate catch is ranked. T's indicate Tuft's Plain samples.

relationship out of many which has received the greatest consideration by deep-sea biologists, because of the lack of a primary producer population in the abyss. It is hoped that something can be inferred as to the origins, forms, and routes of food input to the deep through investigation of the number of organisms present in samples from different areas of the ocean floor.

Due to the vagaries of the beam trawl used in this study it is not possible to convert catch sizes into densities. This does not, however, prevent cautious comparison of the number of holothurians collected in each area. The average number of holothurians collected per trawl at TP-C (27.4) is approximately a full order of magnitude smaller than the average catch at CP-3-E (300.2). Unless the beam trawls collect specimens exponentially with area sampled, then this ten-fold difference is greater than the possible two or three fold difference in actual square meters sampled. If the entire invertebrate catch at TP-C was low, then unusually brief on bottom times might be suspected. However, the total catches were not markedly reduced, and there were no other indications of low sampling intensity such as very low odometer counts. It is therefore reasonable and informative to examine the average holothurian catch in each area as an actual estimate of abundance relative to the other sample areas.

Cascadia Basin and Tuft's Plain samples represent approximately the same span in depth and distance from land yet they are wholly different with respect to the areal variation in the total number of holothurian specimens collected per trawl. In spite a 1000 m depth range

and 100 km distance from land range the number of specimens collected in the Cascadia Basin series shows only a large scatter, Figures 13 and 14. There are no discernable trends in catch size either either depth or distance from land. The fewest specimens taken were 29 in BMT's 90 and 160. These two outliers may represent two of the few times that the trawl-odometer system worked. They have the lowest recorded odometer readings, suggesting that the trawls sampled an unrepresentatively short time and do not reflect the abundance of holothurians on bottom. The largest number of specimens were taken at BMT-119 in the E series at the base of the slope where 452 specimens were collected. The other samples in the E area and all along the entire slope base were not distinctly higher than those collected elsewhere. When samples were averaged together to represent an area, CP-3-E was the highest area due largely to the large catch in BMT-119. The average catch and the range in each area are shown in Table 2. These values confirm the lack of consistent pattern found when individual samples are examined. It is important to note that the offshore trend in average catch is different from one series of samples to another; no one series can represent the whole basin. Across the breadth and depth of the entire basin no trends can be detected in total holothurians other than a range of catch varying over about one order of magnitude and showing no consistent localized high or low values.

On Tuft's Plain an entirely distinct and different pattern is immediately obvious in Figures 13 and 14. Depth and distance from land here increase together so that plotting of abundance against both

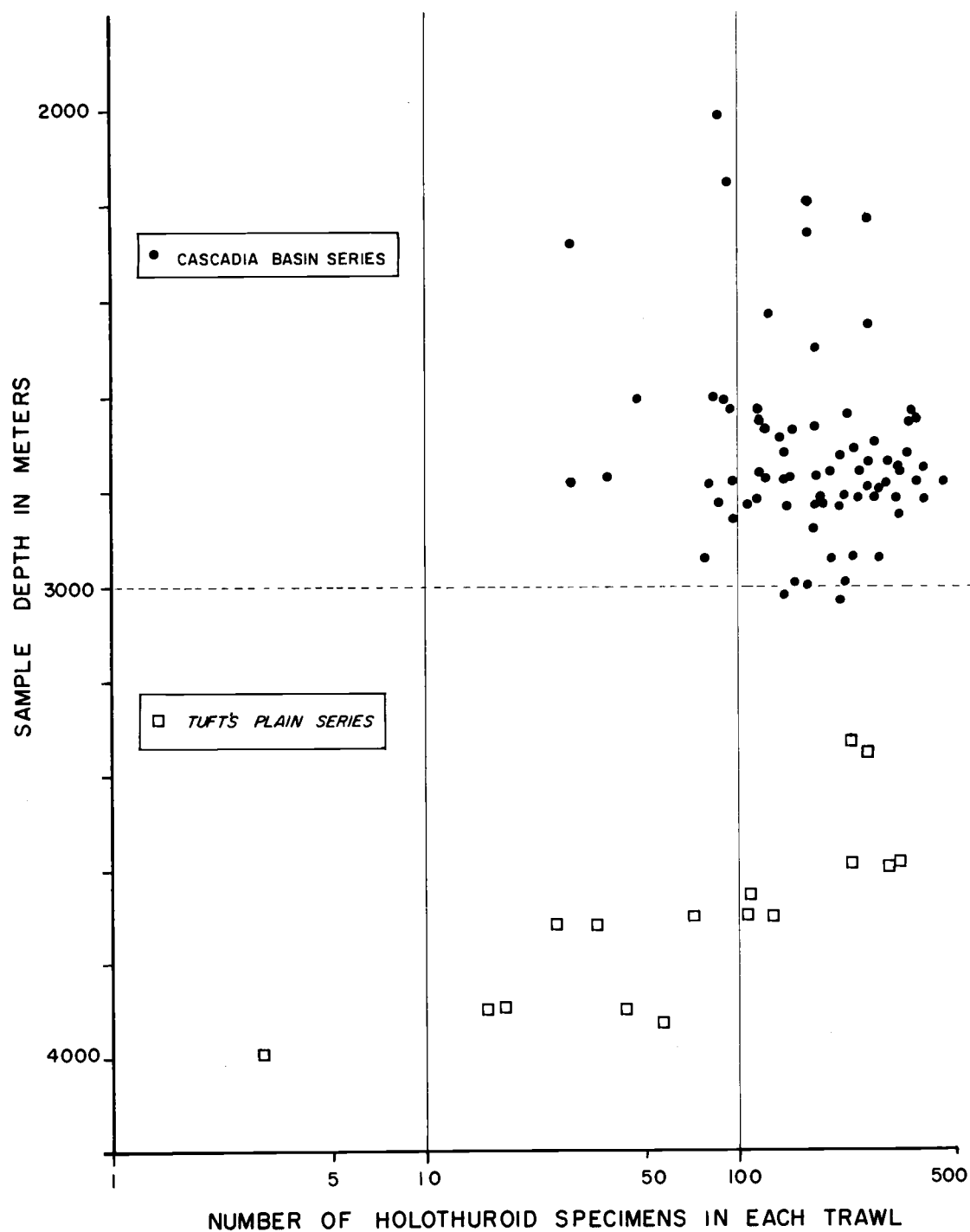


Figure 13. The number of holothurians per trawl versus the depth of collection. The catch of holothurians apparently decreases exponentially with depth only on Tuft's Plain.

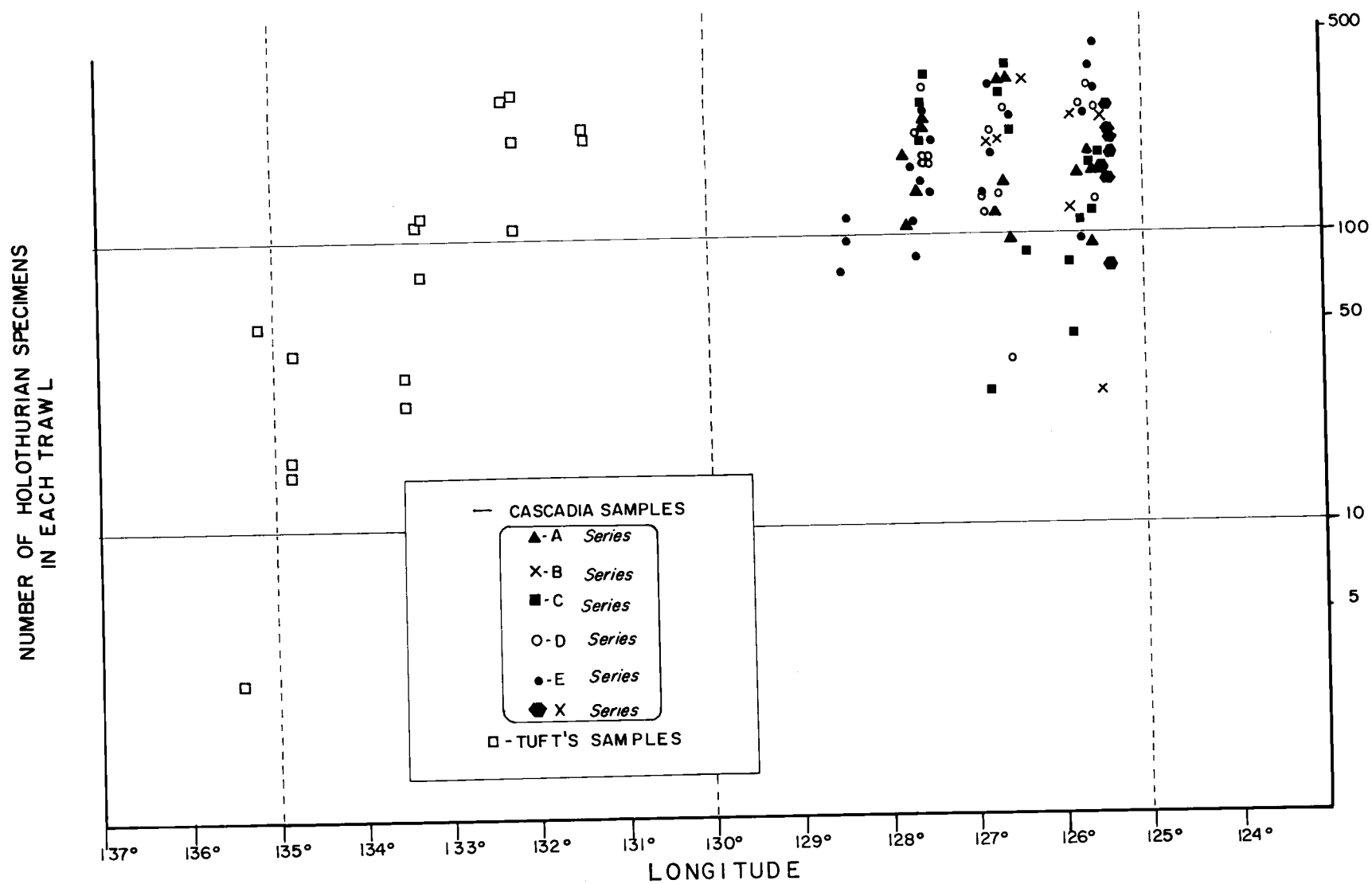


Figure 14. Plot of holothurians per trawl versus position seaward. The decrease across Tuft's Plain is obvious.

Table 2. The average, maximum, and minimum catch of Holothuroids per trawl at each sampling area.

Ave.							
(Max.)							
(Min.)							
TP-C	TP-B	TP-A	CP-4	CP-3	CP-2	CP-1	
27 (58) (3)	73 (124) (27)	240 (311) (112)		193 (259) (117)	205 (313) (91)	128 (167) (88)	A
					223 (342) (137)	168 (262) (29)	B
				275 (367) (214)	236 (394) (29)	106 (177) (47)	C
				212 (331) (174)	156 (274) (38)	224 (274) (118)	D
			107 (127) (79)	162 (266) (85)	231 (333) (141)	300 (452) (99)	E
							183 (276) (77)

variables is redundant but has been done to facilitate comparison.

The total number of holothurians per trawl decreases exponentially with depth and distance from land in such a manner that the catch diminishes by approximately two orders of magnitude for each 1000 meters increase in depth or 100 kilometers movement seaward. At the shallow and landward end of the Tuft's series catch sizes were similar to the values seen all over the Cascadia Basin. If the low values found at CP-4 are taken as representative of the density in that area, then the eastern Tuft's samples reflect comparable numbers of holothurians to those on the shallower and more landward western Cascadia Basin. The extreme low of 3 specimens in BMT-310 is not simply reflective of a poor total catch because a representative number of about 5000 total invertebrates were in that sample. Although it must be considered only a preliminary observation, because all the trawl contents have not been sorted to the level of species, the total invertebrate catch does not seem to show the same distribution as the holothurian catch. As is clearly seen in Figure 11, the total invertebrate catch in both the Tuft's and Cascadia series fall within the same range of from about 1000 to 10,000 specimens but in the Cascadia series there is not the depth or distance from land decreases so obvious for holothurian's on Tuft's.

When the summed counts of holothurians per trawl are broken down into the component species the results for the Cascadia and Tuft's series again are distinctly different. On Tuft's the exponential decrease can be found in the major species, Abyssocucumis albatrossi, Benthodytes sanguinolenta, and Onierophanta mutabilis (Figure 15).

In the Cascadia series the apparent uniformity seen in the data for total holothurian catch obscures considerable variation in abundance shown by individual species. Both Peniagone cf. dubia and Paelopatides confundens have high catches at the base of the slope, CP-1, while the third most abundant Cascadia species, Scotoplanes globosa is not common in this region (Figures 16-18). West of the slope base large catches of both the former two species become less common while Scotoplanes reaches its greatest concentrations at the CP-2 line off-setting the decrease in the number of the other two species (Figure 17). Scotoplanes is somewhat lower in number in the CP-3 series of samples (Figure 18) but sporadic highs for Peniagone and Paelopatides combine with lesser numbers of the other species to maintain the usual one order of magnitude range in holothurian catch. typical of the rest of the basin. The manner in which the species counts relate to one another at the same stations is, however, a topic covered more appropriately under the discussion of relative abundance relationships.

Within Sample Relative Abundance

AIDN Analysis of Variance

Due to the southward tilt of Cascadia Basin both the sample series perpendicular to land and those parallel to land lie along a depth gradient. Therefore it is not possible to structure a factorial analysis of variance in which depth variation is associated with a single position factor. However, it is still possible to determine

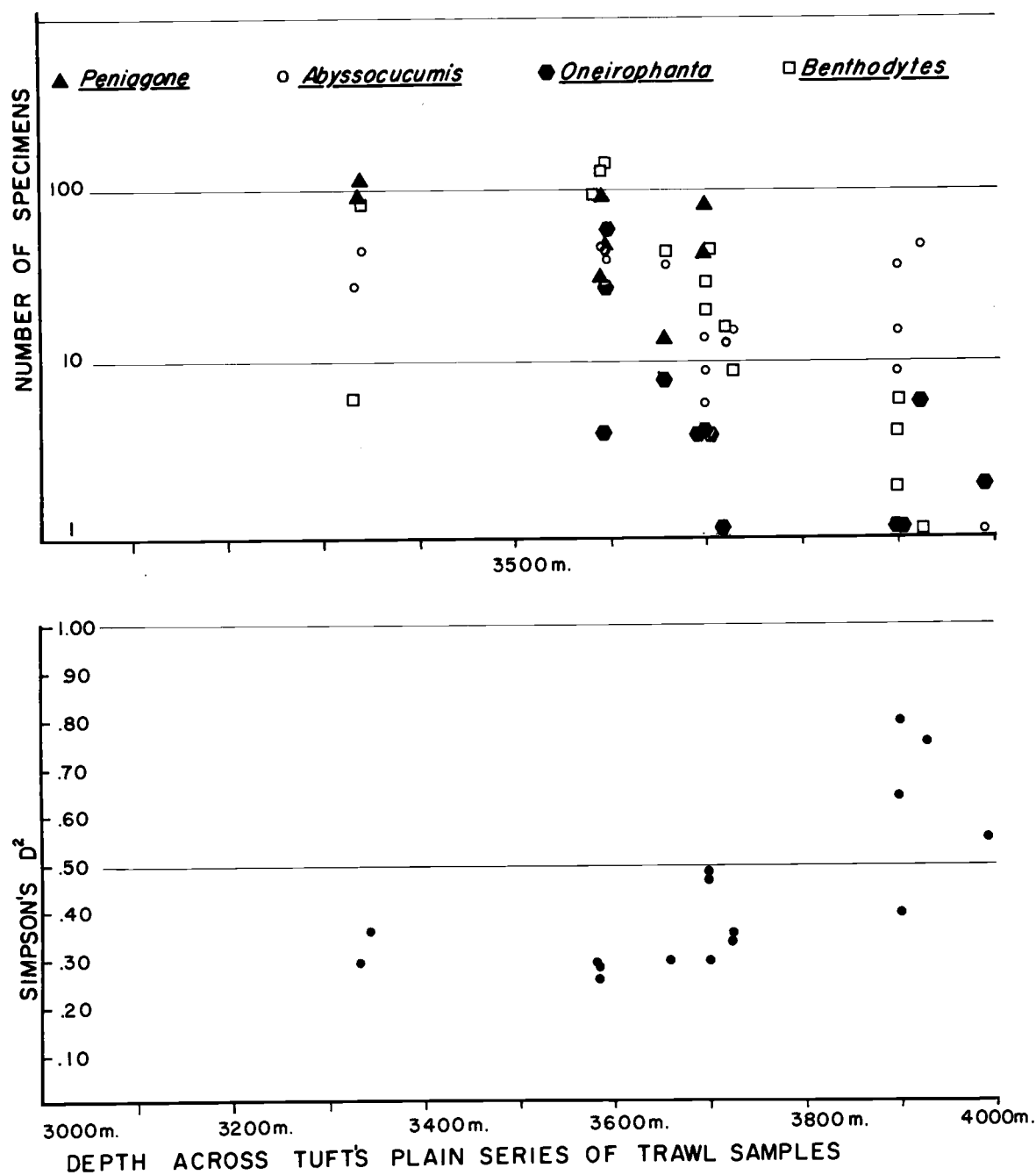


Figure 15. Change in abundance of the four major species on Tuft's Plain with the accompanying change in Simpson's D squared.

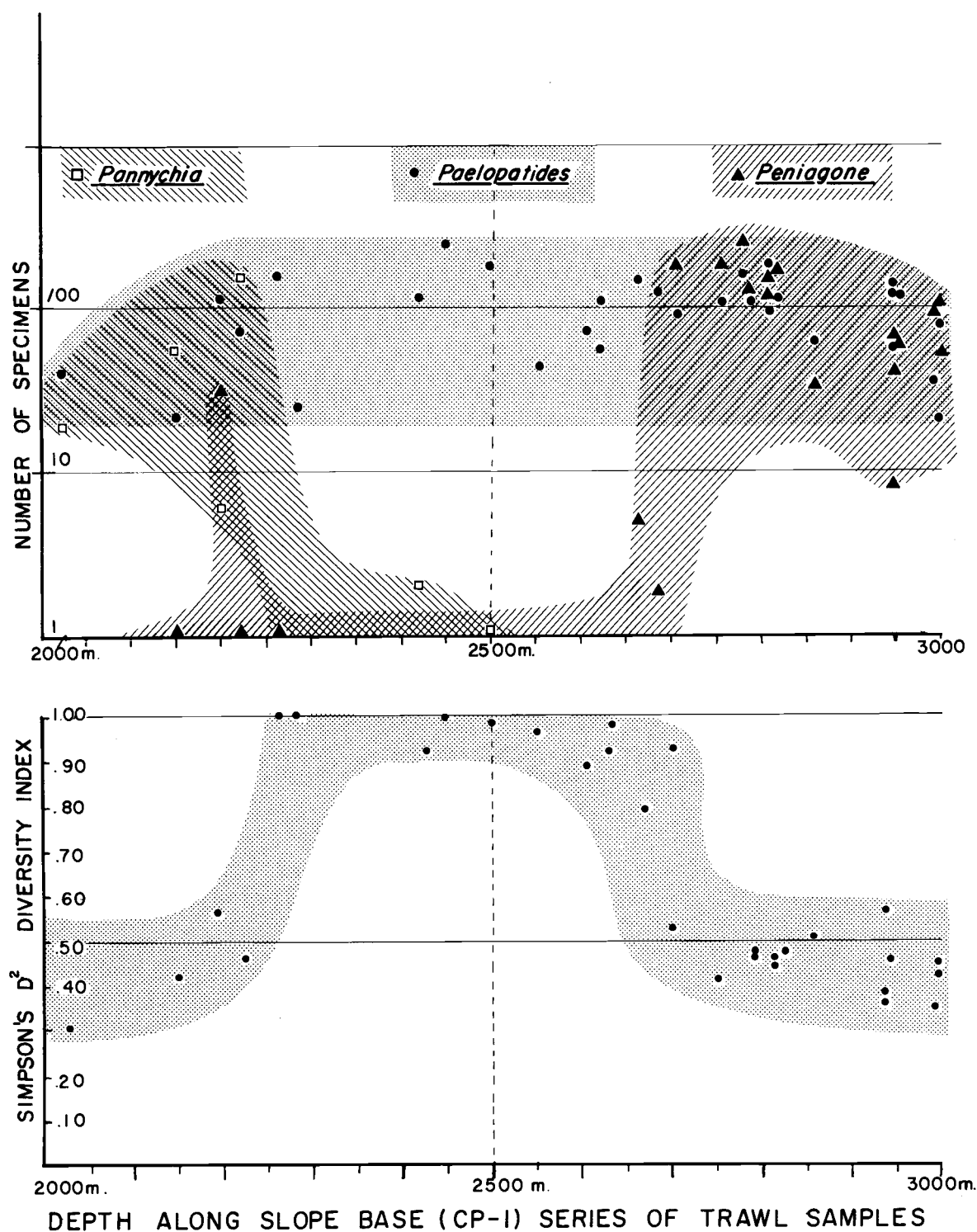


Figure 16. Change in abundance of three major species at CP-1 (slope base) series with accompanying changes in Simpson's D squared.

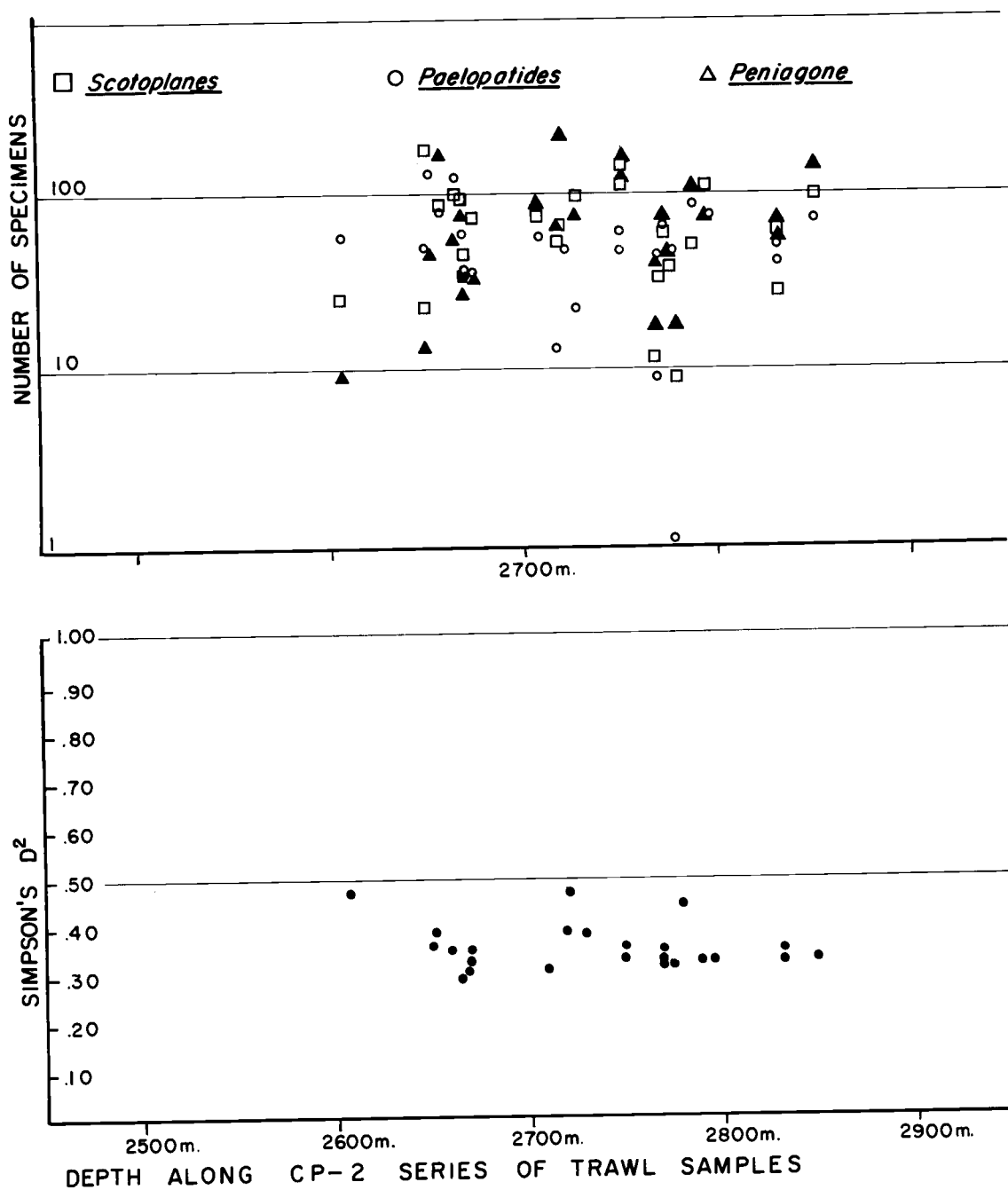


Figure 17. Change in abundance of three major species at CP-2 series with accompanying changes in Simpson's D squared.

