

AN ABSTRACT OF THE THESIS OF

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in Oceanography presented on April 13, 1979

Title: DISPERSION OF THE SANDY-BEACH AMPHIPOD EOHASTORIUS BREVICUSPIS

BOSWORTH

Abstract approved:

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Redacted for privacy

The microdistribution of the amphipod Eohastorius brevicuspis was examined over a 19 month period. Field sampling was conducted principally at Lost Creek State Park, Oregon, and on one occasion at Driftwood State Park, Oregon. Both are high-energy, fine sand beaches which appear to be uniform. Stratified random samples were taken with each of a series of corers of varying diameters. For the samples obtained for each size of corer, indices of dispersion were calculated and evaluated to obtain information on the size of patches, the distribution of individuals within patches, and the distribution of the patches. E. brevicuspis From Lost Creek at natural densities were placed in a box of thoroughly sieved, well-mixed sand in the laboratory, together with natural densities of other macrofauna, or with other macrofauna excluded. The positions of individuals in the box were determined by partitioning the sand into 192 blocks (2 cm by 2 cm) horizontally, and into 3 layers (6.6 cm deep) vertically. In two of five experiments, the length and sex of every individual were also recorded. Additional experiments were conducted to examine the predation rate of the isopod Cirrolana harfordi on E. brevicuspis, to test for endogenous tidal periodicity in the depth in the sand at which E. brevicuspis is found, and to determine the direction of burrowing during downward migration.

Patches of higher density were variable in size, but occurred most frequently with diameters near 15 cm. In the field, larger-scale patches with diameters of two meters were also found. In laboratory experiments, the number of individuals per patch and the number of patches varied with the overall density. Patches were surrounded by low-density areas containing from 1/4 to 1/10 as many individuals per unit area. Individuals within patches tended to be spaced uniformly. It was not possible to determine the distribution of patches. Patches were formed in the laboratory in the absence of predators, other macrofauna, and observable environmental heterogeneity. They appear to be present at all times, although downward migration at low tide and upward migration at high tide was indicated. Over six hours, an artificially created patch of dyed amphipods migrated downward but did not spread horizontally, suggesting that individual patches could remain intact through one or more tidal cycles. There was no segregation of different sexes or sizes into different patches, although smaller individuals tended to be located nearer the surface of the sand. Patchiness in this species is probably not caused by responses to physical environmental heterogeneity, or to other macrofauna (including both predators and competitors), nor by behavior associated with reproduction. Some possible consequences of the observed distribution of this species were discussed.

DISPERSION
OF THE SANDY-BEACH AMPHIPOD
EOHAUSTORIUS BREVICUSPIS BOSWORTH

by

Paul F. Kemp

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed April 13, 1979

Commencement June 1979

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Date thesis is presented April 13, 1979

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ACKNOWLEDGMENTS

Theses, I am told, inevitably cause a certain amount of grief to their authors. I would like to express my appreciation of the support which my advisor, Dr. J. J. Gonor, gave me while I was getting my share. I would also like to thank Dr. Gonor and James Kopp for their assistance in field sampling, and several friends (notably Ruth Phinney) for helping me bounce ideas back and forth. Most of all, I would like to thank Linda Neubauer for patiently doing all of the above, and caring too.

CONTENTS

	<u>Page</u>
I. INTRODUCTION	
A. Ecological significance of patchiness	1
B. Statement of the goal of the thesis	16
II. METHODS USED IN THIS STUDY	
A. Methods for the analysis of patchiness	18
1. Morisita's index	18
2. Iwao's index	23
3. Regression of mean crowding: mean	26
4. Hierarchal ANOVA of contiguous quadrats	27
5. Random-pair analysis of contiguous quadrats	30
6. Methods for definition of patches	33
a. Iyer method	33
b. Decision-rule method	34
c. Usher's method	35
7. Principal components analysis	36
8. Intra-patch dispersion chi-square	38
B. Description of the study area	40
C. Field sampling methods	44
1. Preliminary sampling	44
2. Sampling program	46
D. Laboratory studies	48
1. Patch size, distribution, and composition	48
2. Tidal rhythmicity	53
3. Predation by <u>Cirolana</u> on <u>Eohaustorius</u>	54
III. OBSERVATIONS AND RESULTS	55
A. Field sampling	55
1. Preliminary sampling	55
2. Sampling program	56
a. Scale of patchiness	57
b. Distribution of patches	57
c. Distribution within patches	57
d. Minimum size of patches	58
3. Generality of field results	59
B. Laboratory studies	59
1. Patch size	59
2. Distribution of patches	65
3. Distribution within patches	65
4. Patch composition	66
a. Correlations analysis	66
b. Principal components analysis	68
5. Patch size and density	69
6. Stability and persistence during downward migration	71
7. Tidal migration	72
8. Predation by <u>Cirolana</u> on <u>Eohaustorius</u>	73
9. Sizes of individuals in LP5 and LP6	74
IV. SUMMARY	76

	<u>Page</u>
V. DISCUSSION	79
A. Methods used	79
B. Patchiness	83
VI. BIBLIOGRAPHY	88
Appendix: Figures	94
Appendix: Tables	140

APPENDIX : FIGURES

<u>Figure</u>		<u>Page</u>
1	Distribution maps of contiguous-core arrays in the NE sample, 11/20-21/76	95
2	Graph of composite Morisita's index versus block size for the NE sample	97
3	Plot of per-core density versus core position for LN1 sample, Lost Creek beach, 11/20/76	99
4	Plot of per-core density versus core position for LN2 sample, Lost Creek beach, 12/4/76	101
5	Graphs of Morisita and Iwao indices for PS1, Lost Creek beach, 1/29/77	103
6	Graphs of Morisita and Iwao indices for PS2, Lost Creek beach 6/5-6/77	105
7	Graph of Morisita and Iwao indices for PS3, Lost Creek beach, 12/22/77	107
8	Graph of Morisita and Iwao indices for PS4, Driftwood State Park, 7/11/78	109
9	Graph of mean square to mean density ratio versus block size for LP3 trial, 8/15-18/77	111
10	Graph of mean square to mean density ratio versus block size for LP4, 8/21-24/77	113
11	Graph of mean square to mean density ratio versus block size for LP5, 8/31-9/3/77	115
12	Graph of mean square to mean density ratio versus block size for LP6, 10/16-19/77	117
13	Graph of pooled variance between paired units versus distance between units for LP3	119
14	Graph of pooled variance between paired units versus distance between units for LP4	121
15	Graph of pooled variance between paired units versus distance between units for LP5	123
16	Graph of pooled variance between paired units versus distance between units for LP6	125

<u>Figure</u>		<u>Page</u>
17	Graph of pooled variance between paired units versus distance between units for LP7	127
18	Distribution map of LP3 by layers	129
19	Distribution map of LP4 by layers	131
20	Distribution map of LP5 by layers	133
21	Distribution map of LP6 by layers	135
22	Distribution map of LP7	137
23	Distribution map of LP7 on second recovery showing positions of dyed amphipods as superscripts. Units under original location outlined.	139

APPENDIX : TABLES

<u>Table</u>		<u>Page</u>
1	Mean square variances for LN2 data	140
2	Calculated indices for the PS1 study	141
3	Calculated indices for the PS2 study	142
4a.	Calculated indices for the PS3 study	143
4b.	Calculated indices for the PS4 study	144
5	Values of mean square/mean for the LP series	145
6a.	Values of pooled variance for LP series	146
6b.	Values of pooled variance for LP areal distribution maps	147
7	Values of pooled variance for LP series excluding highest-variance pairs	148
8	Bartlett's test statistic M for homogeneity of pooled variances	149
9	Values of intra-patch dispersion chi-square for LP series distribution maps	150
10	Summary of LP6 patch composition variables	151
11	Matrix of correlations for LP6	152
12	Correlations between principal components and patch composition variables	153
13	Patch dimensions versus layer density for LP series distribution maps	154
14	Patch dimensions versus total density for LP series distribution maps	155
15	Number of expected and observed joins between dense units for LP series distribution maps	156

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INTRODUCTION

A. Ecological significance of aggregated distributions

In early studies on marine communities, the species composition rather than the functional organization of the community was emphasized. Petersen (1914) set a precedent for considering that the more numerous a species, the more likely that it was important in the interactions within the community. In subsequent quantitative studies, attempts were made to gain increasingly detailed and reliable information on the relative abundance of species in marine communities. In the earliest studies it was assumed that species were distributed randomly within the sampling area and methods suitable for random distributions were used. In many cases, the spatial distribution of individuals was such that the variance of counts between sample units was greater than the mean count, where, if the Poisson distribution was used as the mathematical model for randomness, the variance would be expected to be equal to the mean. A number of statistical and sampling methods were devised to minimize the effects of non-random species distributions. Among these were increase in the sample size, to approach a normal distribution (by the Central Limit Theorem); the use of transformations to convert non-random data into approximately normally distributed equivalents; the use of frequency distributions other than the normal or Poisson models to describe data; and the use of distribution-free statistics. In studies using these methods the presence of non-randomness was recognized but this was regarded as a problem to be overcome rather than as an object of study.