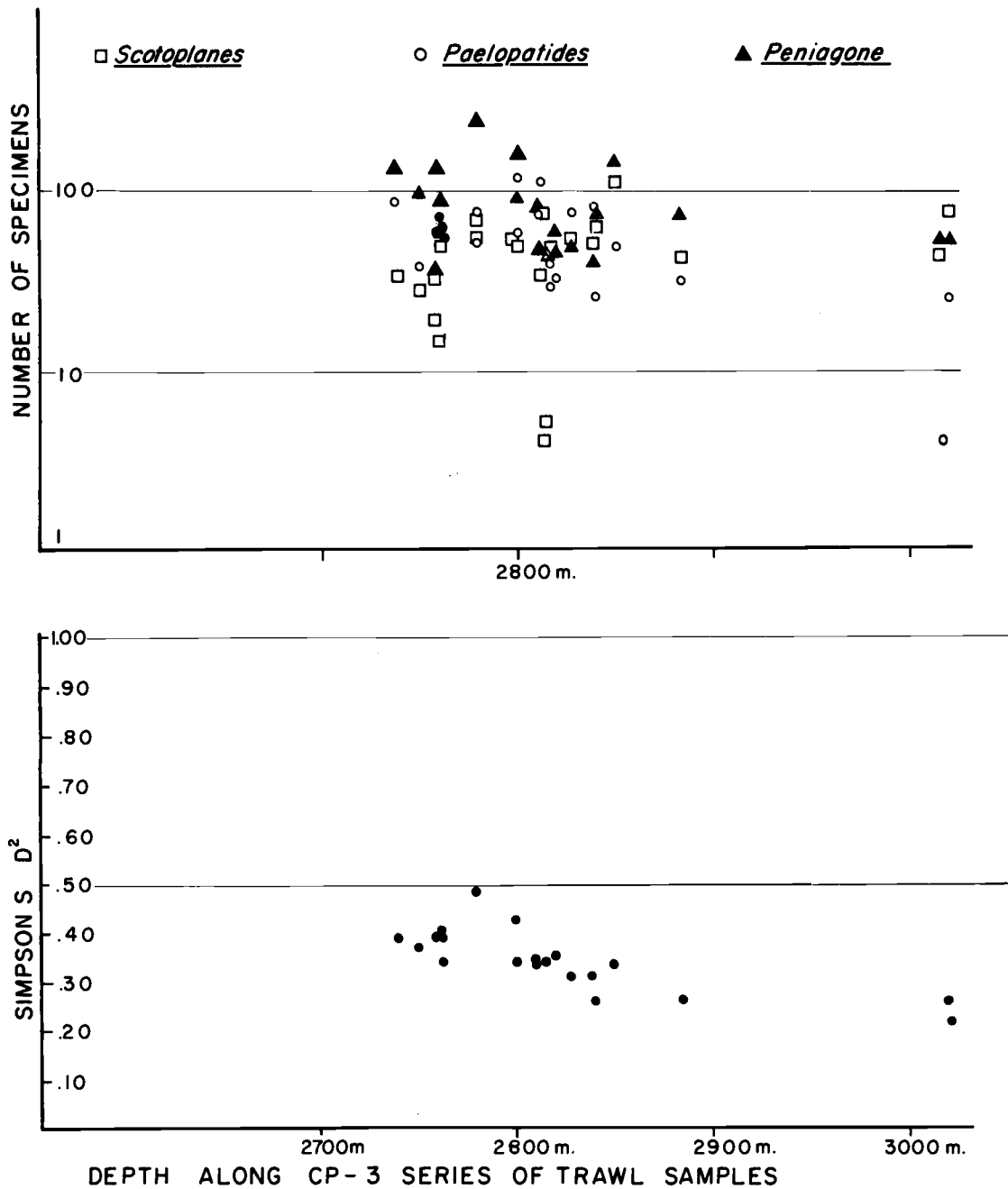


Figure 18. Changes in abundance of three major species at CP-3 series with accompanying changes in Simpson's D squared.

the significance of depth effects upon the fauna because each sample series lies along depth gradients of appreciably different slope. Of the three series parallel to land, CP-1 spans 970 m; CP-2 spans 244 m and CP-3 spans 285 m. Actually, all but two samples in the CP-3 series fall within a relatively narrow 110 m range, and I consider it to be the flattest of the three sample series. If the faunal variation along these three series is independent of the depth gradient, the effect of north-south position within the series should be independent of the effect due to position offshore. However, if depth is an important factor, then there should be strong interaction between the effects due to north-south position and those due to offshore position.

Through use of the AIDN factorial analysis of variance the total variability of the proportional data was partitioned, and the following null hypotheses tested:

1. That there are no significant differences in the composition of the holothuroid fauna at different positions in the sample grid.
2. That there is no interaction between faunal variation due to offshore position and that due to north-south position.

The results are shown in Table 3. There is a significant ($p < .005$) effect due to position in the grid, and there is significant interaction between the two factors.

The interaction between north-south effects and offshore effects is quite apparent in Table 4. When separate analyses were conducted on each of the CP-1, 2, and 3 series the effect of north-south

Table 3. AIDN Analysis of Variance for Cascadia Basin Series

Source of Variance	Degrees of Freedom	Sums of Squares Corrected	Mean Square	F
POSITION	14	6.8111	.4865	6.9105 *
Offshore	2	3.8920	1.9460	
North-South	5	.9712	.1942	
Interaction	7	1.9478	.2783	3.9531 *
RESIDUAL	61	4.2935	.0704	
TRAWLS	75	11.1046		
17 spp. * p. < .005				

Table 4. Separate Analyses of Variance for Each Offshore Series

Source of Variance		Degrees of Freedom	Sums of Squares Corrected	Mean Square	F
CP-1 12 spp.	North-South Pos.	5	2.3660	.4732	4.083 *
	Residual	24	2.7808	.1159	
	Trawls	29	5.1468	.1775	
CP-2 11 spp.	North-South Pos.	4	.39956	.0999	3.000 *
	Residual	20	.66691	.3230	
	Trawls	24	1.06647	.04444	
CP-3 14 spp.	North-South Pos.	3	.15295	.05098	1.085
	Residual	18	.84576	.04699	
	Trawls	21	.99871	.04756	

* p. < .005

Table 5. AIDN Analysis of Variance for Tuft's Plain Samples

Source of Variance	Degrees of Freedom	Sums of Squares Corrected	Mean Square	F
Position	2	1.3565	.6782	5.9745 *
Residual	13	1.4953	.1150	
Trawls	15	2.8518	.1901	
17 spp., *p. < .005				

position within each series can be seen to decrease across the basin. The north-south position has a significant effect at CP-1, a significant, but smaller effect at CP-2, and no significant effect in the CP-3 series. The total variances at CP-2 and CP-3, as estimated by the trawl mean square, are approximately the same. At CP-2, which is closer to land, there appears to be greater north-south structure to the faunal variation than is seen at CP-3. The greatest total variance, north-south effects, and unexplained residual are all associated with CP-1. In that series there are both the greatest depth range and the greatest terrestrial effect.

A similar single factor analysis was performed on the available Tuft's Plain data (Table 5). As with the Cascadia results, there is a significant effect due to position. Most interesting is the fact that the total variance, position effect and residuals at CP-1 closely resemble those on Tuft's Plain. The depth span on Tuft's is 636 m; not greatly different than that at CP-1.

Inter-Area Similarities

The triangular similarity matrix needed to fully display all possible pairs of samples in this study contains 4500 separate entries. During data analysis this large array was generated, but its full inclusion here is unnecessary. The preceeding analysis of variance contains much of the information in that table and the examination of the much smaller similarity matrix for pooled sample areas is equally informative, Table 6.

Table 6. Inter-sample Area SIMI Similarity Values, Part I.

	CP-1-A	CP-2-A	CP-3-A	CP-1-B	CP-2-B	CP-1-C	CP-2-C	CP-3-C
CP-1-A	1.0000							
CP-2-A	.5873	1.0000						
CP-3-A	.4737	.7758	1.0000					
CP-1-B	.7865	.6675	.6112	1.000				
CP-2-B	.3074	.8456	.8880	.3389	1.0000			
CP-1-C	.7830	.6791	.5920	.9987	.3333	1.0000		
CP-2-C	.3225	.8222	.9283	.3739	.9940	.3637	1.0000	
CP-3-C	.4515	.8363	.9883	.5612	.9452	.5473	.9700	1.0000
CP-1-D	.5962	.7407	.9616	.7846	.7476	.7648	.8010	.9206
CP-2-D	.4780	.9322	.9274	.5585	.9685	.5550	.9681	.9694
CP-3-D	.4282	.9014	.9354	.5016	.9817	.4961	.9839	.9776
CP-1-E	.4992	.6844	.9815	.6685	.7863	.6439	.8439	.9412
CP-2-E	.4374	.8626	.9710	.5296	.9684	.5186	.9839	.9544
CP-3-E	.4795	.8325	.9857	.6010	.9196	.5868	.9475	.9912
CP-4-E	.3750	.9226	.8290	.4017	.9760	.4048	.9534	.9024
CP-1-X	.6201	.7636	.9371	.8060	.7343	.7895	.7819	.9015
TP-A	.0157	.1769	.4350	.0473	.3931	.0295	.4334	.4237
TP-B	.0042	.2139	.5372	.0396	.4909	.0179	.5279	.5249
TP-C	.0000	.0024	.0014	.0001	.0013	.0004	.0012	.0062

Table 6. Part 2.

	CP-1-D	CP-2-D	CP-3-D	CP-1-E	CP-2-E	CP-3-E	CP-4-E	CP-1-X
CP-1-D	1.0000							
CP-2-D	.8484	1.0000						
CP-3-D	.8386	.9934	1.0000					
CP-1-E	.9851	.8484	.8528	1.0000				
CP-2-E	.8893	.9853	.9905	.9096	1.0000			
CP-3-E	.9338	.9570	.9670	.9472	.9835	1.0000		
CP-4-E	.7050	.9722	.9701	.7136	.9370	.8852	1.0000	
CP-1-X	.9820	.8451	.8300	.9564	.8738	.9179	.7087	1.0000
TP-A	.3657	.3429	.4124	.4276	.4092	.5075	.3417	.3482
TP-B	.4441	.4217	.5005	.5243	.5049	.5916	.4088	.4161
TP-C	.0001	.0007	.0205	.0000	.0014	.0604	.0401	.0414

Table 6. Part 3.

	TP-A	TP-B	TP-C
TP-A	1.0000		
TP-B	.9745	1.0000	
TP-C	.4357	.3755	1.0000

The greatest dissimilarities are for comparisons between areas most separated in depth and distance. TP-C and CP-1-A have a similarity of .000000, so they share absolutely no holothurian fauna in common. TP-C also has low values of similarity with the other two stations in the Tuft's Plain series. It can be seen that the similarity between CP-1-A and the farthest Cascadia stations, CP-3-E and CP-4-E, are comparable to the similarities between TP-C and the other TP stations. These comparison span about the same depth difference of 1000 meters.

The increasing similarity between samples in the CP-1 series and those seaward on the basin with increasing depth along the CP-1 line is evident. When each of the C-1-A through CP-1-E areas' similarities are examined it is seen that all three of the deeper CP-1 stations, CP-D, E, and X are actually more similar to the stations seaward on Cascadia Basin than they are to the shallower stations in CP-1.

Results of Cabfac, Vector Analysis

The 22 species dimensions in which the angles of the full similarity matrix are arrayed was reduced to a smaller number of orthogonal reference axes by CABFAC. The relatively high proportions of Paelopatides confundens, Peniagone cf. dubia, Scotoplanes globosa, Abyssocucumis albatrossi, and Benthodytes sanguinolenta resulted in the formation of relatively few new axes or "Factors".

From the principal factor score matrix, Table 7, the first new axis is seen to lie between Paelopatides confundens, and Peniagone

Table 7. Unrotated Factor Scores (Cosine of Angle Between Factor and Species)

Species Axis	Factor (Orthogonal Assemblages)						
	1	2	3	4	5	6	7
<u>Paelopatites confundens</u>	.647	-.729	.207	-.039	.036	-.057	.001
<u>Peniagone cf. dubia</u>	.658	.571	-.104	-.464	-.095	.061	.002
<u>Scotoplanes globosa</u>	.376	.205	-.320	.838	.050	-.041	.005
<u>Psychropodes longicaudata</u>	.043	.046	.054	.061	.094	-.028	.002
<u>Abyssocucumis albatrossi</u>	.033	.176	.686	.245	-.639	.039	-.165
<u>Benthodytes sanguinolenta</u>	.049	.247	.584	.081	.748	-.066	-.090
<u>Oneirophnata mutabilis</u>	.007	.051	.171	.045	-.038	.003	.981
<u>Pseudostichopus nudus</u>	.006	.006	-.004	.010	-.002	-.001	-.002
<u>Caphiera sulcata</u>	.006	.005	-.002	.016	.011	-.004	-.007
<u>Synallactes gilberti</u>	.006	.007	.010	-.003	.019	-.003	-.025
<u>Pannychia moesleyi</u>	.014	-.056	.018	.059	.087	.979	-.002
<u>Molpadia musculus</u>	.009	-.012	.003	.005	.011	.159	-.000
<u>Molpadis granulata</u>	.002	.006	.007	-.000	.011	-.001	-.003
<u>Ypsilothuria bitentaculata</u>	.015	.004	.004	-.064	-.034	.012	-.008
<u>Pseudostichopus villosus</u>	.000	.002	.002	.003	.009	-.001	-.000
<u>Mesothuria murrayi</u>	.000	.002	.011	.005	-.009	.000	-.025
<u>Amperima rosea</u>	.000	.001	.001	-.001	.001	.000	-.000
<u>Amperima narsei</u>	.003	-.001	-.001	.009	.005	.038	.000
<u>Benthodytes incerta</u>	.000	.000	.003	.002	-.006	.000	-.005
<u>Peniagone gracilis</u>	.000	.003	.013	.005	-.006	.000	-.008
<u>Laetmogone wyville-thompsoni</u>	.000	.000	.002	.001	.005	-.001	-.001
<u>Scotoplanes clarki</u>	.000	.003	.012	.005	.001	-.001	-.022
Percent of Variance	63.76	15.54	9.61	5.31	2.52	1.83	.90

cf. dubia and to a much lesser extent towards Scotoplanes. It accounts for 64% of the sample vector length. The distribution of the individual sample's loadings on to this first axis are interesting in that they show the uniformity of faunal composition suggested in the ANOVA. In Figure 19a the samples in CP-1 can be seen to be increasingly nearer this axis as they are progressively closer to the deeper end of that series. The CP-2 line consists of two different values of loading. While the samples in the northern half of CP-2 have loadings in the .80's, those at the southern end of CP-2 have loadings typically in the .90's. The CP-3 and the CP-E series can be seen to be quite similar with regard to this single most important factor.

The second factor, or new axis, reflects only 15.54% of the sample vector length, about 1/4th that of the first principal factor. It is bimodal and can be seen from the factor score matrix to be a combination of Paelopatides and Peniagone. Large negative loadings on this factor, Figure 19b simply reflect sizable abundance of Paelopatides in the absence of Peniagone so this is interpretable as Paelopatides alone. This band in the CP-1 series of high Paelopatides dominance is obvious in the map of loadings.

The third factor reflects the combination of Abyssocucumis albatrossi and Benthodytes sanguinolenta which are characteristically the most abundant species taken on Tuft's Plain. The map of this factor simply reflects that the major fauna on Tuft's Plain is different from that on Cascadia Basin (Figure 19c).

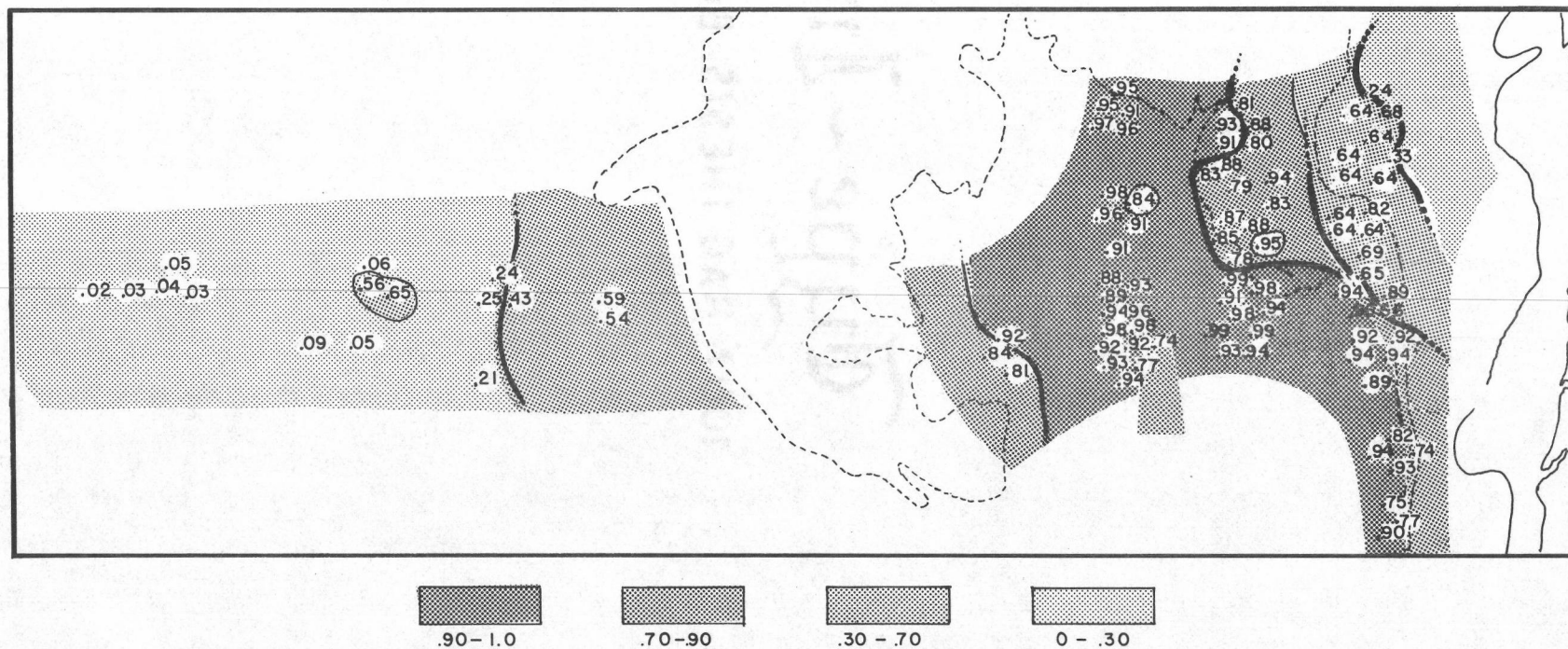


Figure 19a. SIMI, cosine of angle, between each sample vector and the first reference vector (principal component).

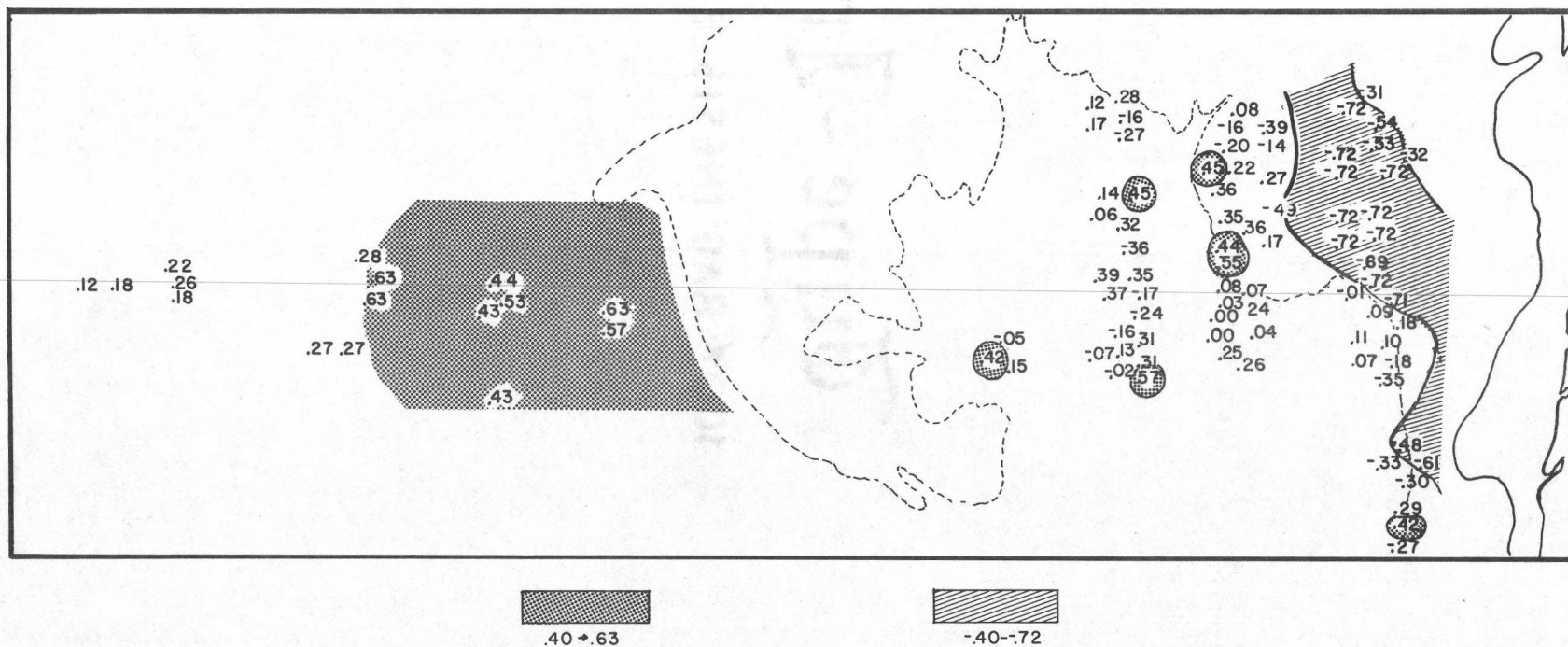


Figure 19b. SIMI, cosine of angle, between each sample vector and the second reference vector (principal component).

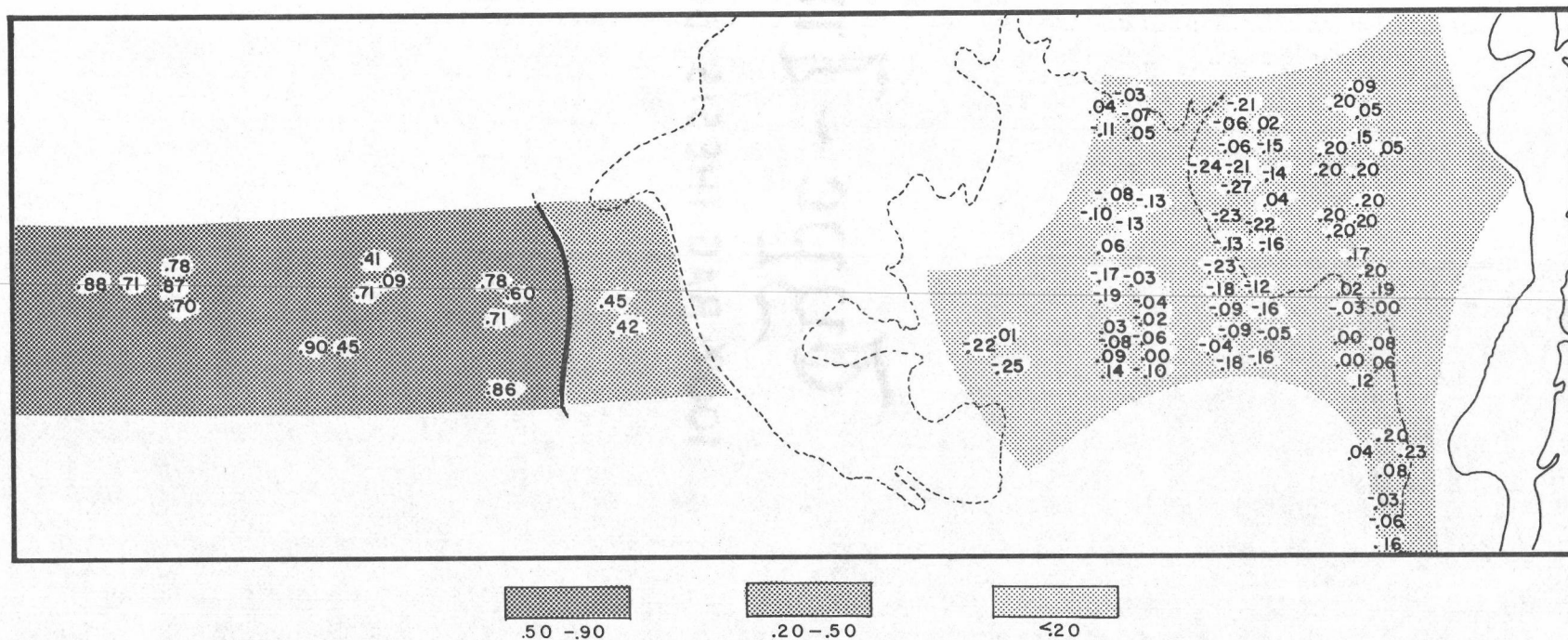


Figure 19c. SIMI, cosine of angle, between each sample vector and the third reference vector (principal component).

The remaining factors explain very little variance, but are interesting in the pattern of species occurrence that they reflect. Factor 4 is obviously Scotoplanes globosa in the absence of Peniagone cf. dubia and thus has high loadings in the trawls of CP-2-A where Scotoplanes was the dominant holothurian. While factor 3 was a combination of Abyssocucumis and Benthodytes sanguinolenta, factor 5 reflects that these two species do not have the same distribution in their extension onto Cascadia Basin, and reflects the separate occurrence of each without the other. Factor six and seven reflect the distributions of Pannychia moeselyi and Onierophanta mutabilis respectively.

As none of the new axes or factors had more than two species highly loaded upon them, they were not especially more informative than direct examination of the distributions of the individual species themselves. Since the analysis was greatly affected by the more abundant and variable species, it tends to de-emphasize the importance of examining the distributions of the rarer forms, which might be quite informative.

Diversity Patterns

The number of holothurian species taken in each individual trawl was generally lower in trawls containing few holothurian specimens than in trawls containing many. As suggested in Figures 20 and 21 the number of species may possibly decreased linearly with a decrease in the number of holothurians collected. This inverse relationship with abundance is most obvious in the Tuft's Plain series of samples due

to the greater range in abundances. The diversity, as measured by number of species collected, does not appear to be similarly related to the total number of invertebrates collected.

The rank abundance curves for Tuft's Plain and Cascadia Basin are strikingly similar when compared in Figure 22. In both areas three species of holothurians comprise the greatest portion of the sampled holothuroid fauna while the most species represent only 1.0% to .10% of the sample. As indicated on the diagrams, the rank of the species comprising the two curves are markedly different. The curve for the separate CP-1, CP-2, and CP-3 series are shown in Figure 23, along with three measures of diversity previously discussed. CP-1 clearly has the greatest dominance by a single species. The three most abundant species are the most equable at CP-2. At CP-3 there is the greatest number of species in the range below 1%, representing a relatively diverse fauna of rare holothurians.

The Simpson's D squared diversity measure versus depth in each of the CP-1 through CP-3, plus Tuft's Plain, are shown in Figures 16, 17, and 18. The diversity does not change regularly with depth, but reflects the dominance of species over the depth range sampled. In the CP-1 series the zone of Paelopatides confundens dominance clearly controls all diversity trends. Below about 2500 m the Simpson's D squared decreases slightly with depth, indicating an increased diversity, until the far Tuft's Plain samples are reached. At these samples diversity is low due to dominance by a few species.

In Table 8 three diversity measures are presented for the pooled samples in a form suggestive of their map orientations. While the

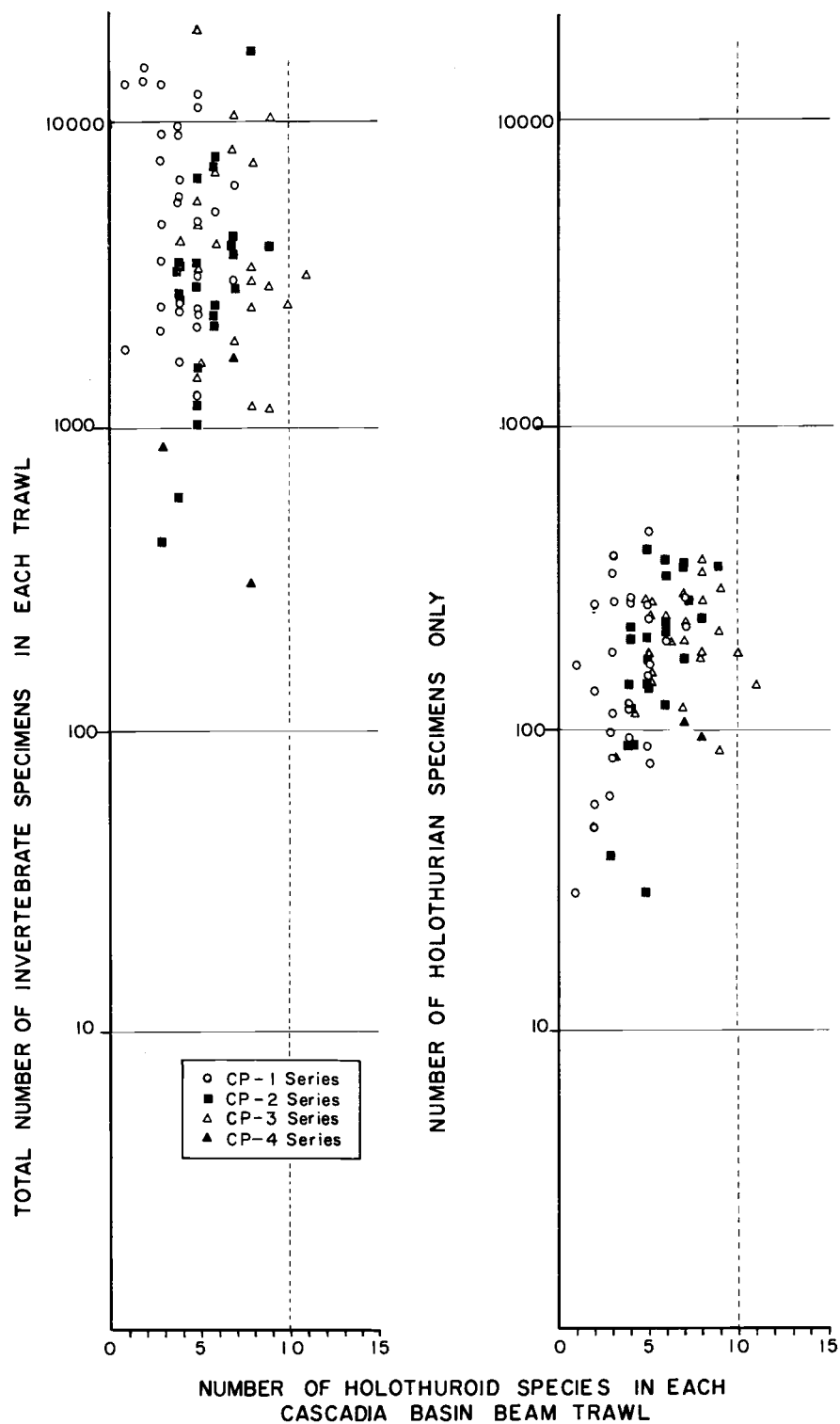


Figure 20. The number of holothurians species per trawl versus the log of both the number of holothurian specimens and the total number of specimens.

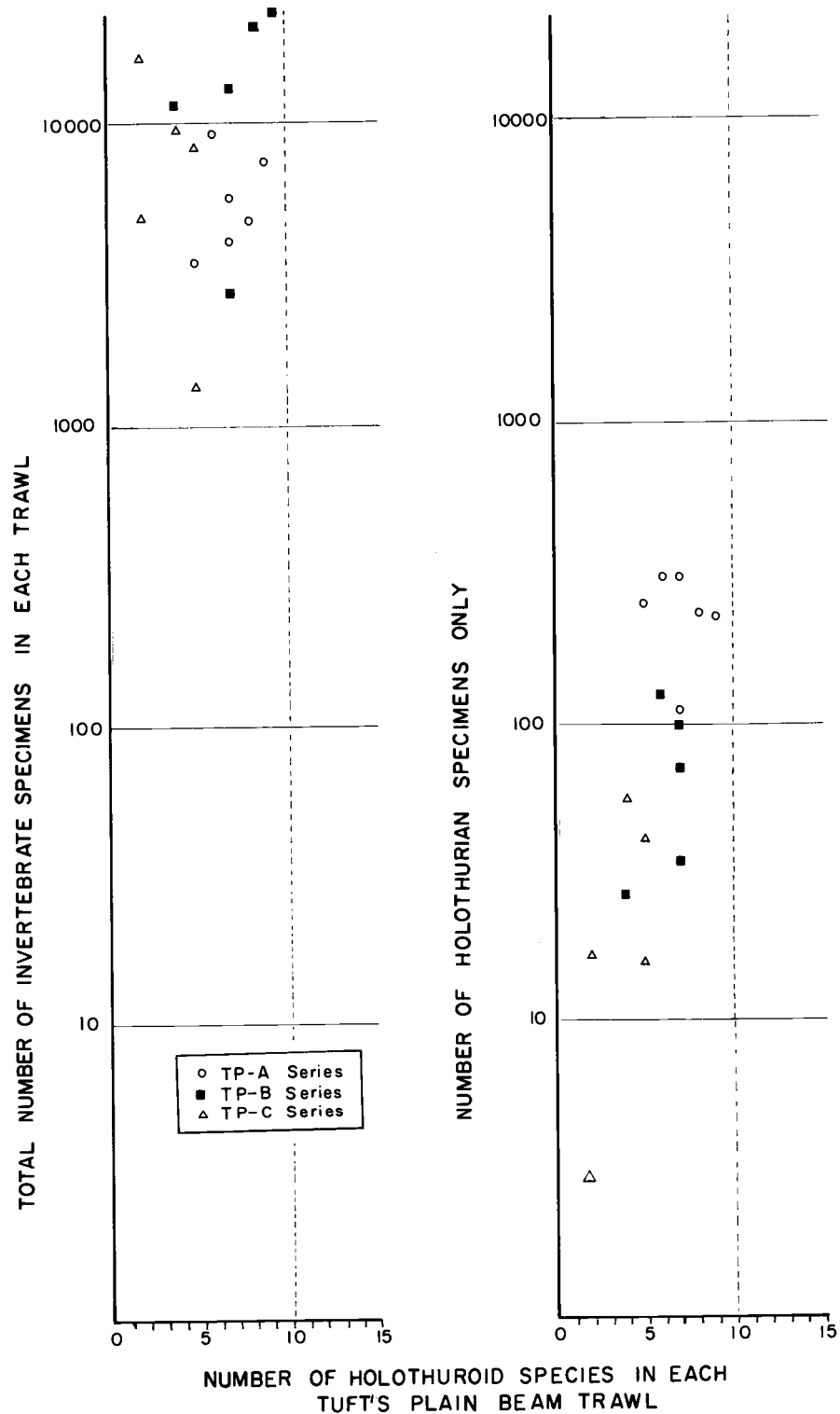


Figure 21. The number of holothuroid species per trawl plotted against the log of the number of holothurian specimens and total invertebrates for Tuft's Plain samples.

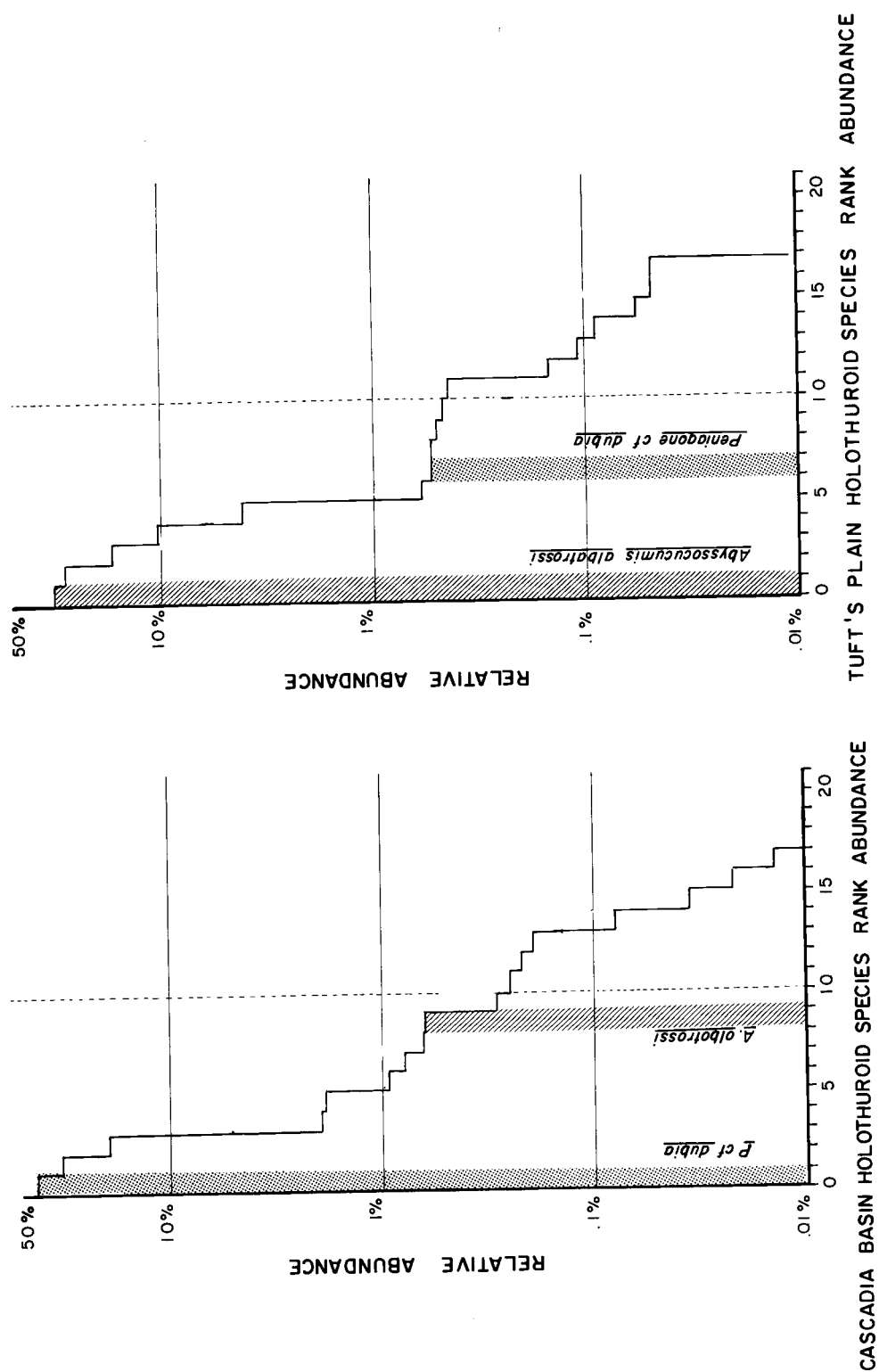


Figure 22. The Rank-abundance diagrams for the pooled samples of Tuft's Plain and Cascadia Basin showing the similarity in form.

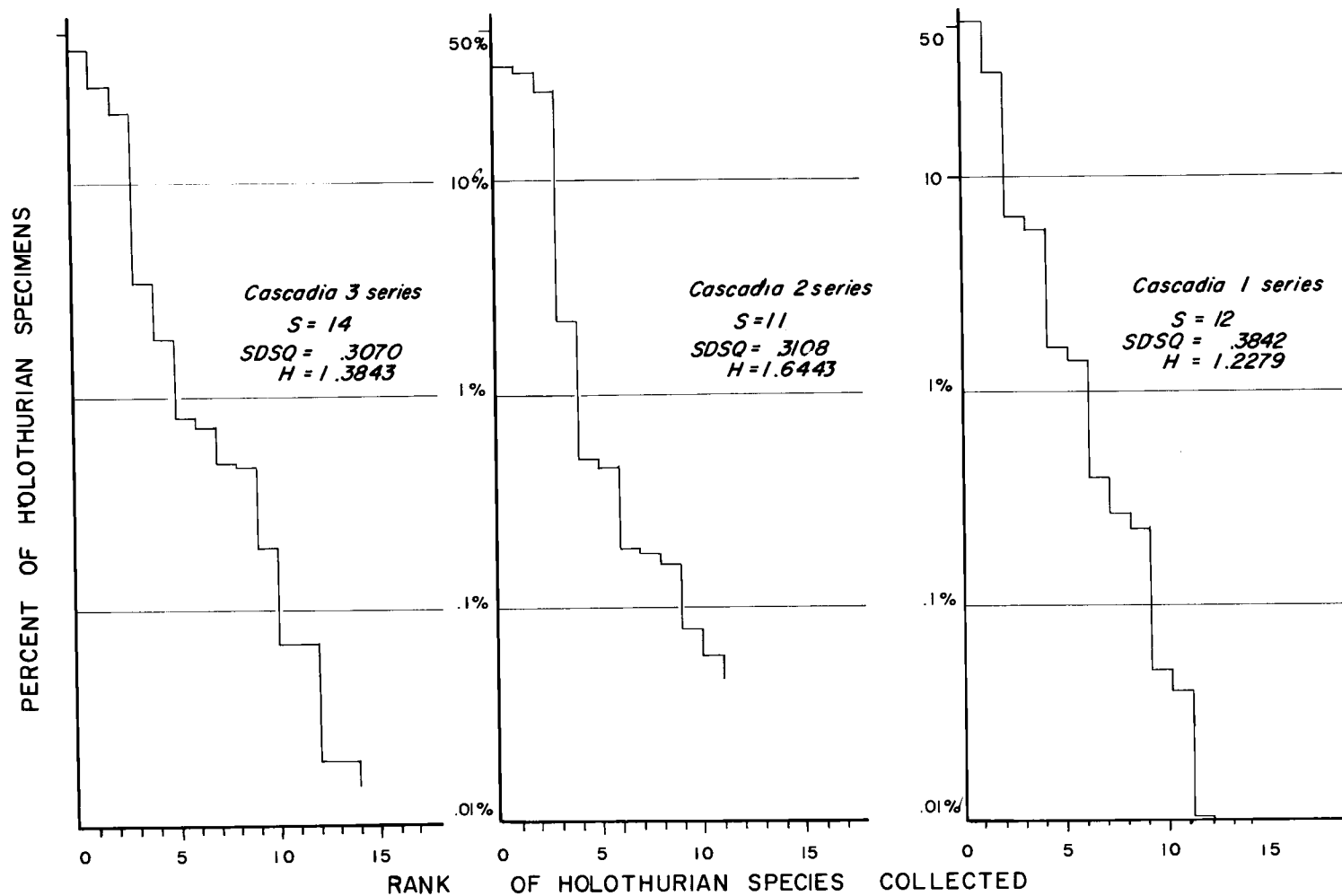


Figure 23. The rank of abundance diagrams for holothurians in the pooled samples from each Cascadia Basin offshore series. Three measures of diversity, S = no. species, Simpson's D squared, and H_e are shown.

Table 8. Three measures of diversity in each sample area.

NUMBER OF SPECIES							
TP-C	TP-B	TP-A	4	3	2	1	
				8	9	6	A
					7	6	B
				10	9	6	C
				9	8	5	D
6	13	12	9	14	9	6	E
						8	X

Simpson's D^2 (Dominance)

				.3597	.3199	.4116
					.3453	.6803
				.3361	.3256	.9059
				.2808	.3218	.4830
.5161	.2593	.2627	.3100	.2706	.3229	.4547
						.3422

 H_e Information Measure

				1.1543	1.6995	1.2067
					1.4427	.6054
				1.2450	1.2629	.2624
				1.4236	1.6453	.8601
.9417	1.6000	1.5420	1.3648	1.5914	1.3313	.8759
						1.3022

Number of Specimens in the Above Indices

				963	1024	511
					902	671
				1373	1413	531
				1061	781	1119
137	364	1440	292	1134	925	1501
						1280

diversity of each sample is given in Table 8, the pattern seen in the pooled samples is essentially the same and easier to present.

On the basis of number of holothurian species taken, the extreme sample areas with respect to depth and distance apart stand out as lowest diversity. TP-C and CP-1 are marked by the lowest number of species. The highest number of species are seen to have been taken at TP-A & B and only at the deepest area of Cascadia Basin, CP-3-E. The same pattern of diversity highs and lows is seen in an examination of both Simpson's D squared and H_e , the information measure.

Distribution of Species

Schematic maps showing the locations at which each of the 22 species were collected are shown in Table 9. Through examination of these charts in conjunction with the larger depth range chart (Table 1) drawn from all available data, four distribution groups may be constructed. Slope species which extend partially on to Cascadia Basin are the first distinct group and consist of Pannychia moeslyei, Molpadia musculus, Ypsilothuria bitentaculata, and Amperima narsei. This last species has not been recorded from the slope in any Oregon State University sample, but has been collected off the coast of Washington State at slope depths (Alton, 1972). At the other extreme there is a distinct group which is mostly collected on Tuft's Plain, but also occurs at the deepest and farthest from land stations along the CP-3 series. These species are Abyssocucumis albatrossi,

Table 9. Proportion of Each Species In Each Pooled Sample Area

Species found only at the CP-1 series of samples

Pannychia moesleyi

TP-C	TP-B	TP-A	CP-4	CP-3	CP-2	CP-1	
				0	0	.2077	A
					0	.1568	B
				0	0	.0011	C
				0	0	0	D
				0	0	0	E
0	0	0	0			0	X

Ypsilothuria bitentaculata

				0	0	0	
					0	0	
				0	0	0	
				0	0	0	
0	0	0	0	0	0	0	
						.0997	

Species found in greatest proportion at CP-1 series of samples

Paelopatides confundens

				.3717	.3796	.5982	
					.1579	.8094	
				.2883	.2227	.9415	
				.2624	.3010	.6049	
0	0	.0157	.2055	.2649	.2894	.4540	
						.4625	

Peniagone cf. dubia

				.4455	.1751	.0524	
					.4120	0	
				.4583	.4243	.0059	
				.3476	.3627	.3389	
0	.2164	.2670	.3082	.4019	.4124	.4967	
						.3380	

Species found in greatest proportion at CP-1 series of samples (con't)

Molpadia musculus

				0	.0006	.0608
					.0068	.0019
				0	.0096	.0166
				0	.0053	.0051
0	0	0	0	.0010	.0061	.0044
						.0095

Amperima naresi

				0	.0023	.0195
					.0007	0
				0	.0083	0
				0	0	0
0	.0019	0	0	0	0	0
						0

Species found only in the CP-2 series of samples

NONE

Species found in greatest proportion at CP-2 series of samples

Scotoplanes globosa

				.1499	.3772	.0615
					.3867	.0248
				.2042	.3089	.0141
				.2969	.3155	.0490
0	0	0	.4144*	.1868	.2618	.0437
						.0719

Pseudostichopus nudus

				.0018	.0058	0
					.0044	0
				.0043	.0073	0
				.0035	0	0
0	0	0	.0100	.0066	.0015	.0004
						0

Species found only in CP-3 series of samples

NONE

Species found in greatest proportion at CP-3 series of samples

Caphiera sulcata

				.0044	.0045	0
					0	.0041
				.0044	.0007	0
				.0077	.0017	0
0	0	.0013	.0068	.0121	0	0
						0

Species found only at TP-A series of samples

NONE

Species found in greatest proportion at TP-A series of samples

Synallactes gilberti

				0	0	0
					0	0
				.0028	0	0
				0	.0017	0
0	0	.0157	.0068	.0123	.0055	0
						.0056

Species found only , or in greatest proportion at TP-B.