The significance of aggregated distributions of organisms has been of considerable interest to theoretical ecologists because of the important effects of patchy distributions on many major ecological processes. In early models of the interactions of individuals and species it was assumed that all individuals were distributed randomly. This assumption and the implications of patchiness for predation, competition, and coexistence, development of feeding strategies, and speciation were tested in later models, as the following examples will demonstrate.

Hastings (1977) and Murdoch (1977) have recently examined the behavior of model predator-prey systems when the environment was assumed to be patchy. Hastings used a model proposed by Caswell (1977) in which empty patches are colonized by prey first, then by predators. The patch is assumed to crash when the predator eats all of the prey in the patch, and is then empty and ready for new colonists. Caswell (1977) justified these simple dynamics on the basis that most other factors (e.g. dispersal, growth within patches) of the dynamics within patches occur on a much faster time scale than the elimination time, and may therefore be considered instantaneous. Hastings' one-predator, one-prey version of Caswell's model predicts that slow-moving predators go extinct, especially if the prey species is also slow-moving. Equilibrium was reached when both the predator and the prey were highly mobile.

Murdoch's (1977) model uses a single predator species which has the option of two patch types occupied by two prey species. The model predicts that a predator will always utilize the more abundant prey, regardless of the time spent in transit between the patches.

Models describing the behavior of two competing species in a patchy environment have been proposed by Cohen (1970), Levins and Culver (1971), and Horn and MacArthur (1972). Cohen demonstrated that stochastic fluctuations in the interactions between two competing species in a patch-work environment could lead in some cases to stable coexistence. Levins and Culver (1971) developed a differential equation model for the proportion of patches occupied by each of two competing species, given the migration rate between patches and the rate of extinction within patches for each species. As a consequence, they were led to the interesting conclusions that rare species can exclude one another, and that coexistence of rare species can occur under some conditions. Horn and MacArthur (1972) developed equilibrial theories for the occupation of patches by species which are characteristically fugitive or opportunistic. In each of the above modeling studies, it was suggested that a mosaic of environmental types would have a profound effect on the community which would develop in that location.

Foraging strategies in patchy environments have been examined by several theoretical ecologists (Tullock, 1970; Emlen, 1973; Krebs et al., 1974; Charnov, 1976; see summary in Pyke et al., 1977). Many of these are based on the assumption that an animal forages in a given patch until it has gained as much food as it can expect from that patch (Gibb, 1958). Others have examined the possibility that an animal increases the rate of turns or decreases the radius of turns when it encounters higher food densities (Cody, 1971, 1974), in the expectation that in a clumped distribution of food, the presence of one food item increases the probability of more in the same area. Either of these classes of

foraging models are deterministic representations of the expected behavior of the forager.

Oaten (1977), in contrast, proposes that foragers which maintain their feeding effort despite stochastic variation in the rate of capture when feeding in prey patches are more successful than those who do not. In the previous models it was assumed that predators can either directly evaluate the prey density, or that they leave a patch when the capture rate drops to a low level. A random fluctuation in prey capture rate or nearby density would cause this sort of predator to leave the patch. Oaten shows that a predator which averages the last few observations on prey density or capture rate is less likely to abandon a patch of prey which could still be effectively exploited.

Speciation models which include patchiness have been the rule, because in most models of speciation it is required that the environment be sufficiently heterogeneous to provide both differential selection pressures, and to block migration from one gene pool to another. The theory of island biogeography for example, essentially deals with patches of occupied space on a background of empty space (MacArthur and Wilson, 1967; Levin and Paine, 1974).

The effects of patchiness on the estimation of population parameters has also been a stimulus for other types of ecological studies on patchiness. Much of the early literature on patchiness of marine organisms is centered on the distributions of oceanic plankton. The difficulty of separating the effects of sampling error from the effects of patchy plankton distributions stimulated a number of empirical and model studies of patchiness (Hardy, 1936; Cushing and Tungate, 1963; Cassie, 1959a, 1959b; Wiebe, 1970; Levin and Segel, 1976; Riley, 1976; Wroblewski and

O'Brien, 1976; Kamykowski, 1974; Steele, 1973). Planktonic patchiness has been attributed to such causes as minor physical perturbations accentuated by herbivore grazing (Levin and Segel, 1976); diel migration of herbivores interacting with tidal currents (Riley, 1976); and internal waves acting as forcing functions (Kamykowski, 1974). The persistence of a patch, once formed, has been discussed by Wroblewski and O'Brien (1976) and Kierstead and Slobodkin (1953).

The effects of patchiness in estimation of diversity of marine benthic communities was considered by Fager (1972). He evaluated the rarefaction method for estimation of benthic diversity proposed by Sanders (1968), and found that the estimate of diversity by this method was biased when aggregation properties differed between species within the community.

Jumars (1975) discussed the consequences of environmental and biological heterogeneity with regard to diversity. Jumars proposed a model in which organisms with a small "ambit" (sensu Lloyd, 1967) are more likely to have a higher diversity in a given location than organisms with a large ambit. If the ambit is the distance within which an individual extends its influence and is in turn influenced by anything within that radius, then species with small ambits are more likely to encounter a smaller subset of the overall environmental and biological conditions than large-ambit species. Species with small ambits are more likely to be coarse-grained (sensu MacArthur and Wilson, 1967) relative to species with large ambits. If the grain structure of the environment is stable, then species may specialize on the subset of the total environment which they experience (Colwell, 1973), with the consequence that coarse-grained species are potentially more diverse than fine-grained species, having more potential habitats. Jumars proposes that conditions of stable

environmental grain structure are more likely to occur for small-ambit species than for large-ambit species, and therefore communities of species with small ambits are more diverse than those of species with large ambits.

Jumars' model was in part supported by the study of Thistle (1978) who found that the distance over which patchiness benthic harpacticoid copepods occurred was identical to that of environmental heterogeneity. This suggested that the dispersion of the copepods reflected a response to environmental grain on the scale of their ambit.

Increasing interest in patchiness in marine communities as a problem to be examined in itself is reflected in recent papers on models of patch formation, and in studies of the dispersion of species in marine communities. Levin and Paine (1974) proposed a model of the formation and maintenance of a patchy distribution in the rocky intertidal, based on the work of Dayton (1972). Dayton found that battering by logs and wave shock formed holes in what was potentially a solid sheet of mussels in the higher rocky intertidal. Levin and Paine's model allows a patch to grow, shrink, persist for varying lengths of time, and vary in invasibility once created. A patch could also be a bounded maximum of population density rather than a hole in a continuous distribution, provided that the background is relatively homogeneous. For a given set of parameters of patch formation and change, the model may be used to predict the steady-state equilibrium in which a stable distribution of patches of different ages and sizes are present. Levin and Paine proposed that, under conditions where disturbance is the major factor producing patchiness, their model could be used to predict the distributional structure of a community. Levin and Paine also made some predictions concerning the attributes a species would have to have to persist in a

given set of conditions. Whittaker and Levin (1977) discussed disturbance and microhabitat differences as two potential sources of patchiness, and using the assumptions of Levin and Paine's model provided more detailed predictions of the expected nature of patch formation.

Roughgarden (1977) developed a model of patchiness which he felt was simpler in its assumptions than previous models. The environment is considered a mosaic of areas between which individuals may freely migrate. The resource level in each area fluctuates independently of other areas. Roughgarden determined that the distribution of individuals in the overall region would be patchy even though the fluctuations in resource levels were random. This was especially true for species with rapid population growth rates and moderate dispersal rates. Slow-growing populations generally did not differ greatly from random distributions in this model.