Mesothuria murrayi

				0	0	0
					0	0
				0	0	0
				0	0	0
0	.0148	0	0	.0017	0	0
						0

Laetmogone wyville-thompsoni

				0	0	0
					0	0
				0	0	0
				0	0	0
0	.0028	0	0	0	0	0
						0

Species found in greatest proportion at TP-B

Molpadia granulata

				.0010	0	0
					0	0
				.0012	.0009	0
				.0021	.0007	0
0	.0150	.0014	0	.0037	.0008	0
						0

Scotoplanes clarki

				0	0	0
					0	0
				0	0	0
				0	0	0
0	.0131	.0022	0	0	0	0
						0

Pseudostichopus villosus

				0	0	0
					0	0
				0	0	0
				0	0	0
0	.0028	.0007	0	.0024	0	0
						0

Benthodytes sanguinolenta

				.0014	.0017	0
					0	0
				.0005	0	0
				.0255	0	0
.0820	.3816	.3798	.0171	.0436	.0027	0
						0

Psychropodes longicaudata

				.0242	.0532	0
					.0312	.0030
				.0334	.0172	.0109
				.0463	.0115	.0024
.0207	.0664	.03558	.0103	.0270	.0198	.0008
						.0005

Species found only at TP-C

Benthodytes incerta

				0	0	0
					0	0
				0	0	0
				0	0	0
.0048	0	0	0	0	0	0
						0

Species found in greatest proportion at TP-C

Peniagone gracilis

				0	0	0
					0	0
				0	0	0
				0	0	0
.0125	0	.0044	0	0	0	0
						0

Abyssocucumis albatrossi

				0	0	0
					0	0
				.0024	0	0
				.0080	0	0
.6865	.2466	.1948	.0204	.0316	0	0
						.0279

Oneirophanta mutabilis

				0	0	0
					0	0
				0	0	0
				0	0	0
.1935	.0309	.0868	0	.0039	0	0
						0

Amperima rosea

				0	0	0
					0	0
				0	0	0
				0	0	0
0	.0027	0	0	0	0	0
						0

Benthodytes sanguinolenta, Onierophanta mutabilis, Molpadia granulata. There is a group of rare species which appears to be found on Tuft's Plain but they are so rare as to make their distribution obscure. In beam trawl samples these are Laetmogone wyville-thomsoni, Benthodytes incertae, Amperima roseae, Mesothuria murrayi, Pseudostichopus villosus, and three species collected only by otter trawl, Ceroplectana trachyderma, Myriotrochus gigantea, and Myriotrochus bathybius. It is likely that more intensive sampling on Tuft's Plain and the slope base beyond 3000 m will increase information on these distributions. The third major group blankets almost the entirety of the Cascadia Basin and extends to the eastern edge of Tuft's Plain. These are the numerically abundant Paeloptides confundens, Peniagone cf. dubia, and Scotoplanes globosa. The exact extension of these species westward onto Tuft's Plain is partially obscured by taxonomic difficulties surrounding the differences between Peniagone cf. dubia on Cascadia and the presumably separate Peniagone gracilis on Tuft's Plain. Similarly, Scotoplanes clarki on Tuft's Plain may represent a mere morphological variant of Scotoplanes globosa of Cascadia Basin.

The fourth is distinct, but not abundant. It can be seen on Cascadia Basin, sometimes extending westward to the eastern edges of Tuft's Plain, generally absent from the CP-1 line. These are Synalactes gilberti, Caphiera sulcata, and Pseudostichopus nudus. Not conforming to any of these and remarkable for its great range including all but the relatively shallow CP-1-A and CP-1-B areas is Psychropodes longicaudata.

These groupings are intended only as an initial classification of trend; there are exceptions consisting of positive records of specimens collected well beyond the range of most other specimens of that species. Caphiera sulcata which is otherwise noticeably rare or absent at the slope base, has been collected commonly on the continental slope off Washington between 1189 m and 1463 m, but has previously been incorrectly identified as Mesothuria (Zygothuria) lactea (Carney, 1971 and Alton, 1972). A single specimen of Abyssocucumus albatrossi which seems distinctly limited to depths at or below 3000 meters has been collected on the Oregon Continental slope at 2000 meters.

The 22 species of holothurians collected in the beam trawling series on Cascadia Basin and Tuft's Plain may also be grouped according to the series, CP-1 through 3 and TP-A through C, at which they occur solely or in the greatest proportion regardless of the magnitude of the proportion.

Two species occur solely at CP-1, Ypsilothuria bitentaculata at 1-X in the deep end and Pannychia moesleyi at the shallower end, CP-1-A through C. Two species of abundant holothurian are found proportionately most important at the CP-1 series, Paelopatides confundens and Peniagone cf. dubia. Molpadia musculus and Amperima naresi also have their proportionately greatest occurrence at the CP-1 series but show very different pattern seaward. Molpadia musculus is not found at the CP-3-A, C and D areas yet is common in equally deep CP-1 samples. The Amperima naresi is found only at CP-1-A and does not go along the slope base but extends out onto the shallowest portion of the CP-2 series on the apron of Astoria Fan.

No species of holothuroid is found only in the CP-2 series. The abundant species Scotoplanes globosa is most important at the northern and shallow end of this series. Psychropodes longicaudata is similarly most important at the northern and shallow end. Both species are similar in that they are relatively rare along the entire depth of the slope base, CP-1, series, but relatively common at similar depths in the CP-3 series. The rarer species Pseudostichopus nudus is again more important at the northern end of the CP-2 series where samples were taken on the Astoria Fan apron. The proportions there, however, were very similar to those encountered at the CP-3 series.

Molpadia granulata and Caphiera sulcata were most abundant in the CP-3 series, especially at the CP-3-E area. Although no species were collected only at the CP-3 series, four species found there are Tuft's Plain species found nowhere else on Cascadia Basin. Two other species, most common on Tuft's Plain, have their highest Cascadia Basin proportions at CP-3-E. The transition between the fauna of Cascadia Basin and Tuft's Plain is thus most distinct at CP-3-E.

Although CP-2 is undistinctive compared to the other Cascadia Basin or Tuft's series, the fauna which occurs at CP-2 falls into a class in which the highest proportions are in the A through C areas on the apron of Astoria Fan and a class with highest proportions off the apron at D and E. With the highest proportions at either A, B, or C are Scotoplanes globosa, Psychropodes longicaudata, Pseudostichopus nudus, Paelopatides confundens, Amperima naresi, Molpadia musculus ,

and Caphiera sulcata. Peniagone cf. dubia is not appreciably more dominant at CP-2-B and CP-2-C than it is at CP-2-E. However, it has a distinctly low dominance at the relatively shallow CP-2-A area. Molpadia musculus is somewhat similar in that it is most dominant in the CP-2-B and CP-2-C regions yet is markedly low in the CP-2-A area. Those species which have distinctly higher proportions in the CP-2-D and CP-2-E areas are Synallactes gilberti and Molpadia granulata. Benthodytes sanguinolenta has been taken only at CP-2-A and CP-2-E, where it is slightly more common. All three of these species are most abundant and reach their highest proportions on Tuft's Plain below 3000m. Although no specimens of Abyssocucumis albatrossi have been collected along the CP-2 line by beam trawl, a few specimens were taken by otter trawl in the general vicinity of CP-2-E. The presence of these four deeper water holothuroid species at the southern end of the CP-2 sample series is reflective of the significant vertical zonation found in the AIDN analysis of variance previously discussed. However, the proportions of most of the species which do show zonation along CP-2 are too low to have contributed to the results of that analysis.

More extensive sampling in the CP-3-E, CP-2-E, and CP-1-E areas may demonstrate that the deep, southern portion of Cascadia Basin has a holothurian fauna which is more similar to the holothurian fauna of Tuft's Plain than to that of the shallower portions of the basin.

At the easternmost Tuft's Plain area, TP-A, no species were found restricted to that area but Synallactes gilberti was most important there. Benthodytes sanguinolenta was about as equally important at TP-A as at TP-B. TP-B was more distinctive than TP-A. One species is restricted to TP-B and six others taken most abundantly there. Of special interest is the importance of Psychropodes which is of similar importance at the CP-2 series. Only one species was confined to the TP-C area, although two reached their greatest importance there.

Abundance Versus Occurrence

At each of the sample areas the number of specimens (abundance) of each species collected and the number of trawl samples from that area in which it was taken (occurrence) provide two measures of the local distribution of the species in that location. If the species is distributed in some uniform manner over the area sampled then increasingly larger catches should coincide with an increasing proportions of trawl samples which contain that species. This relationship is quite distinctly shown in Figures 24a through 24c where the percent of trawls in each area containing the species are plotted against the average number of specimens found in those trawls containing that species. For all but four species, in any area in which 20 or more animals were taken on the average, the animal was taken in 100 percent of the trawls in that area. On Cascadia Basin Pannychia moesleyi, and Peniagone dubia are taken in numbers much larger than 20 specimens but were not collected in all samples in those areas.

In the former instance, this is simply reflective of inclusion in the sample area of a few very shallow samples in which Pannychia dominated. The case of Peniagone is far more interesting. Those stations where it was captured in fewer trawls than expected from the abundance are in areas at the extreme of its distribution, and these points fall on a very straight line. The high abundance coupled with low occurrence reflects that Peniagone and Pannychia occur in dense but scattered clusters at the extremes of their range. The linear fit of Peniagone is unexplainable at this time, but it may be due to the aggregation pattern of that species. On Tuft's Plain Benthodytes sanguinolenta and Synallactes gilberti show similar indication of dense aggregates, high counts in areas where they were not taken in all the samples.

Psychropodes longicaudata is presented on a separate graph, Figure 24e, because it appears to be a special case. It is the only species which was repeatedly collected at less than 10 specimens per sample, yet was in every trawl in those areas. Only Benthodytes sanguinolenta was ever in such low abundance yet so prevalent in the samples and this was only in a single area. It thus appears that Psychropodes longicaudata is either more uniformly distributed than any other species or it is more available to the trawl. Additionally, Psychropodes was found in more of the sampling areas than any other species.

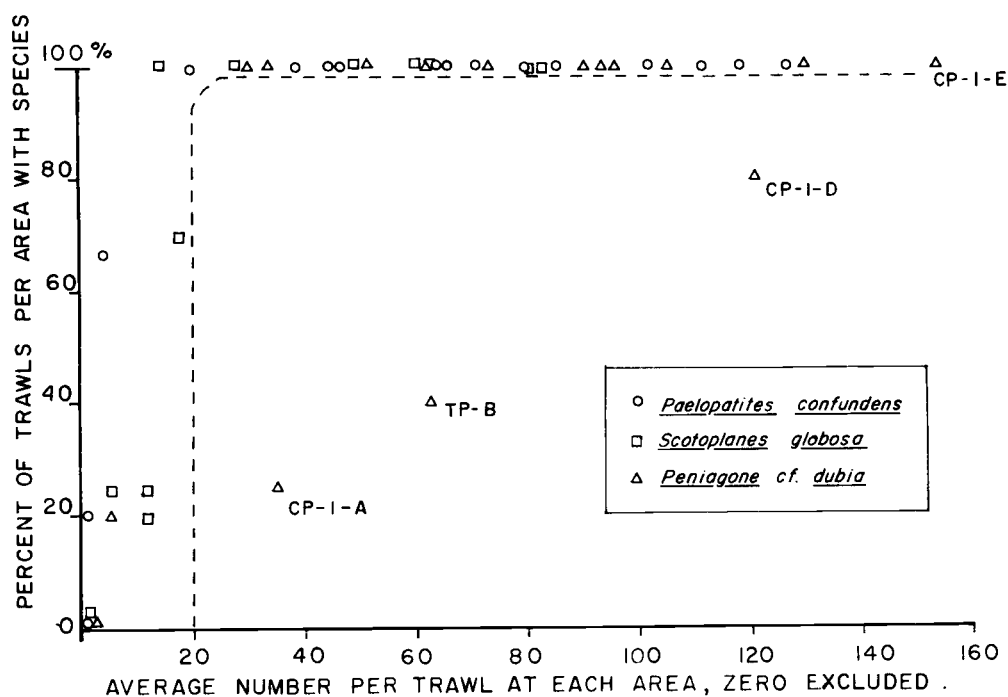


Figure 24a. Abundance (average number of specimens per area when taken) versus Occurrence (percent of trawls in each Area taking at least one specimen) for the three major Cascadia Basin species.

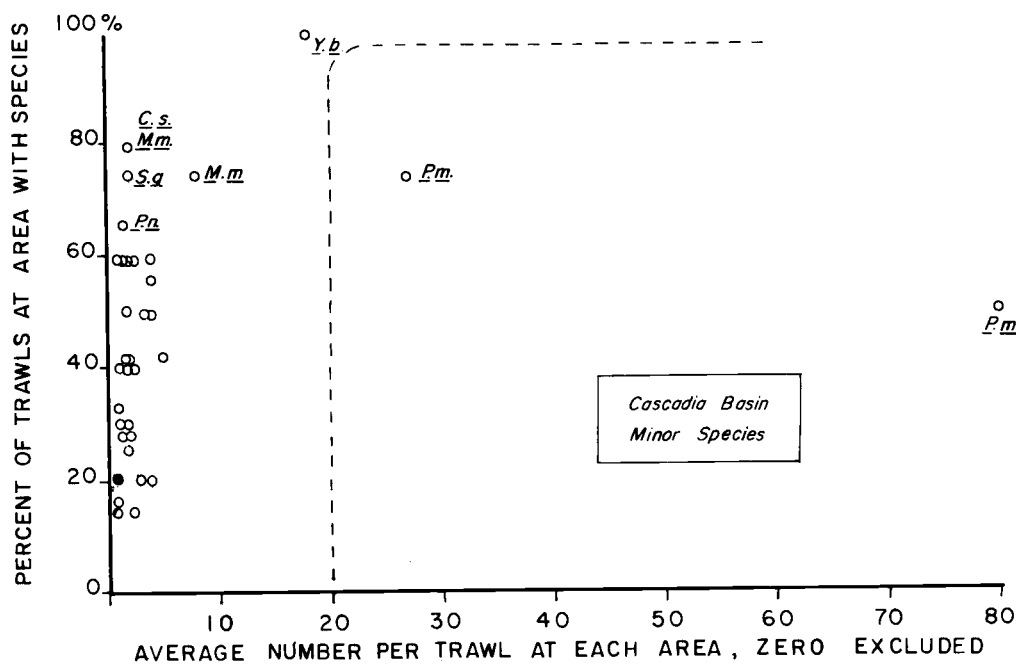


Figure 24b. Abundance versus occurrence for the minor Cascadia Basin species.

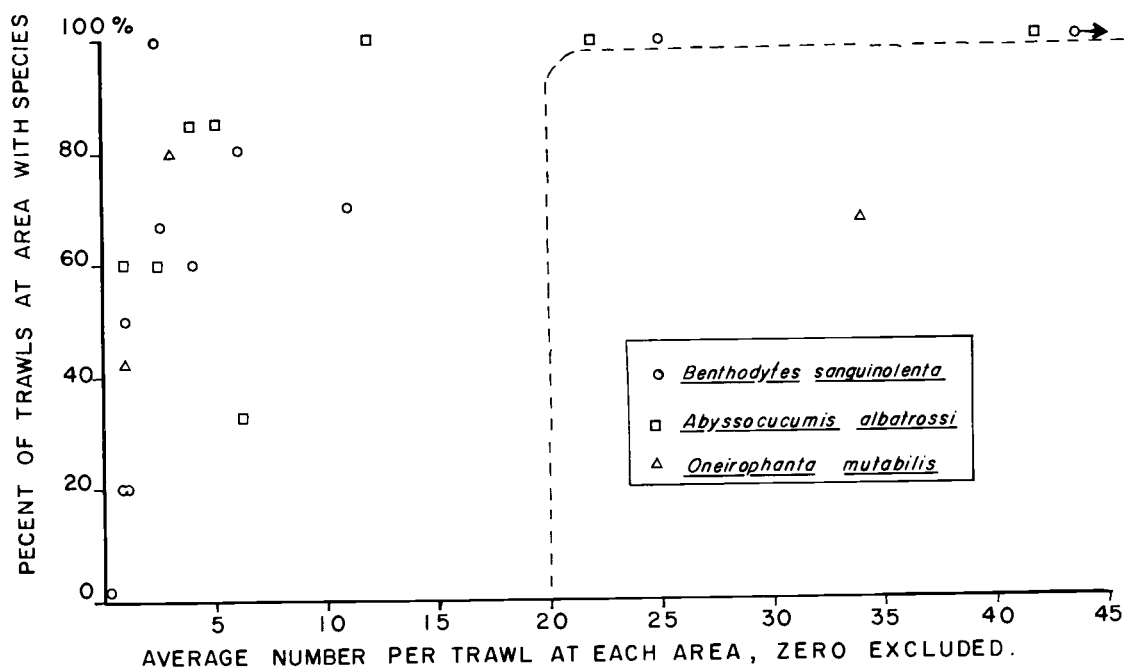


Figure 24c. Occurrence versus abundance for the major Tuft's Plain species.

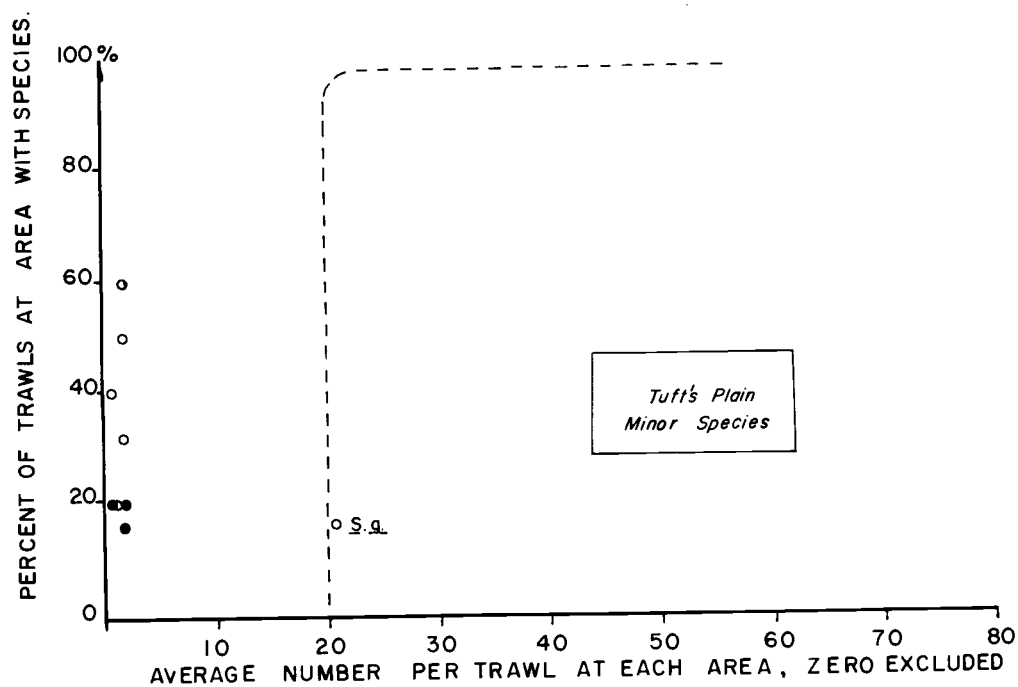


Figure 24d. Occurrence versus abundance for the minor Tuft's Plain species.

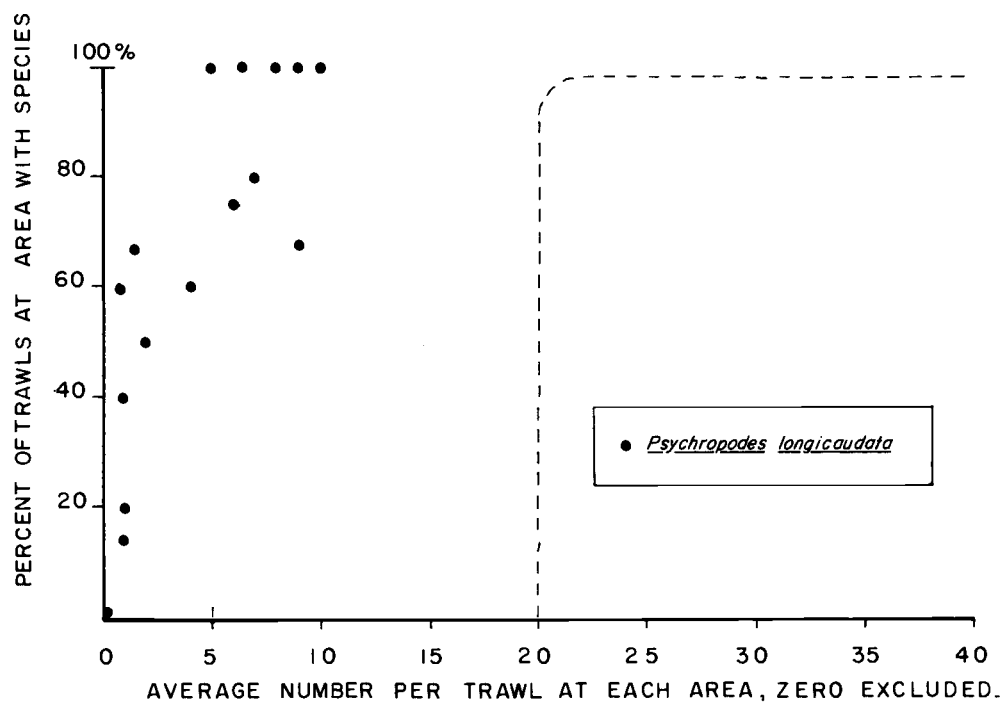


Figure 24e. Abundance versus occurrence for *Psychropodes longicaudata* showing that it is taken a high percent of the time although at relatively low numbers.

Body Sizes

Size Frequency Histograms

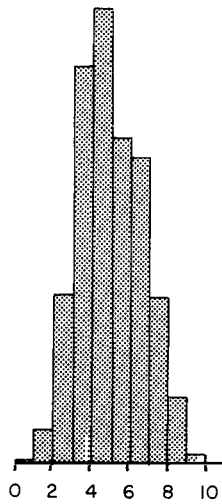
The size-frequency histograms for the seven most abundant species of holothurians on both Cascadia Basin and Tuft's Plain are presented in Figure 25. The area^s under the histograms have been normalized to facilitate comparisons. With the exception of the morphologically spectacular species Psychropodes longicaudata the histograms are similar. Each have^s a modal length located near the midrange of the observed body lengths. Although the histograms suggest that both large and small individuals are relatively rare, both the upper and lower tail of each histogram has^{ve} probably been distorted. As I have discussed, the lower tail may be greatly reduced by size selection of the net, and the largest specimens may represent deformed shorter individuals. Peniagone cf. dubia, Paelopatides confundens, and Benthodytes sanguinolenta are the most mucoid and subject to excessive elongation upon preservation. However, even in these species the largest measured specimens were never more than twice the length of the modal class.

Psychropodes longicaudata shows the least peaked histogram with a slight model^x at lengths between 4 to 8 centimeters long. The maximum length recorded is 3 to 4 times longer than the modal length. This is a firm, muscular species more subject to shrinkage upon preservation. Therefore the largest classes may be somewhat truncated. It is the only species in which there apparently is a greater number of relatively small specimens in the sampled population.

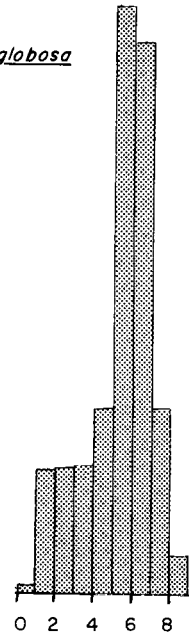
Species most abundant on Cascadia Basin.

Peniagone cf. dubia

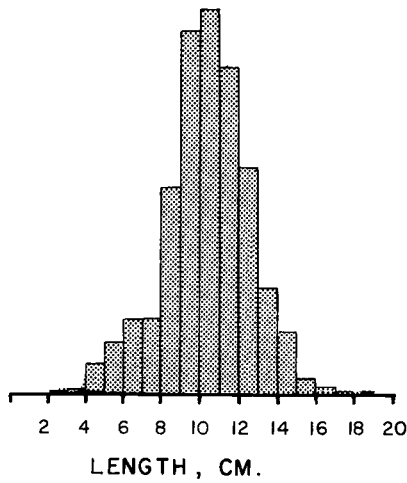
5071

*Scotoplanes globosa*

1173

*Paelopatides confundens*

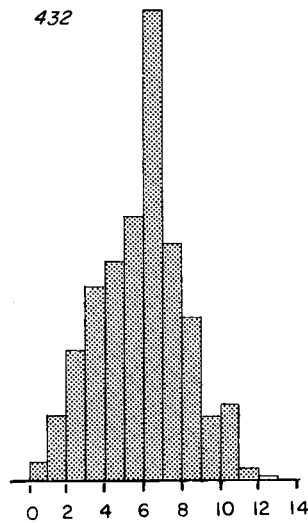
4069



Species most abundant on Tufts Plain.

Abyssocucumis albatrossi

432

*Oneirophanta mutabilis*

82

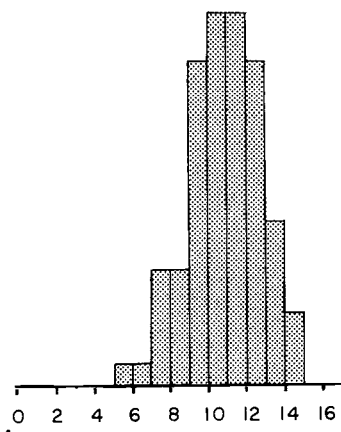
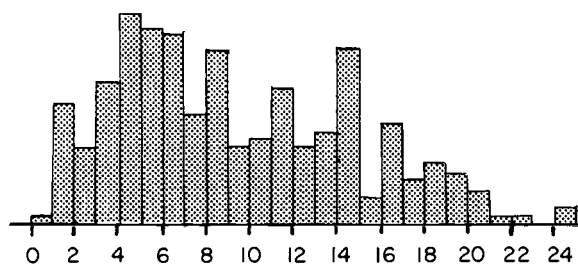


Figure 25. Size frequency histograms of body lengths for the seven most abundant holothurian species. The histograms have been normalized to an area of 1.0. The number of specimens is shown.

Species abundant on both Tufts Plain & Cascadia Basin.

Psychropodes longicaudata
241



Benthodytes sanguinolenta
252

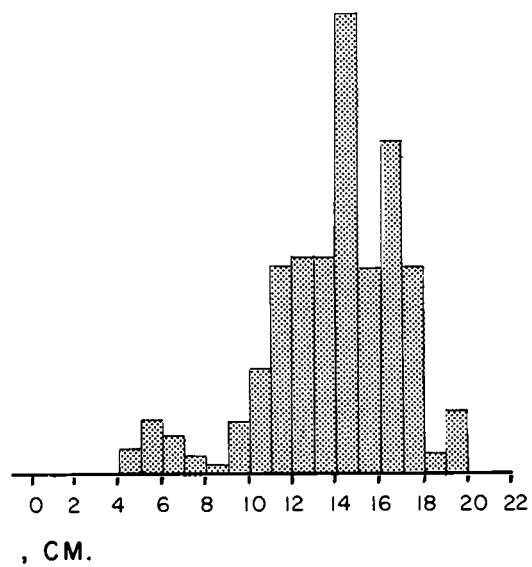


Figure 25. (continued)

Intraspecies Size Distributions

Designation of Small and Large

The subjective impression that several of the species would show polymodal size-frequency histograms proved to be invalid. Only in Benthodytes sanguinolenta is there suggestion of a second mode. Being unable to divide the histograms into small and large size categories on the basis of distinct small and large modes, I made a division on the basis of the following criteria: 1. The division must be at a size class shorter than the modal size ; 2. The division should coincide with a natural break if possible. The small vs. large divisions for A. albatrossi and Psychropodes longicaudata were the most arbitrary. The former shows no natural break, while the latter shows no distinct modal class. The other species were less subjectively divided. In subsequent analyses the small and large categories are:

<u>Peniagone</u> cf. <u>dubia</u>	small = 0-3 cm. long
<u>Paelopatides</u> <u>confundens</u>	small = 0-8 cm. long
<u>Scotoplanes</u> <u>globosa</u>	small = 0-4 cm. long
<u>Psychropodes</u> <u>longicaudata</u>	small = 0-9 cm. long
<u>Abyssocucumis</u> <u>albatrossi</u>	small = 0-4 cm. long
<u>Benthodytes</u> <u>sanguinolenta</u>	small = 0-11 cm. long

Due to the low number of specimens of Oneirophanta mutabilis taken in a single trawl, it was omitted from further analyses.

Dependence of Small:Large Upon the Region Sampled

Contingency tables and computed Chi squared values for the 6 major species are presented in Table 10. The null hypothesis for each test is the same: that the proportion of small specimens collected from each sampling region is the same. The number of regions was determined by the abundance of the species in each sampling series CP-1, CP-2, etc. Series were combined if they contained only a few specimens.

Abyssocucumis albatrossi was the only tested species for which the null hypothesis was accepted. It showed no significant difference in the proportion of small specimens in the collections from Tuft's Plain or Cascadia Basin. All the other species did show significant differences in the proportion of small specimens. Peniagone cf. dubia, Paelopatides confundens, Scotoplanes globosa, and Psychropodes longicaudata specimens collected along the base of the continental slope (CP-1 sample series) had fewer small specimens than expected. Excepting Psychropodes longicaudata the proportion of small specimen was equal or higher than expected away from the slope base. Psychropodes had fewer small specimens than expected on Tuft's Plain as well as at the slope base. However, the significantly large Chi squared value was due primarily to the absence of small specimens from the CP-1 series coupled with the few large specimens in the same region.

Table 10. 2xC Contingency Tables of Large and Small Specimens

Peniagone cf. dubia

	Tuft's Plain	3&4	Cascadia 2	Basin 1	Totals
Small obs. (0-3 cm.)	41	290	167	30	528
exp.	(25)	(190)	(167)	(147)	
Large obs. (3 cm.)	195	1500	1406	1357	4458
exp.	(211)	(1601)	(1406)	(1240)	
Totals:	236	1790	1573	1387	4986
$\chi^2 = 173.6$ $df. = 3$ $p. < .005$					

Paelopatides confundens

	Tuft's Plain	3&4	Cascadia 2	Basin 1	Totals
Small obs. (0-8 cm.)		163	185	158	506
exp.		(107)	(129)	(272)	
Large obs. (8 cm.)		684	853	2025	3562
exp.		(750)	(909)	(1912)	
Totals:		857	1038	2183	4068
$\chi^2 = 117.3$ $df. = 2$ $p. < .005$					

Scotoplanes globosa

Benthodytes sanguinolenta

		Tuft's Plain	Cascadia Basin Combined	Totals
Small	obs.	83	10	93
	exp.	(69)	(24)	
Large	obs.	105	54	159
	exp.	(119)	(40)	
Totals:		188	64	252
$\chi^2 = 16.3$ $df. = 1$ $p. < .005$				

Abyssocucumis albatrossi

		Tuft's Plain	3&4	Cascadia Basin 1	Totals
Small	obs.	59	7	3	69
(0-4 cm.)	exp.	(57)	(7)	(5)	
Large	obs.	280	35	28	343
(4 cm.)		(282)	(35)	(26)	
Totals:		339	42	31	412

χ^2 = 1.04 df. = 2 p. < .500

Summary of Results

The many results presented in this section and its appendices can be summarized as six major findings.

1. Cascadia Basin and Tuft's Abyssal Plain share a common set of holothurian species whose patterns of relative proportions distinguish one area from the other. On Cascadia Basin, Peniagone cf. dubia, Paelopatides confundens and Scotoplanes globosa are the dominant species. On Tuft's Plain Abyssocucumis albatrossi, Benthodytes sanguinolenta, and Oneirophanta mutabilis are the most abundant species.

2. As a taxon the holothurians are the second most abundant group collected from these areas; only the ophiuroids are more numerous. Across Cascadia Basin the holothurian portion of the total invertebrate catch is variable about a median of approximately 5%. Tuft's Plain is distinctly different in that the number of specimens and proportion of the total catch that are holothurians decreases markedly across the Plain. This decrease in numbers is accompanied by a decrease in the number of species collected which greatly affects the proportional composition of the holothurian fauna. The decrease in numbers appears to be exponential with linearly increasing depth and distance from land.

3. When statistical analyses most affected by dominant species are undertaken the greatest variability of faunal composition within any sample series was at CP-1, which is parallel to the continent, and

covers a depth range of 970 meters along the junction of the Astoria Fan and the Continental Slope. Along this depth range three distinctive faunal groups were found: one dominated by a slope species, Pannychia moeselyi; the next dominated solely by Paelopatides confundens; and the deepest dominated by a mixture of Paelopatides and Peniagone dubia, but largely depauperate in Scotoplanes globosa abundant at the very same depths but farther to sea. At CP-2 there was 1/5th the depth range found at CP-1, 1/4th the overall variability in faunal composition, and only slight faunal zonation by depth. The fauna along the whole series was dominated by the three typically abundant, Paelopatides confundens, Peniagone cf. dubia, and Scotoplanes globosa. This last species was distinctly more abundant at the shallower and more northerly samples along the series taken on the apron of Astoria Fan. At CP-3 there was the same overall variability in the faunal composition as at CP-2, but there was no distinct zonation of the dominant fauna along its slight vertical drop of about 110 meters.

4. Analyses of similarity that were most reflective of the dominant species were necessarily complimentary to the results of analysis of variance. CP-1 was found to be increasingly like the deeper fauna at CP-2 and CP-3 with increasing depth. At CP-1-E and CP-1-X the sampled faunas were most similar to the faunas at CP-2 and CP-3. The similarities between the Tuft's Plain and Cascadia Basin sample areas were reflective of the distance and depth between the areas being compared.

5. When all species were mapped and examined for pattern the zonations found coincided with the statistical analysis at CP-1, and CP-2, but were completely different for CP-3. Despite the absence of vertical zonation along the slight 110 meter relief of CP-3 shown for the abundant species, CP-3-E and to a lesser extent CP-3-D to the north were distinct from the other Cascadia Basin areas. At these two areas in the Basin the greatest number of species more common on Tuft's Plain were encountered. Additionally, it was found that the increasing similarity between CP-1 series samples and CP-2 and CP-3 series was largely restricted to the dominant fauna. Rarer species such as Psychropodes longicaudata, Caphiera sulcata, Synallactes gilberti, and Pseudostichopus nudus were rare or absent from the deeper CP-1 series but relatively common at the same depths seaward.
6. The three species which occur in the greatest proportion on Cascadia Basin, Peniagone cf. dubia, Paelopatides confundens, and Scotoplanes globosa have fewer than expected small specimens in the slope base region (CP-1 sample series). The proportion of small specimens of Psychropodes raripes and Benthodytes sanguinolenta is also dependent upon the region sampled, while the proportion of small specimens of Abyssocucumis albatrossi is apparently independent.

VIII. DISCUSSION

Depth Controlled Species Composition

The major factor determining the composition of the holothurian fauna on Cascadia and Tuft's Abyssal Plain appears to be the depth of water. Where depth is relatively constant along any sample series there is minimal change in composition and abundance of major species. Sanders and Hessler (1969) first concluded that depth was the major factor affecting the species composition of the infauna because the greatest between station dissimilarities occurred on the continental slope where the depth gradient is also the greatest. The results of this study show that the same generalization can be extended to the large epifaunal holothurians, although it is not apparent exactly how depth actually limits the distributions.

The large variation in proportional composition of the holothurian fauna at the slope base region (CP-1 series) is another example of sharp bathymetric zonation of fauna on a continental slope. It might be attributable to variation in the sediment, increasing segregation from the productive surface water, or physiological limitations of the component species. It seems unlikely that physiological tolerance of hydrostatic pressure or a hydrographic variable is the sole agent controlling composition. Peniagone cf. dubia, Scotoplanes globosa, Abyssocucumis, Ypsilothuria bitentaculata, and Caphiera sulcata have all been collected sporadically as much as 1000 m shallower than the depths at which they are more commonly encountered. More intensive sampling between 1000 m and 2000 m on the face of the slope might

result in additional unusually shallow capture records. In the Gulf of Mexico the holothurian fauna of the slope is distinctly zoned, but the depth of the zones is variable around the margin of the Gulf (Carney, 1971). Rowe (1968) similarly found that the mega-epifauna off North Carolina were distinctly zoned, but that these faunal zones did not follow isobaths. Instead they appeared to be influenced directly or indirectly by bottom currents.

The faunal variation found in the CP-2 series of samples can not be easily attributed to a single depth related factor. As I have reviewed earlier, the samples located on the slightly shallower Astoria Fan apron are also under the regions in which surface ecology is influenced by the summer extension of the Columbia River plume. The ecological coupling with the surface may be different in this area, the sedimentary regime is slightly different than the adjoining areas, and there may be increased seasonal fluctuations.

When the similarities between samples on Tuft's Plain and those on Cascadia Basin are considered together it appears that there is a complete change in the dominant holothurian fauna for every 1000 m or so increase in depth regardless of distance from land. On Tuft's Plain, there appears to be a decrease in the abundance of holothurian as well as a compositional change. This will be discussed in greater detail when I compare the holothurian fauna with the infauna.

The presence of Tuft's Plain species at CP-3-E&D suggests that there may be a distinct faunal composition associated with Cascadia Sea Channel. Rowe (1972) has suggested submarine canyons may also have a distinct fauna, although he has not presented convincing

evidence. It can not now be determined whether the channel represents a favorable environment for deeper water species, or simply an avenue of migration by larvae and adults. The channel and its associated levies certainly provide a different structural and sedimentary environment than the surrounding basin floor. Griggs et al. (1969) reported an apparent increase of infaunal density in the axis of the channel and suggested that it might be due to a high organic carbon content in the channel sediments. However, the channel is distinct from the surrounding area in so many ways that many combinations of factors might be suggested as causing the faunal distinctiveness.

While some environmental factors which vary with depth may be the cause of the marked faunal zonation at the slope base (CP-1 series), depth can not explain the more subtle difference between the fauna at the deep slope areas, CP-1-D&E and fauna at the same depth seaward. In these areas and the deeper CP-1-X there is a relatively low species richness due to the low densities or absences of species common at the CP-2 and CP-3 series of samples. Additionally, it is in these areas that the unexpectedly low numbers of Peniagone cf. dubia and Paelopatides confundens are found.

Distribution of Size Classes

When patterns of distribution are being related to physical factors all individuals of a certain species are usually considered to be a single variable. Treating all specimens of a species as an ecological entity is of great analytical expediency but it ignores the fact that the organism-environment interactions of a given species

may change radically over a lifetime. This is most obviously the case for benthic invertebrates whose metamorphic stages have radically different ecologies and morphologies. However, even animals like the holothurians, whose post-larval forms are morphologically fixed, must experience a changing set of organism-environment interactions during post-larval growth in size. Additional understanding of both deep-sea life and deep-sea habitats may possibly be derived through the study of the distribution of different life history stages of benthic organisms.

When the distributions of small specimens of the six major species are combined with the distribution of total specimens of those species three patterns are suggested.

1. There are those species in which unexpectedly low proportions of small specimens coincide with regions in which the species are a relatively low proportion of the holothurian fauna.
2. There are species in which unexpectedly low proportions of small specimens coincide with regions in which the species are a relatively high proportion of the holothurian fauna.
3. There are species in which the proportion of small specimens is in expected proportion regardless of the relative abundance of the species.

Scotoplanes globosa and Benthodytes sanguinolenta are clear examples of the first situation. S. globosa is proportionately less important at the CP-1 series than anywhere else on Cascadia Basin. B. sanguinolenta similarly is proportionately unimportant on Cascadia Basin and has the low proportion of small specimens in that area.

Poor reproductive success at the edge of a range is the most likely explanation for this pattern. Psychropodes longicaudata may also be an example, but it is less evident. P. longicaudata shows the same few specimens and low proportion coincidence at the slope base, but also has fewer than expected small specimens on Tuft's Plain where it is a more common species.

While the first situation is basically what one might expect, the second is more intriguing and difficult to explain. The significant rarity of presumid young specimens of Peniagone cf. dubia and Paelopatides confundens from the region adjacent to the base of the slope may be due to a great variety of causes. As I have detailed earlier, sediments in that area have a component of coarse, terrigenous sediment greater than that seaward. Such a sediment may be unsuitable for ingestion by the smallest holothurian specimens, although quite sufficient for larger specimens migrating into the region. The large specimens of Paelopatides confundens in the slope base region undergo a gonad cycle suggestive of active reproduction (Hufford, 1968). However, unknown conditions of larval drift and settlement may result in a low recruitment of larva into the benthic populations at the slope base.

Alternately it may be hypothesized that Peniagone cf. dubia and Paelopatides confundens are subject to size specific predation by opportunistic predators. As individuals grow they become subject to decreasing predation due to size alone, improved avoidance ability, or improved defensive mechanisms. The low numbers of small specimens adjacent to the base of the slope may then be due to an increased level of predation upon smaller forms in that area.

Although general works such as Hymann's (1955) state that virtually nothing except man feeds upon holothurians, specimens have been found in the stomachs of a variety of predators. I have personally found identifiable fragments or whole bodies in abyssal fishes, shallow reef fishes, abyssal nudibranchs, and the stomach of a walrus. Beam trawl sampling on Cascadia Basin has shown that a large nudibranch gastropod, Bathydoris sp. is most abundant in the slope base region. Similarly, the catches of abyssal fishes are greatest in the same region (unpublished data, W. Pearcy). From stomach content examination it has been shown that some deep water fishes do ingest holothurians (Pearcy and Ambler, 1975). During a cursory examination of Bathydoris I found it to contain an entire small specimen of Peniagone cf. dubia, and fragments of the apode holothurian Protankyra pacifica.

The hypothesis that there is size specific predation upon holothurians by predators more abundant at the base of the slope than seaward is supported by the above coincidences in distribution and feeding. A test of the hypothesis may be possible through stomach content and distribution studies which consider the size and identification of the specimens trawled and those ingested.

The only tested species to have the proportion of small specimens appear independent of sample region was Abyssocucumis albatrossi. This species is morphologically and systematically distinct from the other major deep-sea species. As the name implies it is a member of the normally suspension feeding Cucumariidae. Although its feeding type cannot be ascertained with certainty, it morphologically resembles shallow water suspension feeders. Unlike the other major species

which are distinctly bilaterally symmetrical, A. albatrossi is radially symmetric and has no apparent modifications for mobility over the sediment. If this apparent lack of mobility is real, then it may be the cause of the relatively constant proportion of small specimens. As the other species are adapted to moving over the sediments, there is the possibility of considerable post larval mobility. The adults may be capable of dispersing well beyond the range within which reproduction is successful. A. albatrossi may be motile only during the larval phase. If settlement occurs only in areas where reproduction is possible, young and older specimens should occupy the same regions.

Holothuroid Size and Diversity Hypotheses

The size-frequency histograms of deep-sea holothurians are of interest because the size structure of benthic populations have been used in an attempt by Grassle and Sanders (1973) to refute the Cropper hypothesis (Dayton and Hessler, 1972). By extension of the Lotka-Volterra population growth model life history strategies may be classified between two extremes, "r", and "K". Southwood et al. (1974) have developed a discrete model of interest to deep-sea biologist because it defines "r", and "K" as extremes in an adaptive spectrum corresponding to a spectrum of environmental persistence and predictability. In their model an r-selected animal is one that has historically lived below the carrying capacity, has a short generation time, a high reproductive rate, and is reproductively capable of tracking an unpredictable fluctuating environment. At the other extreme are the

K-selected animals living in an environment which is either highly persistent or fluctuates predictably. K animals tend to live at populations near carrying capacity and are modified to make most efficient use of resources for which they must compete. This can be construed to mean long generation time, low fecundity, and long life.

During a generally successful and thorough attack upon the Dayton-Hessler cropper hypothesis (Dayton and Hessler, 1972), Grassle and Sanders (1973) concluded, mainly from egg sizes, that most deep-sea animals are K-selected. On the basis of body size it was further concluded that they are not only K-selected, but do not undergo the extensive predation demanded by the cropper hypothesis. The categorization of the bulk of deep-sea fauna as either r or K suffers from many weaknesses. Firstly, the concepts depend upon knowledge of a complex of life history parameters which are simply unknown for deep-sea animals; in order to know the reproductive success of an animal far more is needed than ova count and maximum diameter. Secondly, deep-sea conditions may be so extreme as to render the models inapplicable. Thirdly, the concepts of r and K are so loaded with relative terms that they can easily be turned into logical circles with little effort. The best review of the factual knowledge of reproduction in the deep-sea is that given by Scheltema (1972). There appears to be a wide range of life history strategies in the deep-sea, rather than all only one kind.

Grassle and Sander's conclusion that a heavily preyed upon species population must show an abundance of small, young forms is offered without supporting reference. They must have assumed that predation

increases with prey size, so that very few individuals live to a large size. The Cropper hypothesis distinctly does not make reference to such a scheme. On the contrary, the predatory pressure envisioned by Dayton and Hessler is a function of the number of predators bigger than a given prey individual. As the animal grows the number of predators sufficiently large to eat it decreases, and so might the overall predatory pressure on that individual. This type of predation would result in a population that was top heavy with large, old individuals who had survived the life cycle stages of intense predation. Therefore, when Grassle and Sanders cited size frequency histograms for deep-sea benthos which showed few small specimens, they were not refuting the presence of intense predation required by the Cropper hypothesis.

The predator apparently intended by Grassle and Sanders must be an archtypical "prudent predator" sensu Slobodkin (1971). This animal is so finely tuned to the reproductive strategy of its prey that it feeds only on large, old senile individuals. In this manner it harvests its crop so as to maximize the productivity of the prey population. A predator which is so "biologically accommodated" to its prey would be expected only in the deep-sea community as envisioned by the Stability-Time hypothesis. By proving that this type of predation is unlikely in the deep-sea, Grassle and Sanders may have refuted the hypothesis that they were attempting to defend.

Of the seven species collected in large enough numbers to compile size-frequency histograms, only Psychropodes longicaudata had more small individuals than large. This species appears to be quite

uniformly distributed across almost the entire width of Cascadia Basin and Tuft's Plain. It is collected in relatively small numbers, and appears to be cosmopolitan. The ovary is small relative to the rest of the body, yet contains a few of the large ova ever measured in an echinoderm, 4 mm in diameter (Hansen, 1975). The morphology is elaborate, indicating considerable specialization of the tube feet. Although this species might be considered to be a "K" strategist, it is the only species with a size-frequency distribution that Grassle and Sanders would consider indicative of a "r" strategist living in a highly unpredictable environment.

In summary, the size distribution of each species, excepting Psychropodes, is similar to that found in many other abyssal benthic invertebrates. The larger size classes predominate. However, unless all the underlying assumptions about the selectivity of holothurian predators can be proved, then compiled size frequencies cannot be used to refute the Cropper hypothesis. Even if the size frequency of trawl collected animals does reflect the actual size frequency of the sampled population, the observed distributions may be obtained by a great variety of hypothetical predatory schemes and reproductive strategies.

Infauna-Holothuroid Comparisons

The infauna of Cascadia Basin and Tuft's Plain have not been as intensively sampled as the mega-epifauna, nor have all samples been processed to the level of species. It is, thus, not yet possible to make a full comparison between epifauna and infauna distribution

patterns. However, a series of anchor box dredge samples have been collected along a transect coinciding with the CP-E series (Carey and Hancock, 1965). Although it is premature to claim that this single narrow transect is typical for the entire Basin, comparisons with the holothurian fauna show very marked differences.

The infaunal polychaetes identified by Hancock (1969) were subjected to similarity analysis by Stander (1970). Among the indices used was SIMI, making possible a comparison of the polychaete and holothuroid results. The polychaete analysis came from five anchor box dredge stations: NAD 21 with 7 samples, NAD 22 with 4 samples, NAD 22A with 2 samples, and NAD 21 and NAD 24 with only a single sample each. This series corresponds to the CP-1-E and CP-2-E beam trawl stations. In Table 11 the SIMI values for both the holothurians and the polychaetes are shown. Only a single pair of the polychaete samples were even as similar as .50000, while none of the pairs of holothurian samples were any less similar than .9075. The polychaete fauna along the CP-E line is extremely variable while the larger epifaunal holothurian fauna is strikingly uniform.

The great variation of the infauna along the CP-E series appears to be found in other groups beside the polychaete worms. Dickinson (1976) examined the amphipod fauna collected by epibenthic sledge (Hessler and Sanders, 1967) at CP-1-E and CP-3-E. Again, while the holothurian faunas between these two areas are highly similar, there is great variation in the amphipod fauna. Barnard (1969) also identified gammarid amphipods of the CP-E line from the same samples along the CP-E line in which Hancock identified the polychaetes.