The dispersion of species in marine benthic environments has been examined in a number of papers. Most of these have concentrated on determining the degree to which the distribution of individuals of one or more species deviated from a random expectation, as measured by an index of dispersion. (Knight-Jones and Stevenson, 1950; Clark and Milne, 1955; Menzies and Widrig, 1955; Jackson, 1968; Gage and Geekie, 1973; Kenchington and Hammond, 1978; numerous others). In many cases, the sampling design of these studies was intended to best examine the density of species, and therefore was inappropriate for estimation of dispersion. Most of the published estimates of patchiness of marine species should be regarded as minimum estimates.

Detailed studies of aggregation in benthic marine species have been published by Holme (1950), Paine (1963), Angel and Angel (1967), Gärdefors and Orrhage (1968), Levinton (1972), Heip (1975, 1976), Jumars (1975),

Hogue (1977), Jumars et al. (1977), Kenchington and Hammond (1978), and Thistle (1978).

Heip (1975, 1976) was able to map aggregates of the ostracod Cyprideis torosa using a systematic grid of 1.4 cm diameter cores spaced 10 cm apart. Objective rules used to map patch boundaries permitted the calculation of the average radius of patches. Rules for defining patch boundaries were described by Krishna Iyer (1949) and have been used by Jumars (1975) to describe deep-sea benthic dispersion. Cores in the grid with densities greater than the mean value are considered part of the background density. An alternative critical density is the median density of all cores in the grid. In either case, these methods may underestimate the size of patches when the patch has a dense center but less dense margins, and the mean density is greater than the density in the marginal parts of patches. This will be more obvious when patches are clearly identifiable against a background of empty space or very low density.

Heip (1975) separately analysed the pattern of distribution of males, females, juveniles, adults, and females with eggs. Using the hypergeometric distribution (Pielou, 1977) as a model for the probability that each of these groups was distributed independently of all the others, Heip found that the probability of independent occurrence was low (maximum of 14%), and on this basis suggested that all members of the species aggregate in the same manner. Heip suggested that it also indicated that environmental heterogeneity was unimportant. However, if such heterogeneity affected all classes in the population equally, the observed concordance of distributions would be expected.

Heip found that correlations between the numbers of females with and without eggs, and between eggless females and males, were lower in a species which reproduces annually than in a species which reproduces every few weeks. Heip suggested that it would be advantageous to breeding success for males to be near females more in the species with a short generation time. He did not explain why these correlations were lower than the correlations between other groups within the same species. Heip also did not explain why juveniles in an annually reproducing species would aggregate long before they were reproductively active. Heip's conclusion that reproduction is the primary cause of patchiness in benthic marine species in uniform environments is poorly supported by his data.

Jumars (1975) used a grid of contiguous cores to examine the distribution patterns of deep-sea benthos. The variance to mean ratio of Fisher (1970), commonly termed the index of dispersion, was used to estimate the degree to which each species deviated from a random dispersion, and a summary statistic was calculated for which each species provided one degree of freedom. This "dispersion chi-square" statistic is approximately equal to its degrees of freedom when the distribution of all species is random, and can be used to test the dispersion pattern of the community as a whole.

Jumars et al (1977) used the autocorrelation method of Cliff and Ord (1973) to analyze the dispersion of species in several sets of data on marine benthic communities. Two of the sets were contiguous-quadrat grids, and one was a set of randomly placed sample units. The spatial locations of samples and the density of species within them were used to evaluate the degree of contagion of species, on the assumption that the interactions between individuals is inversely proportional to the square of

the distance. Aggregation was detected at various scales for different species. A polychaete, Armandia sp., showed greatest aggregation at the more distant unit spacings, while the amphipod Dogielinotus loquax was aggregated on some scale which was smaller than the distance between the closest-spaced sample units.

Thistle (1978) examined the distributions of benthic harpacticoid copepods using samples separated by distances of a few centimeters, several meters, and one hundred meters. He found that harpacticoids were distributed patchily at all scales, and especially at the smaller distance scales.

Kenchington and Hammond (1978) and Paine (1963) have used detailed distribution maps of brachiopod density to provide information on dispersion. Both studies showed that the species considered were distributed patchily, but that within areas of higher density, individuals were distributed at random.

"Gardefors and Orrhage (1968) used a method developed by Hughes (1962) to determine the radius of aggregation and the number of aggregates per unit area of four benthic species. The method uses pairs of cores separated by a constant distance, and compares the densities per core to that expected for a pattern of circular aggregates randomly located in the area. The result is a set of radii of aggregates and associated numbers of aggregates, which are interpreted as "if the radius is x, then there are y aggregates per unit area." Species are then compared at all possible radii for differences in their aggregation patterns, without determining what the actual radius of aggregates is. Since the patchiness detected by sampling units depends to some extent on the sampling unit size (see Analytical Methods), the results of this method are dependent on the sampling unit size.

Angel and Angel (1967) used a method described by Kershaw (1957), modified from the method of contiguous-quadrat analysis of variance developed by Grieg-Smith (1957). A line of contiguous cores was used to construct a hierarchal analysis of variance, where blocks of adjacent cores were combined into successively larger composite cores. The block size which is approximately the same size as the patchiness pattern will usually have the greatest variance between blocks. Angel and Angel were able to determine the scale of patchiness for several species in the marine benthic community studied, although the size of the basic core used was too large to allow evaluation of the minimum patch size.

Nearest-neighbor measurements were used by Holme (1950) to determine the distribution of Tellina tenuis in the laboratory. The distribution was found to tend toward uniformity.

Hogue (1977) used a simple method in which cores were taken at increasing distance from one another to determine the approximate scale of patchiness of marine gastrotrichs. Hogue found that the variance between cores increased sharply between distances of 4 cm and 10 cm, and concluded that patchiness occurred over distances between 4 and 10 cm. Non-concordance of the distributions of two species of gastrotrichs indicated that the species were independently distributed, and probably responded to different causal factors in patch formation.

In a few studies the possible causes of patchiness in a given species or community have been determined. Hairston (1959) proposed that rare species will be aggregated simply because their preferred habitat is rare. Jackson (1968) noted that juveniles may be aggregated because of localized release from parental protection or limited dispersal capability. Berthet and Gerard (1965) suggested that species living in marginal habitats would

be greatly affected by resource fluctuations, and would therefore be responsive to habitat variability. Species might therefore be more patchily distributed at the margins of their distributions, if those margins are determined by physical factors. Menzies and Widrig (1955) felt that the aggregation of burrows of Limnoria served the dual purpose of bringing potential mates together, and increasing the circulation of water within burrows, enabling individuals to burrow deeper into the wood. Heip (1975) concluded that reproduction and the increase in mating success was the primary cause of aggregation in two meiobenthic ostracods. Underwood (1976) was able to correlate the dispersion pattern of prosobranch gastropods with the substratum type, linking the patchy distribution to environmental heterogeneity. Allee (1927) examined the physiological effects of aggregation on Ophioderma brevispina. He found that aggregated individuals were more active than solitary individuals, but that the aggregates were able to survive longer than isolated individuals under conditions of oxygen stress. Similar prolongation of survival was found when glass rods were substituted for other individuals. Allee concluded that aggregation occurred because individuals substituted the aggregate for an unidentified feature of the physical environment of eelgrass. He also speculated that autoprotective secretions may benefit groups more than solitary individuals.

Very few general principles of aggregation have been proposed for marine benthic communities or species. In most cases, these have been based on scattered observations on the properties of aggregation in different taxonomic groups or trophic types, rather than on detailed understanding of the function of aggregation in species.

Connell (1955) proposed that the presence and abundance of infaunal suspension feeders are controlled primarily by environmental factors, because their food source is unpredictable and is not controllable by altering position. Patchiness in these species would be caused by environmental heterogeneity. In contrast, deposit feeders can benefit from territoriality if they are sedentary, so the dispersion pattern of sedentary deposit feeders is more likely to be biologically controlled. Gage and Geekie (1973a) tabulated the proportion of aggregating marine benthic species belonging to different trophic or functional feeding groups. More suspension feeders showed significant aggregation than did deposit feeders (42% versus 34%) supporting Connell's prediction. Motility of species did not affect the number of aggregating species (44.4% motile, 44.9% non-motile). When polychaetes were considered separately, the errant species were less often aggregated than the sedentary species (27% to 61.5%). In contrast, Clark and Milne (1955) indicated that errant polychaetes were more often aggregated than were sedentary polychaetes (62.5% of errant species, 39.1% of sedentary species).