Table 11. Comparison of SIMI matrices of the holothurian fauna and the infaunal polychaetes along the CP-E beam trawl series and the Newport Line anchor dredge series seaward across Cascadia Basin.

	CP-1-E	CP-2-E	CP-3-E
CP-1-E	1.0000		
CP-2-E	.9097	1.0000	
CP-3-E	.9472	.9835	1.000

SIMI of holothurian fauna across the CP-E series of samples, extracted from Table

	NAD 21	NAD 22	NAD 22A	NAD 23	NAD 24
NAD 21	1.0000				
NAD 22	.4229	1.0000			
NAD 22A	.0904	.2319	1.0000		
NAD 23	.6893	.3230	.2040	1.0000	
NAD 24	.1815	.2399	.1373	.4064	1.000

SIMI of polychaete infauna along the Newport Anchor dredge line which coincides with the CP-E series of Trawls. From Stander (1970, Table 3).

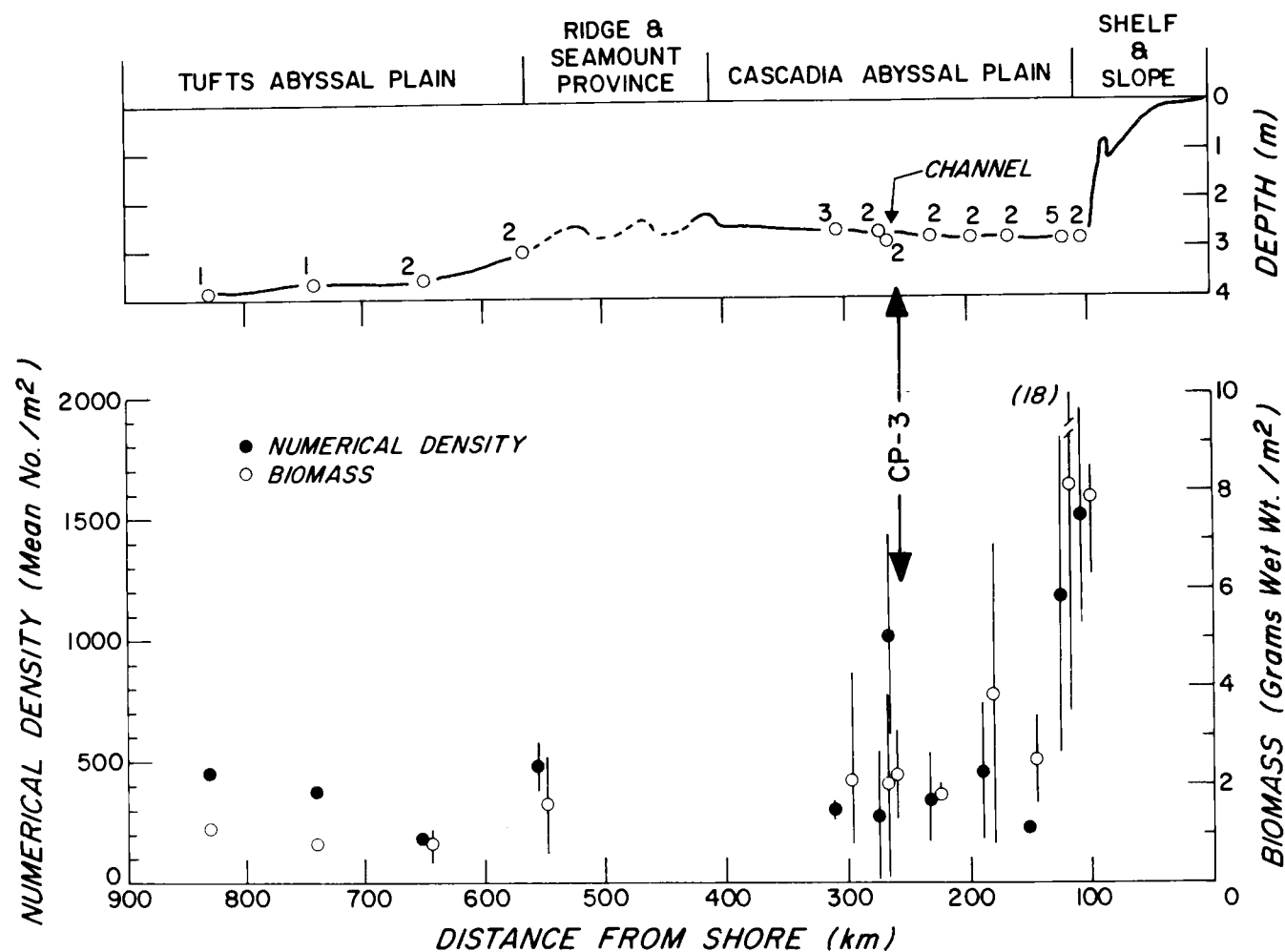


Figure 26. Wet weight and estimated density of infauna across the CP-E series and out onto Tuft's Plain. Each point is the mean, and the vertical line gives the range. The number of samples is shown in the upper figure. Taken from Carey (unpublished ms.).

Although no analysis of similarity was undertaken on the relatively few specimens, an examination of Barnard's findings shows considerable variation in the species composition along the series.

Just as the holothurian fauna shows an entirely different pattern of variation across the Basin when compared to the polychaetes and gammarid amphipods, they show different abundance patterns as well. Carey (unpublished manuscript) has studied the total infaunal densities along the CP-E and outward onto Tuft's Plain. As seen in his figure which is reproduced here (Figure 26) the infauna is most abundant at the slope base stations and decreases in an apparently exponential way across the Basin. The abundance may have reached a fairly uniform low as close to land as CP-3-E (300 km seaward) showing little change out onto Tuft's Plain. The complete opposite may be seen with the holothurians. They show a very variable abundance across the Basin and they undergo a distinct exponential decrease only out on Tuft's Plain.

The differences in sample sizes and techniques used to collect infauna and epifauna makes it difficult to categorically state that the two have distinctly different distribution patterns. Nevertheless there is increasing evidence that infauna and epifauna are distinctly different. In the same areas in which Sanders and Hessler (1969) have found narrowly zoned infauna Haedrick et al. (1975) and Grassle et al. (1975) have found the larger, motile epifauna to have wider zones. Grassle et al. (1975) have also noted that the diversity of the epifauna observed from submersibles does not reflect the high levels of diversity of the infauna collected by epibenthic sledge in the same areas.

Hessler and Jumars (1973) were among the first to directly discuss contradictions between the distributions of feeding types based on epifauna and those based on their own work on meiofaunal polychaetes. While Sokolova (1972) has indicated that the epifauna of the oligotrophic central gyres is predominantly composed of suspension feeders, Hessler and Jumars found that the polychaetes were predominately sediment feeders. Jumars (1975 a, b) has subsequently presented a conceptual framework by which infauna and epifaunal animals can be compared. It is based upon differences in their mobility. It is his opinion that the mobility of the species is of great importance in determining the ecology of that species. It may be assumed that holothurians may be considered highly mobile invertebrates when compared with most infauna. As Grassle et al. (1975) have pointed out, a sediment ingester must be motile because it soon exhausts the resources close at hand. The uniformity of the Cascadia holothurian fauna is thus reflective of organisms which maintain a well mixed fauna through continual movement along the bottom of the Basin while remaining within the physiological limits of each species.

The difference between holothurian and infaunal abundance across the Basin and Tuft's Plain are more difficult to explain. The very high densities of infauna at the base of the slope may simply reflect a much greater input of nutrient material to the bottom in that area (Carey, unpublished manuscript). This is conceivably due to the influence of coastal upwelling which seems to affect the midwater fauna to approximately the CP-1 area (Pearcy, 1976). It is difficult

to explain why the holothurians do not show a similar distinct increase in abundance at the slope base if there is an increased supply of food. It could, of course, be argued that the holothurians obtain their nutrition from some entirely different source than that of the infauna. Alternately, it may be suggested that the form as well as rate of nutrient input determines the fauna on the bottom.

Rowe et al. (1974) have summarized the findings in which an exponential decrease in the number of animals with depth has been noted, and concluded that decrease is due primarily to depth rather than distance from land. His conclusion is based upon a similar decrease in both the zooplankton in the water column and the fauna on the bottom and the assumption that terrestrial input to the bottom proceeds outward from the continent only along the bottom. If terrestrial materials did move seaward in only this way there should be little effect upon the zooplankton in the overlying water. Rowe et al. (1974) reason that since there is a concurrent decrease in zooplankton and bottom fauna with distance from land, it must be due to increasing depth and not the distance. While this logic is not at all compelling, there is so little evidence as to the actual effect of nearby land upon either the bottom or the water column, that I am not able to refute it.

The Suggested Importance of Food Grain Size

Just as the exact ties between terrestrial input to the benthos are not known, even the nature of input from the overlying waters is very poorly understood. Menzel (1967) has concluded on the basis of

the study of dissolved organic carbon that even in the areas of extremely high surface productivity there is very little input of organic carbon to the bottom. He concludes that by far the greatest carbon production and consumption in the ocean occurs above 300 meters. Some support of this can be found in the benthic literature. Frankenberg and Menzies (1968) were not able to find any appreciable increase in the biomass of the infauna below the area of the Peruvian upwelling. Rowe (1971) has partially refuted these findings by comparing the data from the Peru Upwelling area with that from the low productivity Gulf of Mexico. However, the Gulf of Mexico differs from the Pacific Ocean off Peru in so many ways that it hardly seems a valid comparison, and the fact remains that the benthos below upwelling areas has not been categorically demonstrated to be highly productive. In a popular article by Issacs and Schwartzlose (1975) there is a very interesting observation on the results of baited camera studies in the deep-sea. They conclude that beneath areas of very high surface productivity the baited cameras attracted far fewer motile scavengers than they did in areas of much lower productivity. It may be inferred that beneath an upwelling area with its intense surface biological activity that little of the nutrient input making it to the bottom is in the larger particulate form that the scavenger species are adapted to locate.

It can be tentatively suggested that nutrient material both from land and from the overlying water arrives at the bottom in a wide spectrum of sizes ranging from colloidal material to large carcasses. The actual forms reaching the bottom in any given part of the ocean

are determined by the nature of the biological activity in the overlying water. In highly productive upwelling areas consumption of phytoplankton, carcasses, and even fecal material within the water column may be so intense that only very fine particulate material makes it to the bottom. This fine material is probably of such low specific gravity that its distribution over the bottom is greatly affected by deep currents and topography. It would then not simply carpet the bottom, but would probably collect in topographic lows producing patches of high benthic productivity. Progressing away from an area of high productivity the intensity of consumption in the water column may decrease. Thus, a greater proportion of large particulate material such as fecal pellets and carcasses survive to the bottom although total input is less. Thus there may be a gradient in the type of food input with increasing distance from land as well as a decrease in the total amount of material reaching the bottom.

It has been suggested by Jumars (1974 a, b) that many meiofaunal animals gather their resources from an area little bigger than the animal itself. If this is so, then such an animal could exist only in an area where food input from the surface was such as to guarantee having food within reach. This would be the case if the food was raining down in a fine particulate form. If, however, it was in the form of larger particles then most might fall beyond the reach of the individual. A motile animal such as the holothurian could benefit from both types of input, although in areas of high infauna density it would be in competition with the more sedentary infauna. With respect to the results discussed herein, the absence of a distinctly high

holothurian density at the slope base may be due in part to competition with the very abundant infauna which is supported by the seasonal input from high upwelling productivity. Across the plain this fine particulate material decreases and is replaced by input of larger particles that the holothurians are more successful at exploiting. Across Tuft's Plain this larger particle input could progressively decrease as the productivity of the overlying water approaches the oligotrophic conditions of the central gyres. The density of holothurians may thus become progressively lower because they require a larger foraging area to support a single individual. Not only do the faunal densities change in response to the change in form and amount of input, but the species which are present also change. The holothurian fauna which is seen on Tuft's Plain is both less dense than that seen on Cascadia and basically different in composition.

The control of faunal composition by the interaction of resource size and species size is the basic tenant of the Cropper Hypothesis. Although Dayton and Hessler (1972) have primarily limited their discussion of resource to prey species, non-living food material is also a resource whose size spectrum will determine its availability to consumer species. The larger the consumer, the wider the range of sizes of non-living material that may be ingested by it without pre-processing by other consumers. The deep-sea holothurians, which are motile sediment ingesters, are adapted to consume a relatively wide range of non-living food material. The maintenance costs of large size combined with the low levels of food available in the sediments of one locality, however, necessitates that these animals be motile.

Although shallow water holothurians are distinctly sluggish animals, the distinctive morphologies of the deep-sea forms indeed seem to be adaptations to increase mobility (Pawson, in press). Moving over large areas of the bottom to obtain nutrition, holothurians cannot monopolize the food input. A dense, sedentary infaunal population may tend to use all the nutrient and thus partially exclude the slow, motile holothuroids. When the rate of food input is sufficiently high and of the proper grain to support a relatively sedentary infauna, then competition between the infauna and the motile sediment ingesters may be great. This competition may be the reason that species such as Scotoplanes globosa, Psychropodes longicaudata, Caphiera sulcata, Synallactes gilberti, and Pseudostichopus nudus are rare or absent from the base of the slope where infauna density is at its greatest.

IX. CONCLUSIONS

1. The major factor determining the composition of the Holothurian fauna on Cascadia Basin and Tuft's Abyssal Plain appears to be the depth of water. Where depth is relatively constant across the width of the Basin there is minimal change in either composition or abundance of the dominant holothurian species. This constancy of composition of the dominant fauna is found over an area within which there is a change in both sediment facies and terrestrial input to the bottom.
2. Depth is, however, not simply reflective of the extent of removal from the surface productivity. Depth variation due to the sedimentary structure of Astoria Submarine Fan reflects the influence of the Columbia River discharge upon the oceanic ecosystem. Thus the faunal variation which can be seen in comparison of the Fan holothurians to the rest of Cascadia Basin might be due to the slight depth decrease, the different sediment facies, high sedimentation rates, or the variation in food input from the altered ecosystem in the overlying water.
3. Sample areas at the base of the slope but at depths as great as those on the Basin floor contain many of the same species found farther to sea, but are distinctive in the proportions found. It is in these areas that great concentrations of infauna have been collected suggesting an increased input of food. The holothurian abundances do not reflect the same high input rates. Holothurians may not be feeding upon the same food source, or the increased competition with the dense infauna may limit both numbers and species present.

4. Of any Cascadia Basin samples, those from CP-3-E&D bear the greatest resemblance with the Tuft's Plain samples. The proximity of Cascadia Sea Channel with these Cascadia Basin sampling areas suggests that the Channel may be faunally unique.

5. The differences in the change in abundance of holothurians across the sampled areas and in the constancy of composition when compared with the few available data on infauna suggest wholly different ecological strategies for these two extreme components of the benthic ecosystem. It is suggested that species composition and abundance is determined to some extent by the rate of input and the size spectrum of non-living detrital material from the overlying water. While the rate of input may be directly determined by the productivity of the water column, the size spectrum must be determined by far more complex relationships such as the species composition and food web structure in the overlying water. As holothurians are large and motile their species composition is relatively unaffected directly by changes in size structure of the food input. However, through competition with smaller infauna which may be more efficient at feeding on certain size ranges of detritus, the holothurian species and abundance are indirectly determined by the size structure of the resource, as well as the input levels.

6. The areas where unexpectedly few small specimens of Peniagone cf. dubia and Paelopatides confundens are found coincide with the same slope base samples where these two species are numerous. These areas are also sedimentologically distinct, have very high infauna densities, and relatively high occurrences of predatory fishes and

gastropods. The hypothesis that this apparent rareness of small specimens is due to size specific predation as implied by the Cropper hypothesis should be testable.

BIBLIOGRAPHY

- Abele, L. G. 1976. Comparative species richness in fluctuating and constant environments; coral associated decapod crustaceans. *Science* 192:461-462.
- Alton, M. S. 1972. Bathymetric distribution of echinoderms off the northern Oregon coast. Pages 475-537 in A. T. Pruter and D. L. Alverson eds. *The Columbia River Estuary and adjacent ocean waters: bioenvironmental studies*. Univ. Washington Press, Seattle, Washington.
- Anderson, G. C. 1964. The seasonal and geographical distribution of primary productivity off the Washington and Oregon coasts. *Limnol. Oceanogr.* 9:284-302.
- Anon. 1877. Untitled correspondent's report. [news commentary on a meeting of the American National Academy of Science]. *Nature* 16:149.
- Atwater, T. 1970. Implications of plate tectonics for the Cenozoic tectonic evolution of western North America. *Geol. Soc. Amer. Bull.* 81:3513-3535.
- Barnard, J. L. 1971. Gammaridean amphipoda from a deep-sea transect off Oregon. *Smithsonian Contributions to Zool.* 61:1-86.
- Barnes, C. A., A. C. Duxbury, and B. A. Morse. 1972. Circulation and selected properties of the Columbia River effluent at sea. Page 41-80 in A. T. Pruter and D. L. Alverson eds. *The Columbia River Estuary and adjacent ocean waters: bioenvironmental studies*. Univ. Washington, Press, Seattle, Wash.
- Belyaev, G. M. 1970. Ultra-abyssal holothurians of the genus Myriotrochus in V. G. Bogorov ed. *Fauna of the Kurile-Kamchatka Trench and its environment*. [in Russian]. *Trudy Inst. Okeanol. P. P. Shiroshova.* 86:458-488.
- Belyaev, G. M. 1971. Deep water holothurians of the genus Elpidia. in V. G. Bogorov ed. *Fauna of the Kurile-Kamchatka trench and its environment*. [in Russian] *Trudy Inst. Okeanol. P. P. Shiroshova.* 92:326-367.
- Belyaev, G. M. 1972. Hadal bottom fauna of the world ocean (translated from 1966 Russian edition). *Israel Program for Scientific Translation Cat. No. 600107.* Jerusalem. 199 pp.
- Benson, R. H. 1975. The origin of the psychrosphere as recorded in changes of deep-sea ostracode assemblages. *Lethaia.* 8:69-83.

- Beverton, R. J. H. and S. J. Holt. 1957. On the dynamics of exploited fish population. Fishery Investigations, series 2, 19:1-533.
- Boucot, A. 1975. Evolution and extinction rate controls. Developments in paleontology and stratigraphy. I. Elsevier Scientific Publishing Co., Amsterdam. 427 pp.
- Carey, A. G., Jr. unpublished MS. A comparison of benthic infaunal abundance on two abyssal plains in the northeast Pacific Ocean with comments on deep-sea food sources. 30 MS pages.
- Carey, A. G. Jr., D. Hancock, and R. R. Paul. 1972. Initial benthic survey of deep water munitions dump site "G" in the northeast Pacific Ocean two years after dumping. A report to the oceanographer of the Navy. 168 pp.
- Carey, A. G. Jr., and H. Heyomoto. 1972. Techniques and equipment for sampling benthic organisms. Page 378-408 in A. T. Pruter and D. L. Alverson eds. The Columbia River estuary and adjacent ocean waters: bioenvironmental studies. Univ. Washington Press, Seattle, Wash.
- Carey, A. G. Jr. and D. H. Hancock. 1965. An anchor box dredge for deep-sea sampling. Deep-Sea Res. 12:983-984.
- Carlson, P. R. 1968. Marine geology of Astoria submarine canyon. Ph. D. Thesis, Oregon State University, Corvallis, Oregon. 259 numbered leaves.
- Carney, R. S. 1971. Some aspects of the ecology of Mesothuria lactea (Theel), a common bathyal holothurian in the Gulf of Mexico. Master's Thesis. Texas A&M University, College Station, Texas. 91 numbered leaves.
- Carney, R. S. and A. G. Carey, Jr. In prep. An evaluation of odometer wheels in the determination of distance sampled by beam trawls.
- Clark, H. L. 1920. Holothurioidea. Report of the scientific results of the expedition in the tropical Pacific and eastern Pacific. Albatross. Mem. Mus. Comp. Zool. 39:115-154.
- Clifford, H. T. and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, New York. 229 pp.
- Cooley, W. W. and Paul R. Lohnes. 1971. Multivariate data analysis, John Wiley and Sons, New York. 364 pp.
- Cuenot, L. 1948. Anatomie ethologie, et systematique des echinoderms, p. 1-275. in Grasse ed. Traite de Zoologie, v. 2. Masson et Cie Paris.

- Cushing, D. H. 1971. Upwelling and the production of fish. *Adv. Mar. Biol.* 9:255-326.
- Davis, F. M. 1958. An account of the fishing gear of England and Whales. *Fishery Investigations, Series 2*, 21:1-165.
- Dayton, P. K. and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep-sea. *Deep-Sea Res.* 19:199-208.
- Deichmann, E. 1930. The holothurians of the western part of the Atlantic Ocean. *Bull. Mus. Comp. Zool. Harvard* 71:43-226.
- Dickinson, J. J. 1976. Two zoogeographic studies of deep-sea benthic gammarid amphipods. Ph. D. Thesis. Oregon State University, Corvallis, Oregon. 117 numb. leaves.
- Duncan, J. R. 1968. Late pleistocene and postglacial sediments of deep sea environments off Oregon. Ph. D. Thesis, Oregon State University, Corvallis, Oregon. 222 numbered leaves.
- Duncan, J. R., and L. D. Kulm. 1970. Minerology, provenance, and dispersal history of late quaternary deep-sea sands in Cascadia Basin and Blanco fracture zone off Oregon. *J. Sedimentary Petrography* 40:874-887.
- Duncan, J. R., L. D. Kulm, and G. B. Griggs. Clay mineral composition of late pleistocene and holocene sediments of Cascadia Basin, northeastern Pacific Ocean. *J. Geol.* 78:213-221.
- Edwards, C. L. 1907. The holothurians of the North Pacific Coast of North America collected by the Albatross in 1903. *Proc. U. S. Nat. Mus.* 33:49-66.
- Ekman, S. 1953. Zoogeography of the sea. Sidwick and Jackson Ltd., London. 417 p.
- Emery, K. O. 1960. The sea off Southern California John Wiley and Sons, New York. 366 pp.
- Ewing, J., M. Ewing, T. Aitken, W. J. Ludwig. 1968. North Pacific sediment layers measured by seismic profiling, Pages 147-173 in L. Knopoff, L. Drake, and P. J. Hart eds. The crust and upper mantle of the Pacific area. *Amer. Geophys. Union Monogr.* 12.
- Fisher, W. K. 1907. The holothurians of the Hawaiian Islands. *Proc. U. S. Nat. Mus.* 32:637-744.
- Frankenberg, D. and R. J. Menzies. 1968. Some quantitative analyses of the deep-sea benthos off Peru. *Deep-Sea Res.* 15:623-626.

- Frizzel, D. L. and H. Exline. 1966. Holothuriodea, fossil record. Pages U646-U672 in R. C. Moore ed. Treatise on Invert. Paleontology Pt. U, Echinodermata III, v. 2. Geol. Soc. Amer., New York.
- Grassle, J. F. and H. L. Sanders. 1973. Life histories and the role of disturbance. Deep-sea Res. 20:243-259.
- Grassle, J. F., H. L. Sanders, R. R. Hessler, G. T. Rowe, and T. McLellan. 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible Alvin. Deep-Sea Res. 22:457-482.
- Gray, J. S. 1974. Animal sediment relationships. Oceanog. Mar. Biol. Ann. Rev. 12:223-261.
- Griggs, G. B. 1969. Cascadia Channel: the anatomy of a deep-sea channel. Ph. D. Thesis. Oregon State University, Corvallis, Oregon. 183 numbered leaves.
- Griggs, G. B., A. G. Carey, Jr., and L. D. Kulm. 1969. Deep-sea sedimentation and sediment-fauna interaction in Cascadia Channel and on Cascadia Abyssal Plain. Deep-Sea Research 16:157-170.
- Griggs, G. B. and L. D. Kulm. 1970. Sedimentation in Cascadia Deep-Sea Channel. Bull. Geol. Soc. Amer. 81:1361-1384.
- Gross, M. G. 1972. Sediment-associated radionuclides from the Columbia R. Page 736-754 in A. T. Pruter and D. L. Alverson, eds. The Columbia River Estuary and adjacent ocean waters: bioenvironmental studies. Univ. Washington Press, Seattle, Washington.
- Haedrich, R. L., G. T. Rowe, and P. T. Polloni. 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. J. Mar. Res. 33:191-212.
- Hancock, D. R. 1969. Bathyal and abyssal polychaetes (Annelids) from the central coast of Oregon. Master's Thesis, Oregon State University, Corvallis, Oregon 121 numbered leaves.
- Hansen, B. 1975. Systematics and biology of the deep-sea holothurians. Part I. Elasipoda. Galathea Rept. 13:1-262.
- Hansen, B. and F. J. Madsen. 1956. On two bathypelagic holothurians from the South China Sea. Galathea Rept. 2:55-59.
- Hansen, B. 1956. Holothuroids from depths exceeding 6000 meters. Galathea Report. 2:33-54.
- Hartmann, O. 1955. Quantitative survey of the benthos of San Pedro Basin off Southern California. I. Preliminary results. Allan Hancock Pacific Expds. 19:1-187.

- Hedgpeth, J. W. 1957. Concepts of marine ecology. Page 29-52 in J. W. Hedgpeth ed. Marine ecology and paleoecology. I, Ecology Geol. Soc. Amer. Mem. 67.
- Hessler, R. R. 1972. Deep water organisms for high pressure aquarium studies. Page 151-161 in R. Brauer ed. Barobiology and the experimental biology of the deep-sea. North Carolina Sea Grant Program, Chapel Hill, North Carolina.
- Hessler, R. R. and H. L. Sanders. 1967. Faunal diversity in the deep-sea. Deep-Sea Res. 14:65-78.
- Hessler, R. R. and P. Jumars. 1974. Abyssal community analysis from replicate box cores in the Center North Pacific. Deep-Sea Res. 21:185-209.
- Holme, N. A. 1971. Macrofauna sampling. Pages 80-130 in N. A. Holme and A. D. McIntye eds. Methods for the study of marine benthos. Internatl. Biome Prog. Handbook 16.
- Hufford, G. L. 1968. Some aspects of the ecology of the deep sea holothuroid *Paelopatides* sp. Master's thesis, Oregon State Univ. Corvallis, Oregon. 67 numbered leaves.
- Hutchinson, G. E. 1953. The concept of pattern in ecology. Proc. Acadm. Natur. Sci., Phil. 105:1-12.
- Huxley, T. H. 1873. Problems of the life in the deep-sea. Popular Science Monthly [London] 3:451-456.
- Hyman, L. H. 1955. The invertebrates, v. 4, Echinodermata. McGraw-Hill, New York, 763 pp.
- Imbrie, J. and Tj. H. van Andel. 1964. Vector analysis of heavy mineral data. Geol. Soc. Amer. Bull. 75:1131-1156.
- Isaacs, J. D. and A. Schwatzlose. 1975. Active animals of the deep-sea floor. Scient. Amer. 233:84-91.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. Amer. Naturl. 104:501-529.
- Jumars, P. A. 1975a. Methods for measurement of community structure in deep-sea macrobenthos. Mar. Bio. 30:245-252.
- Jumars, P. A. 1975b. Environmental grain and polychaete species diversity in a bathybal benthic community. Mar. Biol. 30:253-266.
- Jeffreys, J. G. 1881. Deep-sea exploration. Nature 21:300-302, 324-326.

- Kinne, O. [ed.]. 1970. Marine Ecology Vol. I Environmental Factors, parts 1-3. Wiley Interscience, New York. 1774 pp.
- Klovan, J. E. and J. Imbrie. 1971. An algorithm and FORTRAN IV program for large scale Q mode factor analysis and calculation of factor scores. *Mathematical Geol.* 3:61-77.
- Kulm, L. D. and G. A. Fowler. 1974. Cenozoic sedimentary framework of the Gorda-Juan de Fuca Plate and Gorda-Juan de Fuca Plate and adjacent continental margin - a review. Pages 212-229 in R. H. Dott, Jr. and R. H. Shaver eds. Modern and ancient geosynclinal sedimentation. Soc. Economic Paleontologists and Mineralogists spec. publ. 19.
- Kulm, L. D., R. C. Rousch, J. C. Harlett, R. H. Neudeck, D. M. Chambers, and E. J. Rungle. 1975. Oregon continental shelf sedimentation: interrelationships of facies distribution and sedimentary processes. *J. Geol.* 83:145-177.
- Kuipers, B. 1975. On the efficiency of a two meter beam trawl for juvenile plaice (Pleuronectes platessa). *Netherlands J. Sea Res.* 9:69-85.
- Levin, S. A. and R. T. Paine. 1975. The role of disturbance in models of community structure. Pages 56-67. in S. A. Levins, ed. Ecosystem analysis and prediction. SIAM, Institute for Mathematics and Society. Philadelphia, Penn.
- Livingstone, D. A. 1975. Late quaternary climatic change in Africa. *Ann. Rev. Ecol. and Systematics* 6:249-280.
- LeDanois, E. [ed.] 1948. Les profondeurs de la mer. Trente ans de recherches sur la fauna sousmarine au large des cote de France. Payot, Paris, 303 pp.
- Ludwig, H. 1894. The holothurioidea. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands...Albatross...1891. *Memoir Mus. Comp. Zool. Harvard* 17:1-183.
- McManus, D. A. 1964. Major bathymetric features near the coast of Oregon, Washington, and Vancouver Is. *Northwest Sci.* 38:65-82.
- McIntye, A. D. 1971. Efficiency of benthos sampling gear. Pages 140-146 in N. A. Holme and A. D. McIntye eds. Methods for studying the marine benthos. Internatl. Biome Prog. handbook 16.
- Menard, N. W. 1955. Deep-sea channels, topography and sedimentation. *Bull. Amer. Assoc. Petrol. Geologists* 39:236-255.

- Menard, N. W. and S. M. Smith. 1966. Hypsometry of ocean basin provinces. *J. Geophysical Res.* 71:4305-4325.
- Menzel, D. W. 1967. Particulate organic carbon in the deep-sea. *Deep-Sea Res.* 14:229-238.
- Menzies, R. J., R. Y. George, and G. T. Rowe. 1973. Abyssal environment and ecology of the world oceans. John Wiley and Sons, New York. 488 pp.
- Mitsukuri, K. 1912. Studies on actinopodus holothurioidea. *J. Coll. Imperial Sci. Univ. Tokyo.* 29:1-284.
- Mooers, C. N., C. A. Collins, R. L. Smith. 1976. The dynamic structure of the frontal zone in the coastal upwelling region off Oregon. *J. Physical Oceanog.* 6:3-21.
- Moseley, H. N. 1880. Dredging and life in the deep-sea. *Nature* 21:543-549, 569-573, 591-593.
- Murray, J. 1895. A summary of the scientific results obtained at the sounding, dredging, and trawling stations of H. M. S. Challenger. Challenger Rept., Summary of Research 2:797-1608.
- Nelson, C. H. 1968. Marine geology of Astoria deep-sea fan. Ph. D. Thesis. Oregon State University. Corvallis, Oregon 287 numbered leaves.
- Oshima, H. 1915. Report on the holothurians collected by the Albatross in the northwestern Pacific. *Proc. U. S. Natl. Mus.* 48:213-291.
- Pawson, D. L. 1969. Ecology of the holothurians. Pages 63-72 in R. A. Boolootian ed. *Physiology of Echinodermata*. Interscience, New York.
- Pawson, D. L. in press. Some aspects of the biology of deep-sea echinoderms. *Thalassia Jugosavica*. 22 MS pages.
- Pawson D. L. and H. B. Fell. 1965. A revised classification of the dendrochirote holothurians. *Brevoria* 214:1-7.
- Pearcy, W. G. 1976. Seasonal and inshore-offshore variations in the standing stocks of micronekton and macrozooplankton off Oregon. *U. S. Nat. Fisher. Serv. Bull.* 74:70-80.
- Pearcy, W. G. and J. Ambler. 1974. Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep-Sea Res.* 21:745-759.
- Rosenberg, D. H. 1962. Characteristics and distribution and water masses off the Oregon coast. Master's Thesis. Oregon State University, Corvallis, Oregon 45 numbered leaves.

- Rowe, G. T. 1968. Distribution patterns in populations of large, deep-sea benthic invertebrates off North Carolina. Ph. D. Thesis, Duke Univ., Durham, North Carolina. 296 numbered leaves.
- Rowe, G. T. 1971. Benthic biomass and surface productivity. in J. D. Costlow ed. Fertility of the sea. Gordon and Breach, New York. vol. 2, pages 441-454.
- Rowe, G. T. 1972. The exploration of submarine canyons and their benthic faunal assemblages. Proc., Roy Soc. Edinburgh, Series B, 73:159-169.
- Rowe, G. T., P. T. Polloni, and S. G. Horner. 1974. Benthic biomass estimates from the northwestern Atlantic Ocean and northeastern Gulf of Mexico. Deep-Sea Res. 21:641-650.
- Sanders, H. L. and R. R. Hessler. 1969. Ecology of the deep-sea benthos. Science 163:1419-1424.
- Sanders, H. L., R. R. Hessler, and G. R. Hampson. 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda Transect, Deep-Sea Res. 12:845-867.
- Scheltema, R. W. 1972. Reproduction and dispersal of bottom dwelling deep-sea invertebrates: a speculative summary. Pages 58-68 in R. Brauer ed. Barobiology and the experimental biology of the deep-sea. North Carolina Sea Grant Program, Chapel Hill, North Carolina.
- Slobodkin, L. B. 1971. Growth and regulation of animal populations. Holt, Rinehart, and Winston. New York. 184 pp.
- Slobodkin, L. and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. Diversity and stability in ecological systems. Brookhaven Symp. Biol. 22: 82-95.
- Small, L. F. and F. A. Cross. 1972. Effects of the Columbia River plume on two copepod species. Pages 344-350 in A. T. Pruter and D. L. Alverson eds. The Columbia River Estuary and adjacent ocean waters: bioenvironmental studies. Univ. Washington Press, Seattle, Wash.
- Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Co. San Francisco, 573 pp.
- Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods, 6th ed. Iowa State Univ. Press, Ames, Iowa. 593 pp.
- Sokolova, M. N. 1959. On the distribution of deep-water bottom animals in relation to their feeding habits and the character of sedimentation. Deep-Sea Res. 6:1-4.

- Sokolova, M. N. 1972. Trophic structure of the deep-sea macrobenthos. *Marine Biol.* 16:1-12.
- Southwood, T. R. E., R. M. May, M. P. Hassell, and G. R. Conway. 1974. Ecological strategies and population parameters. *Amer. Naturalist.* 108:791-804.
- Stander, J. M. 1970. Diversity and similarity of benthic fauna off Oregon. Master's thesis. Oregon State University, Corvallis, Oregon 72 numbered leaves.
- Stuxburg, Anton. 1883. Researches on the deep-sea fauna from a zoogeographical point of view. *Nature* 394-397.
- Theel, Hj. 1882. Report on the holothurioidea, I. Rept. Scient. Reslt. Voyage Challenger, Zool. 4(13):1-176.
- Theel, Hj. 1886. Report of the holothurioidea, II. Rept. Scient. Reslt. Voyage Challenger, Zool. 14(39):1-290.
- VanValen, L. 1974. Predation and species diversity. *J. Theor. Biol.* 44:19-21.
- Webb, D. J. 1974. The statistics of relative abundance and diversity. *J. Theoretical Biol.* 43:277-291.
- Vinogradova, N. G. 1959. The zoogeographical distribution of deep-water bottom fauna in the abyssal zone of the ocean. *Deep-Sea Res.* 5:205-208.
- Wilson, J. T. 1965. Transform faults, oceanic ridges, and magnetic anomalies southwest of Vancouver Island. *Science* 150:482-485.
- Zelinsky, D. 1968. A first course in linear algebra. Academic Press, New York. 266 pp.
- Zinkevitch, L. A. 1963. Biology of the seas of the USSR. Wiley-Interscience, New York. 955 pp.

APPENDICES

Appendix I. Station Data for Beam Trawls

Trawl	Date	Depth	N. Lat.		W. Long.		
BMT 113	Oct. 3 1969	2156 m	46	03.2	125	35.2	CP-1-A
BMT 115	Oct. 4 1969	2195 m	45	48.3	125	38.4	
BMT 194	Mar. 7 1970	2030 m	45	55.5	125	38.8	
BMT 195	Mar. 7 1970	2265 m	45	57.8	125	44.2	
BMT 89	Jul. 14 1969	2225 m	45	43.8	125	26.8	CP-1-B
BMT 90	Jul. 14 1969	2283 m	45	37.5	125	36.4	
BMT 192	Mar. 19 1970	2450 m	45	39.6	125	48.5	
BMT 193	Mar. 19 1970	2425 m	45	38.7	125	48.5	
BMT 93	Jul. 15 1969	2669 m	45	09.3	125	38.3	CP-1-C
BMT 116	Oct. 5 1969	2500 m	45	23.6	125	37.0	
BMT 117	Oct. 5 1969	2633 m	45	18.2	125	40.2	
BMT 190	Mar. 18 1970	2597 m	45	19.5	125	47.4	
BMT 191	Mar. 18 1970	2260 m	45	18.0	125	47.2	
BMT 94	Jul. 16 1969	2688 m	44	58.8	125	34.0	CP-1-D
BMT 95	Jul. 16 1969	2706 m	44	55.0	125	35.0	
BMT 118	Oct. 5 1969	2652 m	45	03.4	125	35.1	
BMT 187	Mar. 17 1970	2760 m	44	56.1	125	39.8	
BMT 188	Mar. 17 1970	2792 m	44	58.5	125	44.3	
BMT 97	Jul. 17 1969	2862 m	44	37.4	125	39.4	CP-1-E
BMT 119	Oct. 5 1969	2779 m	44	42.5	125	35.6	
BMT 120	Oct. 6 1969	2825 m	44	41.7	125	33.5	
BMT 185	Mar. 16 1970	2816 m	44	37.6	125	39.9	
BMT 186	Mar. 16 1970	2816 m	44	35.6	125	35.2	
BMT 288	Jun. 14 1972	2940 m	44	05.3	125	23.6	CP-1-X
BMT 289	Jun. 15 1972	2938 m	44	04.2	125	24.1	
BMT 290	Jun. 15 1972	2938 m	44	04.9	125	24.5	
BMT 291	Jun. 15 1972	2938 m	44	05.0	125	24.0	
BMT 292	Jun. 16 1972	2992 m	43	44.7	125	26.0	
BMT 293	Jun. 17 1972	2997 m	43	34.2	125	29.6	
BMT 294	Jun. 17 1972	3000 m	43	44.0	125	26.0	

Trawl	Date	Depth	N. Lat.		W. Long.		
BMT 154	Jan. 16 1970	2666 m	45	53.1	126	39.0	CP-2-A
BMT 148	Jan. 17 1970	2651 m	45	50.4	126	29.0	
BMT 258	Feb. 15 1971	2670 m	45	56.3	126	35.7	
BMT 259	Feb. 15 1971	2665 m	45	46.9	126	35.5	
BMT 260	Feb. 16 1971	2650 m	45	50.7	126	29.2	
BMT 156	Jan. 17 1970	2661 m	45	35.0	126	20.5	CP-2-B
BMT 261	Feb. 16 1971	2670 m	45	38.5	126	41.5	
BMT 262	Feb. 17 1971	2721 m	45	38.2	126	47.9	
BMT 263	Feb. 17 1971	2730 m	45	36.4	126	42.6	
BMT 157	Jan. 17 1970	2606 m	45	27.8	126	17.4	CP-2-C
BMT 159	Jan. 18 1970	2721 m	45	17.0	126	38.8	
BMT 160	Jan. 18 1970	2784 m	45	10.8	126	43.0	
BMT 264	Feb. 17 1971	2750 m	45	20.6	126	35.7	
BMT 265	Feb. 18 1971	2750 m	45	18.7	126	34.4	
BMT 266	Feb. 18 1971	2710 m	45	18.0	126	26.4	
BMT 161	Jan. 19 1970	2770 m	44	55.0	126	29.9	CP-2-D
BMT 162	Jan. 19 1970	2774 m	44	54.4	126	35.0	
BMT 267	Feb. 18 1971	2795 m	44	58.0	126	35.8	
BMT 268	Feb. 19 1971	2770 m	44	59.3	126	39.6	
BMT 269	Feb. 19 1971	2770 m	44	57.3	126	37.3	
BMT 163	Jan. 19 1970	2787 m	44	45.2	126	30.1	CP-2-E
BMT 270	Feb. 20 1971	2850 m	44	38.5	126	40.6	
BMT 271	Feb. 20 1971	2832 m	44	39.1	126	43.6	
BMT 272	Feb. 20 1971	2832 m	44	40.0	126	46.6	

Trawl	Date		Depth	N. Lat.		W. Long.		
BMT 276	May	17 1971	2761 m	45	56.3	127	36.6	CP-3-A
BMT 277	May	17 1971	2765 m	45	55.3	127	35.0	
BMT 321	Mar.	11 1973	2763 m	45	56.6	127	31.6	
BMT 322	Mar.	12 1973	2740 m	46	01.4	127	31.0	
BMT 323	Mar.	13 1973	2763 m	45	56.0	127	37.1	
BMT 278	May	18 1971	2811 m	45	23.4	127	36.9	CP-3-C
BMT 280	May	18 1971	2800 m	45	21.5	127	33.0	
BMT 318	Feb.	03 1972	2783 m	45	27.1	127	29.0	
BMT 319	Feb.	04 1972	2780 m	45	27.5	127	26.3	
BMT 324	Mar.	14 1973	2809 m	45	13.2	127	32.0	
BMT 332	Nov.	4 1973	2826 m	44	55.0	127	28.5	CP-3-D
BMT 333	Nov.	4 1973	2838 m	44	53.0	127	27.3	
BMT 334	Nov.	5 1973	2838 m	45	01.0	127	32.0	
BMT 335	Nov.	5 1973	2884 m	45	00.7	127	28.8	
BMT 336	Nov.	5 1973	2850 m	45	00.2	127	30.0	
BMT 281	May	19 1971	2816 m	44	38.8	127	36.8	CP-3-E
BMT 282	May	19 1971	2816 m	44	37.6	127	33.4	
BMT 315	Feb.	2 1972	2803 m	44	44.4	127	28.6	
BMT 316	Feb.	2 1972	2749 m	44	36.1	127	36.5	
BMT 317	Feb.	3 1972	2818 m	44	43.1	127	29.3	
BMT 359	Jun.	11 1974	3025 m	44	42.3	127	23.0	
BMT 360	Jun.	12 1974	3021 m	44	41.8	127	22.7	
BMT 328	Nov.	3 1973	2780 m	44	42.0	128	23.5	CP-4-E
BMT 330	Nov.	3 1973	2794 m	44	40.0	128	25.5	
BMT 331	Nov.	3 1973	2820 m	44	34.5	128	21.5	

Trawl		Date		Depth	N. Lat.		W. Long.		
BMT 228	May	30	1970	3354 m	44	46.3	131	25.6	TP-A
BMT 229	May	31	1970	3358 m	44	52.9	131	25.1	
BMT 230	Jun.	1	1970	3655 m	44	27.0	132	14.0	
BMT 298	Oct.	5	1972	3585 m	44	59.0	132	12.0	
BMT 300	Oct.	6	1972	3580 m	44	57.6	132	11.5	
BMT 299	Oct.	5	1972	3585 m	44	58.6	132	11.5	
BMT 232	Jun.	3	1970	3724 m	44	40.2	133	35.7	TP-B
BMT 233	Jun.	4	1970	3717 m	44	40.7	133	28.1	
BMT 302	Oct.	7	1972	3700 m	44	58.6	133	14.2	
BMT 303	Oct.	7	1972	3700 m	45	04.3	133	10.9	
BMT 304	Oct.	8	1972	3700 m	45	05.9	133	11.0	
BMT 305	Oct.	9	1972	3900 m	45	05.0	132	42.8	TP-C
BMT 306	Oct.	9	1972	3900 m	45	03.3	134	43.4	
BMT 307	Oct.	10	1972	3900 m	45	01.8	134	44.2	
BMT 308	Oct.	10	1972	3932 m	45	01.1	135	12.0	
BMT 309	Oct.	10	1972	3990 m	45	00.3	135	22.7	

Appendix II. Faunal Composition of Each Beam Trawl

Sample Area CP-1-A

Species	BMT 113	BMT 115	BMT 194	BMT 195	Pooled
<u>Paelopatites confundens</u>	.2316 *	.7066 *	.4545 *	1.0000 *	.5982
<u>Peniagone cf dubia</u>	0	.2096 *	0	0	.0524
<u>Scotoplanes globosa</u>	0	.0299 *	.2159 *	0	.0615
<u>Psychropodes longicaudata</u>	0	0	0	0	0
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	0	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	0	0	0	0
<u>Caphiera sulcata</u>	0	0	0	0	0
<u>Synallactes gilberti</u>	0	0	0	0	0
<u>Pannychia moesleyi</u>	.5789	.0359	.2159	0	.2077
<u>Molpadia musculus</u>	.1682	.0180	.0568	0	.0608
<u>Molpadia granulata</u>	0	0	0	0	0
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0
<u>Amperima naresi</u>	.0211	0	0	0	.0195
<u>Benthodytes incerta</u>	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0
Total Holothurians	95	167	88	161	511
Approximate Total Invertebrates	5054	4772	12738	13841	
Simpson's D Squared	.4176	.5457	.3063	1.0000	.4116
H _e Information	1.0365	.8697	1.3462	0	1.2067

*Specimens included in size study.