Based on systematic samples taken within Lochs Etive and Creran, Scotland, Gage and Geekie (1973a) proposed that species in a muddy-sand habitat were more aggregated than species in a mud habitat. However, later work (Gage and Geekie, 1973b) within Loch Etive did not show significant differences in species aggregation between sandy and muddy habitats.

Heip (1975) proposed that aggregation in benthic invertebrates represents a compromise between two conflicting interests: the need to find food, and the need to contact other individuals for present or future reproduction. This implies that in energy-rich environments, reproduction

should take precedence, while in energy-poor environments, feeding should take precedence. This last generalization presents a basis for broad predictions concerning the function of aggregation in species for which patchiness cannot be attributed to spatial heterogeneity. This generalization could be tested in uniform environments which differ in the availability of food resources, but which are otherwise uniform. The species present should be more uniformly distributed when food is scarce, and aggregated when food is abundant.

The question arises, however, as to whether the presence of aggregation can materially increase the likelihood of finding a mate. Under sufficiently high density, or with close spacing of aggregates, a mobile species should be able to locate mates as effectively in a random distribution as in an aggregated one. Under conditions of uniformity of environment, high density, close spacing of aggregates, and high mobility, aggregation should have some function other than increasing reproductive success.

Conditions similar to these were described for species of the amphipod genus Eohaustorius present on open-coast, high energy sandy beaches of the central Oregon coast (Bosworth, 1976). Two of the four species present in the region are found in the intertidal. E. brevicuspis is found in the middle to upper intertidal, while E. washingtonianus is found in the lower intertidal to shallow subtidal. E. brevicuspis was selected for the present study because its entire intertidal distribution can be sampled using the same techniques.

E. brevicuspis is found at maximum densities of 15,000/m² and the location of maximum abundance is usually found between six and eleven

feet above mean lower low water (MLLW). Reproduction is seasonal, with a pronounced peak in fecundity between February and April (Bosworth, 1976). Bosworth suggested that the species probably has a univoltine generation, with seasonal reproduction and death following reproduction. The timing of release of juveniles from the marsupium is coincident with the timing of maximum instability of the beach sand in winter, when storms may remove up to seven feet of sand from the beach. Bosworth suggested that this timing served to increase the dispersal capability of the species, since the juveniles are non-planktonic but might migrate passively with the sand. Aggregation due to located release of brooded young appeared unlikely. This is supported by the contention of Green and Hobson (1968) that aggregations of juveniles in soft intertidal sediments would be broken up by tidal action alone. High-energy wave mixing could be added to tidal action as a factor in breaking up such aggregates.

The Oregon beach sands appear to be very uniform, over small scales of centimeters to meters. While this was not rigorously tested, the high rate of wave mixing, coupled with the description of the sand as well-sorted (Bosworth, 1976) suggested that microhabitat variability would probably not be important in aggregation in this species.

Bosworth calculated values of Lloyd's (1967) index of "mean crowding" which estimates the average number of other individuals per quadrat experienced by a subjective individual. The ratio of the mean crowding to the mean density per quadrat is a measure of patchiness. The ratio can be interpreted as the number of times as crowded an individual is, on the average, as it would be if it were in a random distribution of the same density. This measure of patchiness indicates the degree to which aggregation influences the actual density experienced by a given individual.

Typical values of patchiness for Eohaustorius were between two and four. Aggregation, then, increases the probability of encounter of mates by at most two to four times. Observations of E. brevicuspis indicated that a mature adult could burrow on the order of ten centimeters during a single tidal immersion. If preliminary information indicated that the scale of aggregation was less than this distance, then it could be assumed that the density and spacing of aggregates was such that any adult could always locate a mate with or without aggregation. Preliminary sampling for the scale of patchiness suggested that aggregation did occur at such a small scale that the chances of locating a mate could not be materially better than if the distribution were random.

B. Statement of the problem

Judging by the available information on density of Eohaustorius brevicuspis, and on its food availability, this species does not fit the generalization proposed by Heip (1975). The goal of the present study was to determine what other factors might be of primary importance in inducing patchiness when neither environmental heterogeneity, reproductive success, nor aggregation of locally released juveniles appeared to be likely causes of patchiness. Examination of the problem required information on the attributes of patchiness in E. brevicuspis in greater detail than has been obtained by previous studies of aggregation in marine benthos. Past studies have been severely handicapped by a lack of sufficient information to generate testable hypotheses on the functional significance of patchiness and the effects of aggregation. The use of methods extracted from the literature of plant and insect ecology permitted a detailed study of the size, distribution, and composition of aggregates of E. brevicuspis.

The purpose of my research was:

1. To characterize the patchy distribution of a model species,
Eohaustorius brevicuspis, with emphasis on
 - a. patch size
 - b. distribution of individuals within patches
 - c. distribution of patches
 - d. composition of patches
 - e. response of attributes of patchiness to changes in overall density.
2. To begin investigation of the consequences of aggregation through understanding of patch stability and persistence, and other aspects of the dynamics of patch formation.
3. To begin investigation of the function of aggregation through analysis of the composition of patches and correlations between population classes present in patches.
4. To evaluate the effectiveness of selected methods for the analysis of the pattern of distribution of the species, including two new methods proposed in this study.

A. Methods for the analysis of patchiness

1. Morisita's index

Morisita (1959, 1962) developed an index of dispersion based on Simpson's (1949) index of diversity. The intent of the index was to provide an estimator of dispersion which was unaffected by the mean density of a species.

Simpson's diversity index is

$$\frac{\sum_{i=1}^s n_i (n_i - 1)}{N (N - 1)}$$

where N individuals of species 1, 2, 3, ..., s are present and each species has n_i individuals. The index expresses the probability that two individuals picked at random (without replacement) from the collection of N individuals will be of the same species. The diversity is high if this probability is low.

Suppose that s quadrats are sampled, and the quadrat in which each individual is found is noted. The i^{th} quadrat will have a total of x_i individuals. The probability that two individuals selected at random from the collection of N individuals will be in the same quadrat is

$$\delta = \frac{\sum_i x_i (x_i - 1)}{N (N - 1)}$$

The diversity of quadrats is high if this probability is low. An inverse expression of the diversity of quadrats is the degree of aggregation. The population of N individuals is more aggregated when most individuals are located in a few quadrats.

To standardize the index of dispersion, the value observed is divided by the value which the index would take in a completely random distribution pattern. The probability that two individuals picked at random from s quadrats, if the N individuals are randomly distributed among quadrats, is $1/s^2$. The sum over s quadrats is simply $s(1/s^2)$, or $1/s$. Morisita's index of dispersion is defined as $\delta/\delta_{\text{random}}$ and takes a value of 1.0 in a completely random distribution, a maximum value of s in a completely aggregated distribution and a minimum value of:

$$1 - \frac{s-1}{N-1}$$

in a completely uniform distribution.

For simpler computation, an equivalent expression is

$$I = \frac{s(\sum x_i^2 - \sum x_i)}{(\sum x_i)^2 - \sum x_i}$$

In many cases it is appropriate to think of an aggregated population as being concentrated in areas or patches of higher density surrounded by areas of lower density. Morisita's index may be used to evaluate the approximate size of high-density patches and the distribution pattern of such patches, by means of samples taken with a range of quadrat sizes.

When the area enclosed by a sampling device (e.g., a corer) is small relative to the area of patches, a given sample unit can contain at most a few individuals if it falls within a patch, and generally none if it falls outside of a patch. Larger quadrats will contain many more individuals when taken within a patch than when taken outside a patch. Both quadrats will have about the same value of I_δ if the majority of individuals are concentrated in the same number of quadrats. The contrast

between the numbers of individuals in sample units taken within and outside of patches remains high until the sample unit area equals the size of patches. Beyond this point the value taken by the index depends on the distribution of patches. The index value will remain unchanged until the quadrats become large enough to include more than one patch. This requires a greater increase in quadrat size when the patches are widely separated than when they are close together.

The value of I_δ will be small for samples taken with large quadrats if the distribution of patches is random or uniform, and larger if patches are themselves aggregated. I_δ approaches 1.0 for random patch distribution and 0.0 for uniform distribution of patches.

Morisita's index is also affected by the distribution of individuals within patches, the sharpness of the patch boundaries, the contrast between the density within and between patches, the shape of patches, and the variability of patch size.

The distribution of individuals within patches (intra-patch distribution) affects the value of I_δ at small quadrat sizes. If patches are uniform internally, quadrats taken within patches will have uniform numbers of individuals and the value of I_δ will be lower. The index is more sensitive to quadrats which contain individuals than to those which are empty, and therefore will indicate uniformity even though at least some quadrats will have been taken from inter-patch areas.