Sample Area CP-1-B

Species	BMT 89	BMT 90	BMT 192	BMT 193	Pooled
<u>Paelopatites confundens</u>	.2824 *	1.0000 *	.9961 *	.9590 *	.8094
<u>Peniagone cf dubia</u>	0	0	0	0	0
<u>Scotoplanes globosa</u>	.0992 *	0	0	0	.0248
<u>Psychropodes longicaudata</u>	0	0	.0039 *	.0082 *	.0041
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	0	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	0	0	0	0
<u>Caphiera sulcata</u>	0	0	0	.0164	.0030
<u>Synallactes gilberti</u>	0	0	0	0	0
<u>Pannychia moesleyi</u>	.6107	0	0	.0164	.1568
<u>Molpadia musculus</u>	.0072	0	0	0	.0019
<u>Molpadia granulata</u>	0	0	0	0	0
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0
Total Holothurians	262	29	258	122	671
Approximate Total Invertebrates	2480	1270	14012	9096	
Simpson's D Squared	.4642	1.0000	.9923	.9203	.6803
H _e Information	.9247	0	.0254	.2143	1.2067

Sample Area CP-1-C

Species	BMT 93	BMT 116	BMT 117	BMT 190	BMT 191	Pooled
<u>Paelopatites confundens</u>	.8824 *	.9887 *	.9825 *	.9787 *	.9250 *	.9514
<u>Peniagone cf dubia</u>	.0294 *	0	0	0	0	.0059
<u>Scotoplanes globosa</u>	.0706	0	0	0	0	.0141
<u>Psychropodes longicaudata</u>	.0118	0	.0175 *	0	.0250 *	.0109
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	0	0	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	0	0	0	0	0
<u>Caphiera sulcata</u>	0	0	0	0	0	0
<u>Synallactes gilberti</u>	0	0	0	0	0	0
<u>Pannychia moesleyi</u>	0	.0056	0	0	0	0
<u>Molpadia musculus</u>	.0059	.0056	0	0	0	.0011
<u>Molpadia granulata</u>	0	0	0	0	0	.0166
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	170	177	57	47	80	531
Approximate Total Invertebrates	16611	25211	21211	15675	5844	
Simpson's D Squared	.7846	.9776	.9655	.9584	.8588	.9059
H _e Information	.4838	.0697	.0883	.1030	.3141	.2624

Sample Area CP-1-D

Species	BMT 94	BMT 95	BMT 118	BMT 187	BMT 188	Pooled
<u>Paelopatites confundens</u>	.9470 *	.3285 *	.9576 *	.3595 *	.4318 *	.6049
<u>Peniagone cf dubia</u>	.0076	.6460 *	0	.5166 *	.5227 *	.3386
<u>Scotoplanes globosa</u>	.0455	.0219	.0085	.1239	.0455 *	.0490
<u>Psychropodes longicaudata</u>	0	.0036 *	.0085	0	0	.0024
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	0	0	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	0	0	0	0	0
<u>Caphiera sulcata</u>	0	0	0	0	0	0
<u>Synallactes gilberti</u>	0	0	0	0	0	0
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	0	.0254	0	0	.0024
<u>Molpadia granulata</u>	0	0	0	0	0	0
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	132	274	118	331	264	1119
Approximate Total Invertebrates	2963	1672	2466	4753	3550	
Simpson's D Squared	.8989	.5257	.9178	.4115	.4618	.4830
H _e Information	.2291	.7521	.2157	.9677	.8422	.8601

Sample Area CP-1-E

Species	BMT 97	BMT 119	BMT 120	BMT 185	BMT 186	Pooled
<u>Paelopatites confundens</u>	.6364 *	.3584 I	.3805	.3760 *	.5187 *	.4540
<u>Peniagone cf dubia</u>	.3535	.5819 *	.5786	.5388 *	.4305 *	.4967
<u>Scotoplanes globosa</u>	.0101	.0487 *	.0314	.0775 *	.0314 *	.0437
<u>Psychropodes longicaudata</u>	0	0	0	0	0	.0008
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	0	0	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	.0022	0	0	0	.0004
<u>Caphiera sulcata</u>	0	0	0	0	0	0
<u>Synallactes gilberti</u>	0	0	0	0	0	0
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	.0088	.0094	.0039	0	.0044
<u>Molpadia granulata</u>	0	0	0	0	0	0
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	99	452	318	258	374	1501
Approximate Total Invertebrates	1043	2304	2465	8134	9382	
Simpson's D Squared	.5300	.4695	.4807	.4377	.4570	.4547
H _e Information	.7017	.8853	.8370	.9423	.8547	.8759

Sample Area CP-1-X

Species	BMT 288	BMT 289	BMT 290	BMT 291	BMT 292	BMT 293
<u>Paelopatites confundens</u>	.6397	.5181 *	.7403 *	.5217	.1676 *	.5333
<u>Peniagone cf dubia</u>	.2154 *	.2536 *	.1169 *	.2783 *	.5081 *	.3533 *
<u>Scotoplanes globosa</u>	.0103 *	.1377	0	.1652	.0270	0
<u>Psychropodes longicaudata</u>	0	.0036 *	0	0	0	0
<u>Abyssocucumis albatrossi</u>	.0462 *	.0217 *	.0519 *	0	.0108 *	.0467 *
<u>Benthodytes sanguinolenta</u>	0	0	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	0	0	0	0	0
<u>Caphiera sulcata</u>	0	0	0	0	0	0
<u>Synallactes gilberti</u>	0	0	.0390	0	0	0
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	.0103	.0181	0	.0043	.0270	.0067
<u>Molpadia granulata</u>	0	0	0	0	0	0
<u>Ypsilothuria bitentaculata</u>	.0872	.0471	.0519	.0304	.2595	.0600
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	195	276	77	230	185	150
Approximate Total Invertebrates	5186	6939	1319	3362	3128	2386
Simpson's D Squared	.4542	.3548	.5686	.3779	.3551	.4151
H _e Information	1.0700	1.2818	.9072	1.1228	1.2375	1.0481

Sample Area CP-1-X Continued

Species	BMT 294	pooled
<u>Paelopatites confundens</u>	.1257 *	.4625
<u>Peniagone cf. dubia</u>	.6407 *	.3380
<u>Scotoplanes globosa</u>	.0539	.0563
<u>Psychropodes longicaudata</u>	0	.0005
<u>Abyssocucumis albatrossi</u>	.0180 *	.0279
<u>Benthodytes sanguinolenta</u>	0	0
<u>Oneirophanta mutabilis</u>	0	0
<u>Pseudostichopus nudus</u>	0	0
<u>Caphiera sulcata</u>	0	0
<u>Synallactes gilberti</u>	0	.0056
<u>Pannychia moesleyi</u>	0	0
<u>Molpadia musculus</u>	0	.0095
<u>Molpadia granulata</u>	0	0
<u>Ypsilothuria bitentaculata</u>	.1617	.0997
<u>Pseudostichopus villosus</u>	0	0
<u>Mesothuria murrayi</u>	0	0
<u>Amperima rosea</u>	0	0
<u>Amperima naresi</u>	0	0
<u>Benthodytes incerta</u>	0	0
<u>Peniagone gracilis</u>	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0
<u>Scotoplanes clarki</u>	0	0
Total Holothurians	167	1280
Approximate Total Invertebrates	2436	
Simpson's D Squared	.4557	.3422
H _e Information	1.0702	1.2919

Sample Area CP-2-A

Species	BMT 154	BMT 158	BMT 258	BMT 259	BMT 260	pooled
<u>Paelopatitides confundens</u>	.3917*	.3636 *	.2365 *	.3898 *	.5165 *	.3796
<u>Peniagone cf. dubia</u>	.2167*	.1278 *	.2095 *	.1789 *	.1429 *	.1751
<u>Scotoplanes globosa</u>	.3250*	.4886 *	.5000 *	.3195 *	.2527 *	.3772
<u>Psychropodes longicaudata</u>	.0417*	.0057 *	.0541 *	.0767	.0879 *	.0532
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	.0083*	0	0	0	0	.0017
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	0
<u>Pseudostichopus nudus</u>	.0167	.0028	0	.0096	0	.0058
<u>Caphiera sulcata</u>	0	0	0	.0224	0	.0045
<u>Synallactes gilberti</u>	0	0	0	0	0	0
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	0	0	.0032	0	.0006
<u>Molpadia granulata</u>	0	0	0	0	0	0
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima naresi</u>	0	.0114	0	0	0	.0023
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	120	352	148	313	91	1024
Approximate Total Invertebrates	2544	7639	577	4012	3270	
Simpson's D Squared	.3081	.3875	.3527	.2925	.3588	.3199
H _e Information	1.3043	1.0777	1.1727	1.3845	1.1806	1.2800

Sample Area CP-2-B

Species	BMT 156	BMT 261	BMT 262	BMT 263	pooled
<u>Paelopatitides confundens</u>	.2281 *	.2009 *	.0949 *	.1078	.1579
<u>Peniagone cf. dubia</u>	.4825 *	.3333 *	.4745 *	.3578 *	.4120
<u>Scotoplanes globosa</u>	.2544 *	.4155 *	.3869 *	.4902 *	.3867
<u>Psychropodes longicaudata</u>	.0117 *	.0502 *	.0292 *	.0343 *	.0314
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	0	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0
<u>Pseudostichopus nudus</u>	.0175	0	0	0	.0044
<u>Caphiera sulcata</u>	0	0	0	0	0
<u>Synallactes gilberti</u>	0	0	0	0	0
<u>Pannychia moesleyi</u>	0	0	0	0	0
<u>Molpadia musculus</u>	.0029	0	.0146	.0098	.0068
<u>Molpadia granulata</u>	0	0	0	0	0
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0
<u>Amperima naresi</u>	.0029	0	0	0	.0007
<u>Benthodytes incerta</u>	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0
Total Holothurians	342	219	137	204	902
Approximate Total Invertebrates	3922	2771	3516	1169	
Simpson's D Squared	.3500	.3267	.3848	.3812	.3543
H _e Information	1.1941	1.2038	1.1095	1.1185	1.1959

Sample Area CP-2-C

Species	BMT 157	BMT 159	BMT 160	BMT 264	BMT 265	BMT 266	pooled
<u>Paelopatites confundens</u>	.6180 *	.1391 *	.0345	.1415 *	.1523 *	.2511 *	.2227
<u>Peniagone cf. dubia</u>	.1011 *	.6464 *	.5862 *	.4031 *	.4365	.3723 *	.4243
<u>Scotoplanes globosa</u>	.2697 *	.1739 *	.3103 *	.3908 *	.3756	.3333 *	.3089
<u>Psychropodes longicaudata</u>	0	.0203 *	0	.0360 *	.0330	.0130 *	.0172
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	0	0	0	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	.0058	0	.0123	0	.0260	.0073
<u>Caphiera sulcata</u>	0	0	0	0	0	.0043	.0007
<u>Synallactes gilberti</u>	0	0	0	0	0	0	0
<u>Pannychia moesleyi</u>	0	0	0	0	0	0	0
<u>Molpadia musculus</u>	.0112	.0116	.0345	.0154	0	0	.0096
<u>Molpadia granulata</u>	0	.0029	0	0	.0025	0	.0009
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0	0
<u>Amperima naresi</u>	0	0	.0345	.0154	0	0	.0083
<u>Benthodytes incerta</u>	0	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0	0
Total Holothurians	157	345	29	325	394	231	1413
Approximate Total Invertebrates	2634	3033	1021	2461	2929	2297	
Simpson's D Squared	.4650	.4680	.4435	.3370	.3560	.3136	.3256
H _e Information	.9330	1.0382	1.0245	1.2503	1.1440	1.2558	1.2629

Sample Area CP-2-D

Species	BMT 161	BMT 162	BMT 267	BMT 268	BMT 269	pooled
<u>Paelopatites confundens</u>	.2368	.3429 *	.2737 *	.3388 *	.3125 *	.3010
<u>Peniagone cf. dubia</u>	.4474 *	.3429 *	.2810 *	.3719 *	.3702 *	.3627
<u>Scotoplanes globosa</u>	.3158 *	.2786 *	.4124 *	.2727 *	.2981 *	.3155
<u>Psychropodes longicaudata</u>	0	.0214 *	.0219 *	0	.0144 *	.0115
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	0	0	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	0	0	0	0	0
<u>Caphiera sulcata</u>	0	0	0	.0083	0	.0017
<u>Synallactes gilberti</u>	0	0	0	.0083	0	.0017
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	.0143	.0073	0	0	.0053
<u>Molpadia granulata</u>	0	0	.0036	0	0	.0007
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	38	140	274	121	208	781
Approximate Total Invertebrates	419	1595	4230	3449	7679	
Simpson's D Squares	.3560	.3134	.3245	.3276	.3238	.3218
H _e Information	1.0650	1.2331	1.2167	1.1682	1.1789	1.6453

Sample Area CP-2-E

Species	BMT 163	BMT 270	BMT 271	BMT 272	pooled
<u>Paelopatites confundens</u>	.3448 *	.2192 *	.2105 *	.3830 *	.2894
<u>Peniagone cf. dubia</u>	.4100 *	.4354 *	.4000 *	.4043 *	.4124
<u>Scotoplanes globosa</u>	.1992 *	.3003 *	.3421 *	.2057 *	.2618
<u>Psychropodes longicaudata</u>	.0192 *	.0180 *	.0421 *	0	.0198
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	.0038 *	0	0	.0070	.0027
<u>Oneirophanta mutabilis</u>	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	.0060	0	0	.0015
<u>Caphiera sulcata</u>	0	0	0	0	0
<u>Synallactes gilberti</u>	.0077	.0090	.0053	0	.0055
<u>Pannychia moesleyi</u>	0	0	0	0	0
<u>Molpadia musculus</u>	.0153	.0090	0	0	.0061
<u>Molpadia granulata</u>	0	.0030	0	0	.0003
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0
Total Holothurians	261	333	190	141	925
Approximate Total Invertebrates	4145	17446	7214	3437	
Simpson's D Squared	.3273	.3284	.3232	.3524	.3229
H _e Information	1.2526	1.2614	1.2225	1.0941	1.2436

Sample Area CP-3-A

Species	BMT 276	BMT 277	BMT 321	BMT 322	BMT 323	pooled
<u>Paelopatites confundens</u>	.5214 *	.4861 *	.2398 *	.3320 *	.2792 *	.3717
<u>Peniagone cf. dubia</u>	.3077 *	.3958	.5650 *	.5174 *	.4416 *	.4455
<u>Scotoplanes globosa</u>	.1538 *	.0972 *	.1301 *	.1197	.2487 *	.1499
<u>Psychropodes longicaudata</u>	.0171 *	.0139 *	.0528 *	.0270 *	.0102 *	.0242
<u>Abyssocucumis albatrossi</u>	0	0	0	0	0	0
<u>Benthodytes sanguinolenta</u>	0	.0069	0	0	0	0
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	.0014
<u>Pseudostichopus nudus</u>	0	0	.0041	.0	.0051	0
<u>Caphiera sulcata</u>	0	0	.0081	.0039	.0102	.0018
<u>Synallactes gilberti</u>	0	0	0	0	0	.0044
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	0	0	0	0	0
<u>Molpadia granulata</u>	0	0	0	0	.0051	0
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	.0010
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima naresii</u>	0	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	117	144	246	259	197	963
Approximate Total Invertebrates	4123	4758	7176	20776	10397	
Simpson's D Squared	.3905	.4027	.3966	.3930	.3351	.3597
H _e Information	1.0598	1.0380	1.1472	1.0802	1.2101	1.1543

Sample Area CP-3-C

Species	BMT 278	BMT 280	BMT 318	BMT 319	BMT 324	pooled
<u>Paelopatites confundens</u>	.3133	.2210 *	.2568 *	.1362 *	.5140 *	.2883
<u>Peniagone cf. dubia</u>	.3433 *	.5843 *	.4897 *	.6594 *	.2150 *	.4583
<u>Scotoplanes globosa</u>	.3348 *	.1798 *	.1815 *	.1662 *	.1589	.2042
<u>Psychropodes longicaudata</u>	0	.0112 *	.0445 *	.0272 *	.0841 *	.0334
<u>Abyssocucumis albatrossi</u>	0	.0037 *	.0034 *	0	.0047 *	.0024
<u>Benthodytes sanguinolenta</u>	0	0	0	.0027 *	0	.0005
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	0
<u>Pseudostichopus nudus</u>	.0086	0	.0103	.0027	0	.0043
<u>Caphiera sulcata</u>	0	0	.0034	0	.0187	.0044
<u>Synallactes gilberti</u>	0	0	.0068	.0027	.0047	.0028
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	0	0	0	0	0
<u>Molpadia granulata</u>	0	0	.0034	.0027	0	.0012
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima narsei</u>	0	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	233	267	292	367	214	1373
Approximate Total Invertebrates	1571	3467	10048	7472	3064	
Simpson's D Squared	.3282	.4227	.3409	.4818	.3431	.3361
H _e Information	1.1378	1.0275	1.2865	1.0070	1.2976	1.2450

Sample Area CP-3-D

Species	BMT 332	BMT 333	BMT 334	BMT 335	BMT 336	Pooled
<u>Paelopatites confundens</u>	.4031 *	.4520 *	.1366	.1724 *	.1480 *	.2624
<u>Peniagone cf. dubia</u>	.2449 *	.2260 *	.4208 *	.4080 *	.4381 *	.3476
<u>Scotoplanes globosa</u>	.2755 *	.2825 *	.3497 *	.2356 *	.3414	.2969
<u>Psychropodes longicaudata</u>	.0561	.0339 *	.0328 *	.0632 *	.0453 *	.0463
<u>Abyssocucumis albatrossi</u>	0	0	.0055 *	.0287 *	.0060 *	.0080
<u>Benthodytes sanguinolenta</u>	0	.0056 *	.0437	.0690 *	.0091 *	.0255
<u>Oneirophanta mutabilis</u>	0	0	0	0	0	0
<u>Pseudostichopus nudus</u>	0	0	0	.0115	.0060	.0035
<u>Caphiera sulcata</u>	.0153	0	.0055	.0115	.0060	.0077
<u>Synallactes gilberti</u>	0	0	0	0	0	0
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	0	0	0	0	0
<u>Molpadia granulata</u>	.0051	0	.0055	0	0	.0021
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	196	177	183	174	331	1061
Approximate Total Invertebrates	3990	1482	2518	1171	8402	
Simpson's D Squared	.3017	.3363	.3211	.2616	.3326	.2808
H _e Information	1.3185	1.1961	1.3379	1.5731	1.2867	1.5534

Sample Area CP-3-E

Species	BMT 281	BMT 282	BMT 315	BMT 316	BMT 317
<u>Paelopatites confundens</u>	.3846 *	.3412	.4511	.2204	.3092
<u>Peniagone cf dubia</u>	.4231 *	.4706 *	.3421 *	.5424 *	.4539 *
<u>Scotoplanes globosa</u>	.0385 *	.0588 *	.1541 *	.1582 *	.2171 *
<u>Psychropodes longicaudata</u>	.0192 *	.0235 *	.0263 *	.0226 *	.0066 *
<u>Abyssocucumis albatrossi</u>	.0865 *	.0588	.0038	.0056*	0
<u>Benthodytes sanguinolenta</u>	0	.0118	.0150 *	.0282 *	0
<u>Oneirophanta mutabilis</u>	.0096	.0118	0	.0056	0
<u>Pseudostichopus nudus</u>	0	.0118	0	.0056	0
<u>Caphiera sulcata</u>	0	0	.0038	0	0
<u>Synallactes gilberti</u>	0	0	.0038	.0056	0
<u>Pannychia moesleyi</u>	.0385	0	0	0	0
<u>Molpadia musculus</u>	0	0	0	0	0
<u>Molpadia granulata</u>	0	0	0	.0056	.0132
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	.0118	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0
Total Holothurians	104	85	266	177	152
Approximate Total Invertebrates	1662	1158	3051	8559	5519
Simpson's D Squared	.3378	.3459	.3453	.3692	.3490
H _e Information	1.3145	1.3522	1.2361	1.2894	1.1431

Sample Area CP-3-E (continued)

Species	BMT 359	BMT 360	Pooled
<u>Paelopatites confundens</u>	.1190 *	.0286 *	.2649
<u>Peniagone</u> cf. <u>dubia</u>	.1952	.3857	.4019
<u>Scotoplanes globosa</u>	.3667 *	.3143 *	.1868
<u>Psychropodes longicaudata</u>	.0381 *	.0571 *	.0276
<u>Abyssocucumis albatrossi</u>	.0095 *	.0571 *	.0316
<u>Benthodytes sanguinolenta</u>	.1857 *	.0643 *	.0436
<u>Oneirophanta mutabilis</u>	0	0	.0039
<u>Pseudostichopus nudus</u>	0	.0286	.0066
<u>Caphiera sulcata</u>	.0381	.0429	.0121
<u>Synallactes gilberti</u>	.0381	.0429	.0123
<u>Pannychia moesleyi</u>	0	0	0
<u>Molpadia musculus</u>	0	.0071	.0010
<u>Molpadia granulata</u>	0	.0071	.0037
<u>Ypsilothuria bitentaculata</u>	0	0	0
<u>Pseudostichopus villosus</u>	.0095	.0071	.0024
<u>Mesothuria murrayi</u>	0	0	.0017
<u>Amperima rosea</u>	0	0	0
<u>Amperima naresi</u>	0	0	0
<u>Benthodytes incerta</u>	0	0	0
<u>Peniagone gracilis</u>	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0
<u>Scotoplanes clarki</u>	0	0	0
Total Holothurians	210	140	1134
Approximate Total Invertebrates	2981	3194	
Simpson's D Squared	.2258	.2618	.2706
H _e Information	1.7149	1.6788	1.5914

Sample Area TP-A

Species	BMT 228	BMT 229	BMT 230	BMT 298	BMT 299	BMT 300	Pooled
<u>Paelopatites confundens</u>	.0359 *	0	0	.0043	.0161	.0032	.0099
<u>Peniagone cf. dubia</u>	.4215	.4603	.1250	.1379	.3023 *	.1548 *	.2670
<u>Scotoplanes globosa</u>	0	0	0	0	0	0	0
<u>Psychropodes longicaudata</u>	.0179	.0159 *	.0446 *	.0560	.0256 *	.0548 *	.0358
<u>Abyssocucumis albatrossi</u>	.1300	.1865 *	.3482 *	.2112 *	.1447 *	.1484 *	.1948
<u>Benthodytes sanguinolenta</u>	.2960	.3294 *	.3929 *	.4009 *	.4116 *	.4484 *	.3798
<u>Oneirophanta mutabilis</u>	0	0	.0714	.1724 *	.0868 *	.1903	.0868
<u>Pseudostichopus nudus</u>	0	0	0	0	0	0	0
<u>Caphiera sulcata</u>	0	.0079	0	0	0	0	.0013
<u>Synallactes gilberti</u>	.0942	0	0	0	0	0	.0157
<u>Pannychia moesleyi</u>	0	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	0	0	0	0	0	0
<u>Molpadia granulata</u>	0	0	0	.0086	0	0	.0014
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0	.0007
<u>Mesothuria murrayi</u>	0	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0	0	0
<u>Benthodytes incerta</u>	0	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	.0089	.0043	.0129	0	.0044
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	.0045	0	.0089	0	0	0	.0022
Total Holothurians	223	252	112	232	311	310	1440
Approximate Total Invertebrates	4656	3423	3933	7418	5562	9151	
Simpson's D Squared	.2927	.3555	.2985	.2573	.2903	.2863	.2627
H _e Information	1.4280	1.1403	1.4059	1.5441	1.4355	1.4251	1.7805

Sample Area TP-B

Species	BMT 232	BMT 233	BMT 302	BMT 303	BMT 304	Pooled
<u>Paelopatites confundens</u>	.0032	.0286	0	0	0	.0057
<u>Peniagone cf. dubia</u>	0	0	.6613 *	.4206 *	0	.2164
<u>Scotoplanes globosa</u>	0	0	0	0	0	0
<u>Psychropodes longicaudata</u>	.0571 *	0	.0645 *	.1121 *	.0986 *	.0665
<u>Abyssocucumis albatrossi</u>	.3714 *	.5556 *	.0484	.1308 *	.1268 *	.2466
<u>Benthodytes sanguinolenta</u>	.4571 *	.3333 *	.1613	.2804 *	.6761 *	.3816
<u>Oneirophanta mutabilis</u>	.0286 *	0	.0323 *	.0374 *	.0563 *	.0309
<u>Pseudostichopus nudus</u>	0	0	0	0	0	0
<u>Caphiera sulcata</u>	0	0	0	0	0	0
<u>Synallactes gilberti</u>	0	0	0	0	0	0
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	0	0	0	0	0
<u>Molpadia granulata</u>	.0286	0	.0323	0	.0141	.0150
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	.0141	.0028
<u>Mesothuria murrayi</u>	0	.0741	0	0	0	.0148
<u>Amperima rosea</u>	0	0	0	0	.0093	.0019
<u>Amperima naresi</u>	0	0	0	0	.0093	.0019
<u>Benthodytes incerta</u>	0	0	0	0	0	0
<u>Peniagone gracilis</u>	0	0	0	0	0	0
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	.0141	.0028
<u>Scotoplanes clarki</u>	.0286	.0370	0	0	0	.0131
Total Holothurians	35	27	124	107	71	364
Approximate Total Invertebrates	13322	11661	20857	27073	2597	
Simpson's D Squared	.3534	.4266	.4719	.28672	.4866	.2593
H _e Information	1.2956	1.0076	1.1127	1.4425	1.0971	1.6000

Sample Area TP-C

Species	BMT 305	BMT 306	BMT 307	BMT 308	BMT 309	Pooled
<u>Paelopatites confundens</u>	0	0	0	0	0	0
<u>Peniagone cf. dubia</u>	0	0	0	0	0	0
<u>Scotoplanes globosa</u>	0	0	0	0	0	0
<u>Psychropodes longicaudata</u>	.0238 *	.0625 *	0	.0172	0	.0207
<u>Abyssocucumis albatrossi</u>	.7857 *	.5625 *	.8889 *	.8621 *	.3333 *	.6865
<u>Benthodytes sanguinolenta</u>	.1429 *	.2500 *	0	.0172	0	.0820
<u>Oneirophanta mutabilis</u>	.0230 *	.0625 *	.1111 *	.1034 *	.6667 *	.1935
<u>Pseudostichopus nudus</u>	0	0	0	0	0	0
<u>Caphiera sulcata</u>	0	0	0	0	0	0
<u>Synallactes gilberti</u>	0	0	0	0	0	0
<u>Pannychia moesleyi</u>	0	0	0	0	0	0
<u>Molpadia musculus</u>	0	0	0	0	0	0
<u>Molpadia granulata</u>	0	0	0	0	0	0
<u>Ypsilothuria bitentaculata</u>	0	0	0	0	0	0
<u>Pseudostichopus villosus</u>	0	0	0	0	0	0
<u>Mesothuria murrayi</u>	0	0	0	0	0	0
<u>Amperima rosea</u>	0	0	0	0	0	0
<u>Amperima naresi</u>	0	0	0	0	0	0
<u>Benthodytes incerta</u>	.0238	0	0	0	0	.0048
<u>Peniagone gracilis</u>	0	.0625	0	0	0	.0125
<u>Laetmogone wyville-thompsoni</u>	0	0	0	0	0	0
<u>Scotoplanes clarki</u>	0	0	0	0	0	0
Total Holothurians	42	16	18	58	3	137
Approximate Total Invertebrates	8312	1293	16857	9413	4796	
Simpson's D Squared	.6395	.3906	.8025	.7545	.5556	.5161
H _e Information	1.7344	1.1901	.3488	.5027	.6365	.9417