I_δ is strictly independent of the mean density only for a random distribution; if the intra-patch distribution is uniform, the value of the index will increase until the quadrat size equals the patch size. This reflects the increase in the mean density per quadrat as quadrat size increases.

Both a lack of sharpness of the patch boundaries and a lack of contrast between the density within and between patches decrease the effectiveness of the index. In either case, it is possible to have some quadrats contain intermediate densities (when quadrats fall on patch margins), which tend to increase the likelihood that the sample will appear to have a random distribution of densities. Small quadrats are more likely to fall within a marginal area of intermediate density and might therefore be expected to be more influenced by indistinct boundaries.

Since the Morisita index method indicates only one scalar measure of patch size, elongate patches cannot be fully described. It is likely that very elongate patches would not be correctly evaluated.

Variation in the size of patches decreases the capability to resolve patch area. Morisita (1959) tested an artificial population consisting of large clumps of varying size. The value of I_g peaked at an intermediate quadrat size which was somewhat smaller than the median clump area.

Morisita tested the method on artificial populations with different characteristics. The method correctly assessed the patch size for;

- a. small, randomly placed clumps of points of about the same size,
- b. a single large clump with random intra-patch point distribution,
- c. a random distribution with no patches of higher density (no peak index value),
- d. a uniform distribution (index value increased from near zero to near one),
- e. large clumps with uniform intra-patch distribution.

The distribution of individuals within patches was correctly indicated in every case. In addition, Morisita applied the index method to the analysis of natural populations of three plant species. The results agreed with field observations, and further suggested that plants were distributed uniformly within clumps, which was not previously described.

Morisita has also suggested a modified index to measure the degree of uniformity of a population, isolating the uniformity effects from the influence of changing density. This index is the deviation of the observed I_δ value from the expectation under a completely uniform distribution, scaled by division by the maximum possible deviation the I_δ could have from the random expectation.

The significance of deviations from the random expectation of I_δ in the direction of aggregation can be tested by comparing

$$\frac{\left(\sum_{i=1}^s n_i^2 \right) - N^2/s}{N/s}$$

to the chi-squared distribution with $(s-1)$ degrees of freedom.

In summary, the Morisita method involves:

- a. Sampling with a range of quadrat sizes.
- b. Calculation of the I_δ index for each sample.
- c. Plotting of the I_δ value against the quadrat size.
- d. The patch area should be indicated by a peak value of I_δ , falling to lower values for quadrat sizes just larger than the patch area. Uniform intra-patch distributions should result in low values at small quadrat sizes. Random intra-patch distributions should result in constant values of I_δ until the quadrat size exceeds the patch area. Uniform patch distributions should be indicated by I_δ values near zero for quadrats just

larger than the patch area, and random patch distributions by I_δ values near one. If patches are themselves aggregated, the I_δ value may increase again after quadrat size exceeds patch size.

2. Iwao's index

Iwao (1972) developed a similar method for the analysis of the dispersion pattern of species through changing quadrat size, based on the "mean crowding" index of Lloyd (1967). The crowding per individual is the number of other individuals in the same quadrat. The mean crowding, then, is the average number per individual of other individuals in the same quadrat,

$$\bar{m}^* = \frac{1}{N} \sum_{i=1}^N (X_i) ,$$

where N is the total number of individuals, and X_i is the number of other individuals in the same quadrat as the i^{th} subjective individual. For computational purposes, it is often simpler to express the mean crowding as

$$\bar{m}^* = \bar{m} + (V/\bar{m} - 1)$$

where \bar{m} is the mean density per quadrat, and V is the variance of the mean density. This measure of aggregation can be standardized to eliminate the dependence on the mean by calculating an index of patchiness, \bar{m}^*/\bar{m} . \bar{m}^*/\bar{m} is very nearly the same as Morisita's index of dispersion:

$$I_\delta = \frac{\bar{m}^*}{\bar{m} - (1/n)}$$

The two indices represent independent developments of the same concept.

Iwao (1972) developed an index which, like Morisita's I_g index, expresses the change in the patchiness detected as the quadrat size changes and can be used to determine the size of patches. Iwao's index is:

$$\rho = \frac{\bar{m}_i^* - \bar{m}_{i-1}^*}{\bar{m}_i - \bar{m}_{i-1}}$$

where \bar{m}_i^* is the mean crowding for units of size i , and \bar{m}_{i-1}^* is the mean crowding for units of size $i-1$ (the next smaller size). The means are defined similarly. The index can be approximated at the smallest quadrat size by the ratio \bar{m}^*/\bar{m} . The index takes a value of one in completely random distributions, greater than one in completely aggregated distributions, and (as quadrat size is increased) changes from zero to approximately one in a uniform distribution. Detailed discussion of the expected response of the index under different distribution patterns is given by Iwao (1972).

Like the Morisita index, Iwao's index is sensitive to different aspects of the distribution pattern at different quadrat sizes. For quadrats smaller than the typical patch size, the index reflects the distribution within patches. The index calculated for quadrats just larger than the patch size reflects the distribution of patches. A sharp drop in the index value is expected as the quadrat size exceeds the patch size.

Uniformity in the intra-patch or inter-patch distribution pattern is indicated by zero values of Iwao's ρ . Aggregation of patches is indicated by values greater than one following the peak value. Random intra-patch distributions are indicated by index values greater than one at small quadrat sizes. Random distribution of patches is indicated by index values near one at quadrat sizes just larger than the patch size.

Comments on the effects of indistinct boundaries, irregular patch shapes, variability in patch size, and lack of contrast with the background density made in section IB/1 hold for Iwao's ρ index as well.

Iwao (1972) tested the ρ index on a series of artificial populations with varying distribution patterns of individuals in clumps. The index method correctly assessed the approximate patch size and the distribution of individuals within patches. It also correctly identified distribution patterns of the patches, in the following cases:

- a. randomly distributed small colonies, with random intra-patch distribution,
- b. randomly distributed small colonies with uniform intra-patch distributions,
- c. uniformly distributed small colonies with random intra-patch distribution,
- d. small colonies with random intra-patch distribution distributed in well-separated larger clumps.

"Small" colonies were not more than four times as large in area as the smallest sampling unit, while "large" colonies were on the order of ten times as large.

The method also correctly evaluated an artificial population in which colonies did not overlap, but were otherwise randomly distributed. This distribution deviates from a completely random distribution of patches in the direction of uniform spacing of patches. The quadrat sizes just larger than the patch size had index values between one (random) and zero (uniform), as expected.

The method was not able to define the patch size clearly for high-density populations in which little space occurred between patches. The

index method did, however, correctly indicate uniform intra-patch distribution even when the patch size could not be precisely identified.

3. Mean crowding:mean regression

Iwao (1968) has proposed a regression method for the analysis of pattern. The mean crowding and mean density may be calculated for each of a set of populations of a study species which varies in density. If the attributes of patchiness vary linearly with density, the regression of the mean crowding on the mean can be informative. The regression model is simply $\bar{m}^* = a + bm$. The intercept of the regression is the mean crowding at zero density, which is meaningless, taken literally. Iwao suggests that the intercept may be used to estimate the mean crowding at densities near zero. If the intercept is designated \bar{M}_C^* , then from the definition of the mean crowding, $\bar{M}_C^* + 1$ is an estimate of the minimum number per patch. This assumes that the number per patch is a linear function of density. A large value of \bar{M}_C^* implies that individuals are in large clumps even when the density is low.

The expected slope of the regression for uniform distributions is zero between densities of zero and one, and one for greater densities. The expected intercept is therefore near -1.0, and the value of $\bar{M}_C^* + 1$ near zero. A randomly distributed population, or a population which was aggregated only at higher densities, would have a regression intercept of $\bar{M}_C^* = 0.0$. In special cases, when individuals are distributed in patches but are uniformly distributed within patches, and patches are uniformly distributed, the value of the intercept may be less than -1.0. The actual relation of \bar{m}^* to m is complex.

Since the quadrat size used affects the value of the mean crowding, it is not surprising that changing the quadrat size affects the regression

of m^* on m . The effects of changing quadrat size can be used to evaluate the approximate scale of patchiness. However, the sensitivity of the method, given the inherent variability of regression estimates, is less than that of previously described methods. For this method, the mean crowding is plotted against the mean for a range of quadrat sizes used to sample a single population. Iwao (1968) describes the expected results for a variety of different population distributions.

4. Hierarchal ANOVA of contiguous quadrats

Grieg-Smith (1952) introduced a method for the analysis of grids of contiguous quadrats. The method was independently developed by Goodall (1954). If the grid consists of units of size q , and the size of the grid is $m \times m = n$ units, then there are n units of size q , $n/2$ units of size $2q$ (adjacent pairs), $n/4$ units of size $4q$ (blocks of four units), and so on up to two units of size $nq/2$. The sums of squares for the deviation of counts about the mean can be calculated for pairs of units within two-unit blocks, for two-unit blocks within four-unit blocks, and so on. The sum of squares for blocks of $r = 2^j$ units within blocks of $2r = 2^{j+1}$ is given by:

$$SS_r = \frac{1}{r} \sum_{i=1}^{n/r} x_i^2(r) - \frac{1}{2r} \sum_{i=1}^{n/2r} x_i^2(2r)$$

(see Pielou, 1977). Here $x_i(r)$ is the number of individuals in the i^{th} of the r -unit blocks, and n is the total number of units in the grid.

The sums of squares of counts within blocks are divided by their degrees of freedom to yield a mean square estimate of the variance between adjacent r -unit blocks within $2r$ -unit blocks. The mean square may also be divided

by the mean per r -unit blocks to standardize the mean square. A graph of the mean square against the block size r will generally show a peak when the block size equals the patch size, because adjacent half-blocks within the block are likely to lie such that one is in and one outside of the patch. Smaller blocks would generally have both halves within or outside of patches, and would consequently produce lower mean squares.

The pattern of the graph for r -unit blocks larger than the patch size depends on the distribution pattern of patches. The mean square will remain high if patches are randomly distributed and separated. It will drop if patches are uniformly distributed or are close enough together that blocks can include more than one patch. If patches are themselves aggregated (double-clumped pattern), the mean square will increase as the block size approaches the dimensions of the cluster of patches.

Disadvantages of the method have been summarized by Goodall (1974) and by Pielou (1977). These are:

- a. The sample estimates of variance at the larger block sizes have few degrees of freedom, and therefore low precision.
- b. The estimates of variance at all scales above the smallest are correlated with those immediately smaller, so increases in the mean square cannot be rigorously tested.
- c. The choice of sizes of blocks are severely limited to doubling at each step. Since the distance between centers of r -unit blocks doubles at each step, the mean square for half-blocks would be expected to increase somewhat. This effect would be inseparable from that of patch size.

d. Oblong blocks consistently give reduced mean squares relative to square blocks, resulting in a saw-toothed pattern of changes in the mean square graph.

e. Holes in an otherwise continuous distribution would be measured in almost exactly the same way as higher-density patches on a low-density background. The relative effects of each cannot be distinguished.

A variant of the method was proposed by Kershaw (1957), who applied the same procedure of hierarchical ANOVA to a series of contiguous cores in a line rather than a grid. The advantage of the method is that larger scales and a more varied range of scales of patchiness can be evaluated. A potential disadvantage is that patchiness is measured in one direction only, and elongate patches would possibly be over or underestimated in size, depending on how the line crossed the patches.

Thompson (1958) provided a means of rapidly testing the significance of peaks in a mean-square to mean ratio graph. If a theoretical model can be applied, then the expected values for the mean square/mean ratio can be calculated for any number of degrees of freedom. A peak value falling outside this range (for a given probability level) does not agree with the theoretical distribution, and represents some other distribution pattern. Thompson provided tables of the range of expected values at the 95% and 99% levels, under the assumption of a Poisson distribution model. Grieg-Smith (1961) extended this table to a larger range of degrees of freedom. Division of the mean square by the mean is recommended to remove dependence of the variance on the mean, but that Kershaw (1957) indicated that the dependence is seldom great enough to become a problem.

5. Random-pair analysis of contiguous quadrats

Goodall (1974) proposed an alternative to hierarchical ANOVA analysis of contiguous-quadrat grids, which provided independent, rigorously testable estimates of variance at a more detailed range of spacings, and with greater degrees of freedom for most scales of measurement. Pairs of units are drawn from a grid of quadrat units at each of a range of distances. Units which have already been drawn are not available for future selections. The procedure is repeated for each spacing in sequence, then repeated for the entire range of spacings until all pairs are selected or until no two units are at any of the desired spacings. For each spacing, several pairs of units will have been selected. The variance between each pair is calculated, and the variances for all pairs at that spacing pooled. This pooled estimate of the variance between pairs is calculated for each of the spacings. A plot of the pooled variance between pairs versus the distance between pairs should reflect the distribution pattern of individuals in the grid.

When the distance between paired units is small relative to the patch size, it is likely that both units will lie either within or between patches. The variance between such pairs will be small. The probability that one unit will lie within a patch and one outside the patch should increase until the spacing reaches the patch size, in which case no two units can lie within the same patch. The variance estimates should increase until the spacing reaches the patch size.

For spacings greater than the patch size, the direction of change in the pooled variance will depend on the distribution of patches. For widely distributed patches the probability of only one of a pair of units

lying within a patch is relatively constant until the distance between units is as great or greater than the distance between patches. This range of constant variance is narrower if patches are closer together. If the distance between patches is uniform, a sharp drop in the pooled variance would be expected as the inter-pair distance equals the distance between patches. If the distance between patches is variable, the pooled variance should decrease gradually with increasing distance between units. If patches are aggregated, the pooled variance would be expected to increase again as the distance between units increases, and the probability of one of the units lying within the cluster of patches and one outside the cluster increases.

If the variation between units within the same patch is small (uniform intra-patch distribution), the pooled variance will be near zero for small spacings. If individuals are distributed randomly within patches, the contribution to the pooled variance of pairs lying within a patch will be greater than if individuals were distributed uniformly within patches.

Because the pooled variances are independent, they may be rigorously tested for equality or homogeneity. Bartlett's (1964) test of homogeneity may be used to determine if at least some pooled variances are significantly different from the remainder. Pairs of variances may be compared to test whether a peak variance is significant relative to the neighboring values.

If there are many empty quadrats, the data are not normally distributed and presence-absence methods should be used. For each spacing, the number of pairs with both zero (n_0), both occupied (n_2), or only one occupied (n_1)

are determined. These counts are compared to the expectation under the null hypothesis that the counts in each unit of a pair are independent. The expected values are: $E(n_0) = (1-p^2)N$; $E(n_1) = 2p(1-p)N$; and $E(n_2) = p^2N$; where $N = n_0 + n_1 + n_2$, and p is estimated by $2n_2 + n_1/2N$. The observed and expected values are compared to the chi-squared distribution with 1 degree of freedom. If the number of n_2 pairs is too small to use the chi-square test, then the value of n_2 can be compared to the expectation for a binomial distribution given the binomial probability p^2 and sample size N . Goodall notes that the test is approximate because it assumes an infinite population, but that the rigor of the test is sufficient for practical application without the inclusion of a finite population correction term.

6. Methods for definition of patches

a. Iyer method

Krishna Iyer (1949) presented a method for the objective definition of the boundaries of patches. Given a grid of sample units, each unit of the grid may be thought of as a cell in a lattice with connections along both horizontal and vertical axes, and along diagonals. The number of adjacent cells in which both cells are more dense than the mean density is compared to the expected number under an assumption of a Poisson distribution. If the test shows that the dense cells are aggregated, then patches may be defined as those cells which are more dense than the mean value. If the number of cells more dense than the mean is r_1 , and the size of the grid of units is m by n , then the expected mean number of joins between dense cells is given by

$$m_j = \frac{A r_1^{(2)}}{b^{(2)}},$$

where $A = 2 - 3(m + n) + 4mn$, and $r_1^{(x)}$ stands for the product

$$r_1^{(x)} = r_1(r_1 - 1)(r_1 - 2) \dots (r_1 - x + 1).$$

The value of $b^{(x)}$ is defined similarly to that of $r_1^{(x)}$.

The variance of the expected number of joins is:

$$V(m_j) = 2B \frac{r_1^{(3)}}{b^{(3)}} + 2C \frac{r_1^{(4)}}{b^{(4)}} + m - m^2,$$

where $B = 44 - 36(m + n) + 28mn$ and $C = \frac{A}{2} - mn$.

These formulae are based on the expected number of joins under the hypothesis of a random distribution of dense cells, considering the position of cells in the grid and the number of dense cells. The distribution function of the value of m_j is asymptotically normal, though Pielou (1977) states that the exact size of the grid for which normality can be assumed is unknown.

Although Krishna Iyer (194) originally recommended the mean density, any critical value for dense versus non-dense cells may be used. Heip (1976) used the median density. Pielou recommended that some measure of the center of the distribution of counts be used. Jumars (1975) used presence versus absence to define dense cells.

If a range of critical densities are used, it is possible to determine the lowest critical density (if any) for which the Iyer method indicates significant aggregation. If the contrast between the density within and between patches is great enough, and the size of the grid units small enough relative to the size of patches, then this critical density should approximate the density at the margins of patches. Lower critical densities would include many randomly scattered cells, and higher critical densities would exclude the margins of patches (if the centers tend to be more dense) or lower-density patches.

b. Decision rules

For the present work, it was necessary to define provisional patch boundaries in density distribution maps. A reasonably flexible model of patchiness was adopted and limited assumptions were made to develop a set of objective rules for outlining patches.

The model assumes that patches are areas of higher density surrounded by areas of lower density rather than areas of zero density. The margins of patches of high density may be less dense than the centers, so boundaries are approximate. Patches are assumed to be symmetrical and approximately circular in section. The latter arises from the assumption that patches form by attraction between individuals rather than in response to environmental stimuli. If the initial distribution of individuals is uniform, and attraction uniform and non-directional, the population should form clumps which are not significantly elongate.

The critical density for contouring patch boundaries was selected by applying the Iyer method. A simple rule was used to separate elongate shapes on the assumption that these represented adjacent symmetric patches. No two grid units were included in the same patch if they adjoined on only one side or diagonal, with the exception of pairs of adjacent units. This rule eliminates long extensions from patches. These were few enough to have no significant effect on analyses. In two cases, large patches were contoured with very constricted midsections. On the assumption of symmetry of patches, these were divided in half in a manner which left the largest number of joins intact.

c. Usher's method

Usher (1971) described a method for the determination of the boundaries of patches which may also be applied to testing of patches defined by other means. If the distribution of counts of units in a grid is compared to the Poisson expectation, usually the hypothesis of randomness will be rejected if aggregation is present. Usher recommended that the units defined tentatively as being within patches be eliminated from the frequency

distribution of all units, beginning with the most likely "patches". The remaining units are compared to the random expectation by a chi-squared test, until the hypothesis of randomness is accepted. Usher noted that the method works well when the patches are clearly bounded.

7. Principal components analysis

Principal components analysis may be used as an alternative to analysis of correlations between variables. The data table, consisting (in this study) of observations of p variables on n subjects (patches), is transformed into a similar set of p variables with n observations on each. The transformed variables, however, are mutually uncorrelated, although taken as a whole they express all the variance of the original data. The vector of transformed variables (the principal components) may be correlated back to the vector of the original variables to determine the relative contribution of each original variable to each transformed variable. The percent of the total variance explained by each transformed variable is easily obtained. Principal components which explain only a small part of the total variance are usually ignored.

The original data variables were standardized (made dimensionless) by subtracting the mean and dividing by the variance for each variable. Principal components were obtained by use of the OS-3 computer statistical subsystem SIPS at Oregon State University. The principal components were then correlated to the standardized original variables and the resulting matrix of correlations was interpreted. Because no missing values are allowed for the SIPS program, a reduced data set was used, for which all patches with undefined or missing variable values were dropped.

Detailed discussion of the analytical procedure in principal components analysis is available in many standard texts, such as that of Cooley and Lohnes (1971).

8. Intra-patch dispersion chi-square

A new method is proposed here, based on the dispersion chi-square statistic of Jumars (1975). Jumars' statistic is based in part on the index of dispersion s^2/\bar{x} of Fisher (1970). This ratio is the average square of the deviation from the mean density, divided by the mean density. If the distribution of individuals is random, then the distribution of counts of density should follow a Poisson distribution and the variance would be expected to be equal to the mean. The index of dispersion multiplied by its degrees of freedom is distributed as a chi-square statistic (Snedecor and Cochran, 1967, p. 21). Jumars proposed that the sum of the indices of dispersion for each species, multiplied by their respective degrees of freedom (the number of sample units minus one), is a chi-square statistic which should approximately equal its total degrees of freedom when the distribution of all species is random. That is, if every species is randomly distributed and follows a Poisson distribution, all indices of dispersion for all species will equal one, and the sum of the values will equal the number of degrees of freedom times the number of species:

$$\chi^2_{S(n-1)} = \sum_{i=1}^S \left(\frac{s_i^2}{\bar{x}_i} (n-1) \right)$$

where S = the number of species, n = the number of samples, and the term in brackets is Fisher's index of dispersion for the i^{th} species.

A variation on the dispersion chi-squared statistic would permit evaluation of the distribution of individuals within patches. If by any objective rules, patches can be defined in a grid of quadrats or cores from which densities are estimated, and the basic quadrat is small

enough to partition all or most patches into subareas, then an index of intra-patch dispersion can be calculated for each patch. This index is:

$$I_i = \frac{s_i^2}{\bar{x}_i} ,$$

where I_i is the value of the statistic for a given patch, s_i^2 is the variance between units of the grid which lie within the Patch, and \bar{x}_i is the mean density per unit within the patch. If the distribution of individuals within the patch is random, then the ratio of the variance to the mean will be equal to one for every patch. For a total of P patches, the sum of the values for all patches

$$\chi^2_P = \sum_{i=1}^P (I_i)$$

is a chi-square statistic which should approximate its degrees of freedom P when all intra-patch distributions are random. Values of χ^2_P greater than the associated degrees of freedom indicate aggregation within patches, while values less than the degrees of freedom indicate uniformity in intra-patch distributions. Significance of deviations from equivalence to the degrees of freedom are tested in the usual manner for chi-square statistics.

The statistic proposed above has not been formally and rigorously developed. Its present form is analogous to the dispersion chi-square statistic of Jumars, but does not take into account the variation in patch area normally found. Any conclusions based on the statistic at present are provisional.

B. Description of the Study Area

The site selected for detailed study, Lost Creek State Park, is on the central Oregon coast eight kilometers south of Newport, Oregon. The beach is exposed to wave surf with a typical summer slope of .019 and a winter slope of .031 (elevation change/width of beach). Portions of the underlying Nye mudstone (Baldwin, 1964) are exposed during winter months when storms remove from one to two meters of sand from the beach. The beach is approximately 185 m in width, from mean lower low water (MLLW) to the base of a sandstone cliff, at approximately 4 m (13 feet) above MLLW. Lost Creek drains onto the beach approximately 100 m north of the transect location used for most of the sampling, and is largely restricted to a shallow channel at low tide. The sand is medium in size and is well-sorted, and is skewed toward the finer fraction (Bosworth, 1976). The grain size decreases somewhat in the upper foreshore.

A number of physical factors may produce heterogeneity in beach sands. These include beach cusps, rhomboidal marks, lebensspuren, current crescents, current ripples, rill marks, swash lines, and underlying irregularities of the rock surface, and are discussed in detail by Komar (1976). Beach cusps are crescentic forms with alternating mounds and depressions of the sand. They have been observed at scales as small as 10 cm in ponds and small lakes, but are much larger under high-energy conditions. At the Lost Creek site, no beach cusps were noted at any of the sampling times.

Rhomboidal marks are roughly diamond-shaped patterns developed by wave backwash. These have been observed at Lost Creek on many occasions in the mid-beach area. The scale of the pattern was approximately 20 cm along the longer diagonal of the rhomboids. The pattern was not

felt to be an important factor in producing heterogeneity, since the size-selective sorting of sand extended only a centimeter or less into the sand.

Lebensspuren are the disturbances produced by organisms in the sand, such as burrows or fecal mounds. The only lebensspuren regularly found at Lost Creek were the very shallow surface marks left by the amphipod Dogielinotus loquax. These would at times be very prominent, so that the entire surface of the sand was marked with "squiggles". The very shallow penetration of these marks indicates that they are probably not important.

Current crescents are the rounded-V shaped marks downstream of obstructions such as pebbles or shell. As a rule, the frequency of such obstructions was low enough that current crescents were insignificant.

Rill marks are left by trickles of water seeping out of the sand. These leave dendritic patterns of sand ridges. Although both freshwater and saltwater seepages were noted between 25 and 100 m from the top of the beach, rill marks were seldom observed, possibly because of the low rate of seepage.

The line of debris which marks the swash, or upper extent of penetration of waves, is a common and pronounced feature of the beach at Lost Creek. While this feature undoubtedly contributes to heterogeneity of organisms which feed on debris, it was not felt to significantly affect the distributions of infaunal species in the swash area, and probably not at all those outside of the swash line.

During winter storms, a portion of the underlying mudstone was exposed at Lost Creek. The mudstone surface is irregular, with channels of up to 20 cm depth, large shallow depressions, and domes of several meters width and approximately 10 cm to 20 cm high. When the overlying sand is shallow enough, it seems likely that the irregular surface would channel water flow through the sand. This channeling could affect the temperature, salinity, and oxygen content of the interstitial water, as well as govern the location of seepage. Heterogeneity is the distribution of these factors may result in a patchy distribution of species sensitive to changes in one or more factors. This source of heterogeneity in species abundances could increase the observed patchiness, even if the major source of patchiness is not physical heterogeneity. In Bosworth's (1976) study on patchiness in Eohaustorius brevicuspis, the greatest patchiness was observed immediately after storms had removed much of the sand from the beach. Although irregularities in the underlying rock were not specifically examined as a source of heterogeneity in this study, they remain a potentially important factor.

Another site, Driftwood State Park located approximately 20 kilometers south of Newport, was also studied. The site was selected because of its resemblance to the Lost Creek site, and because the intervening headland of Seal Rocks probably serves to block cross-migration of the populations of Eohaustorius brevicuspis on either side of the headland. The two populations could then be tentatively regarded as separate.

The Driftwood State Park site was not examined in detail for physical properties. The size and sorting of the sand appeared to be nearly

identical to that at Lost Creek. As at Lost Creek, the beach is about 185 m in width, with a sandstone cliff at the top. The maximum elevation at the top of the beach was approximately 4.25 m (14 feet). The transect location was approximately 200 m north of a creek which, like Lost Creek, was confined to a shallow channel.

B. Field Sampling

1. Preliminary Sampling

Preliminary sampling to roughly determine the scale of patchiness in Eohaustorius brevicuspis included a grid of contiguous cores in a five-by-six array, and a line of contiguous cores of larger area. The grid was used to examine distances from two to fifteen centimeters, while the line of cores was used to examine distances from approximately fifteen to 528 centimeters.

1) Grid of cores: This sample was designed NE (for nested sample). On 11/20-21/76, five 5x6 contiguous arrays of cores were taken at random positions along a line parallel to the shoreline at the 3.35 m (11 feet) tidal elevation. This level corresponded to the location of the most dense concentration of amphipod tracks on the surface. These tracks were thought to be caused by E. brevicuspis, though later observation showed that the amphipod Dogielinotus loquax was responsible. Each array of 30 cores was taken with 2.4 cm (1 inch) tubular aluminum corers to a depth of 15 cm. The position of each corer was noted and distribution maps were constructed for each array (Figure 1). The distance between the first and the last array was approximately 13 meters.

The arrays of cores were too small to be effectively analyzed for pattern by the methods of Grieg-Smith (1952) or Goodall (1974). From each array, one core was drawn randomly for a sample of five units. Pairs of adjacent cores were then drawn randomly for a sample of five units with a composite core twice the size of the smallest core. The processes was repeated for a square of four adjacent cores, a rectangle of eight cores, a square of sixteen cores, and finally for the entire

array of thirty cores. Cores or sets of cores were drawn with replacement, so that a given core in an array could be included in several of the samples for different composite core sizes. The entire process was repeated several times. Each time, Morisita's index was calculated for each composite core size. The values for the index for different trials were averaged, and the process was repeated until the averages remained unchanged. This entailed fourteen separate trials for the smallest core sizes, but only one for the largest composite core (that in which all thirty units were used). This procedure was felt to result in an adequate representation of the true distribution of individuals in the grids, although the interdependence of the index values precluded any rigorous testing.

2) Linear series of cores: On 11/20/76, a line of contiguous cores (LN1) 20x20 cm square were taken to a depth of 15 cm, along the same line as used for the NE sample. The first array taken for the NE sample was positioned between the 10th and the 11th core of the LN1 sample, and the second array of the NE sample was located after the last core of the LN1 sample. The totals for the NE-1 and NE-2 sample grids were used to extrapolate additional units for the LN1 sample, the total number of units in the sample being eighteen. Sixteen of the cores in the line were analyzed by the Kershaw (1957) modification of the Grieg-Smith (1952) method, and the starting point for the sixteen cores was varied to examine dependency of the analysis on the position of the line.

A second preliminary linear sample was taken on 12/4/76, using a tubular corer 12.5 cm in diameter. Each core was taken to a depth of 18 cm, and the cores in the line were separated by 4 cm. The sample was

taken in the same location as the previous preliminary samples, at the +11 foot level. A total of 64 cores were taken, to extend the scale which could be examined from 1.8 m (for LN1) to 5.28 m.

2. Sampling program

Following the preliminary sampling, a program was developed to examine the small-scale distribution of Eohaustorius brevicuspis. The larger scale of patchiness which was determined by the linear samples was felt to be less important in understanding the significance of a patchy distribution to the species.

The methods described by Morisita (1962) and Iwao (1972) were selected as the most likely to yield detailed information on attributes of patchiness. For these methods, samples taken with a range of core sizes were required. Each sample would be randomly positioned within the sample area, and the sample size would have to be the same for each core size. In addition, the use of the Morisita index required that the core areas increase by approximately a constant factor.

On 1/29/77, the first detailed samples for determination of patch attributes were taken. These were designated Patch Size (PS1). Four strata were defined at Lost Creek, between 1.83 - 2.44 meters (6-8 feet) above MLLW, 2.44 - 3.05 meters (8-10 feet), 3.05 - 3.66 meters (10-12 feet), and 3.66 - 4.27 meters (12-14 feet). Within each stratum, random samples were taken with each of five corers of different diameters. The inside diameters were 2.4 cm, 3.2 cm, 4.5 cm, 6.35 cm, and 8.25 cm. Each sample consisted of 10 cores, following the calculations of Bosworth (1976), who found that a sample size of 10 units was very conservative for measuring population parameters of E. brevicuspis. All cores were taken to a depth of 15 cm.

The same program was repeated on 6/5-6/77 for the PS2 samples. In this second set of samples, only three strata were sampled, 1.22 - 1.83 meters (+4-6 feet), 1.83 - 2.44 meters (6-8 feet), and 2.44 - 3.05 meters (8-10 feet) above MLLW. Loss of sand from the beach during winter storms exposed mudstone at lower levels. The uppermost stratum, though at a lesser tidal elevation than for the PS1 samples, was again just below the level where the sand was dry. Two additional corers with diameters of 1.5 cm, and 12.5 cm were used to extend the range of distances examined by the field studies.

On 12/22/77, a single stratum was sampled at Lost Creek. The PS3 samples were taken to examine the effects of a severe storm on 12/15/77. A series of such storms had eroded much of the sand from the beach, exposing mudstone from the top of the beach to +3.05 m (+10 feet) above MLLW at about 60 m seaward from the sandstone cliff. Between 3.05 m and 0.91 m (+3 feet), sand was present in a thin layer over the mudstone varying in depth from 10 cm to 30 cm. The sand was deeper in the areas overlying channels or depressions in the mudstone. Seepage from the directed flow of water in the channels prevented efficient sampling in the usual transect location (100 m south of Lost Creek), so the PS3 samples were taken an additional 100 m south of Lost Creek. A limited area of 12 m by 30 m was selected for sampling, in an area which was relatively unchannelled and had low seepage. The elevation was between 1.74 m (+5.7 feet) and 1.92 m (6.3 feet) above MLLW. This represented the second quarter of the remaining sand in the intertidal, from the top of the beach. If Eohaustorius brevicuspis accommodated to the diminished amount of sand, this location would be in the mid-to-upper range of the intertidal distribution of the species.

On 7/11/78, a single stratum was sampled at Driftwood State Park, approximately 20 kilometers south of Newport. The intent of this sampling was to determine if some of the aspects of patchiness at the Lost Creek site could be identified at another location physically separated from the Lost Creek population. The Seal Rocks headland was felt to be an adequate barrier to an upper intertidal species, although sand may be transported around the formation in the deeper sublittoral. A stratum was defined from +6.3 to 8.3 feet above MLLW, and sampled in the same manner as the previous PS samples. The corers used were the 1.5 cm, 2.4 cm, 3.2 cm, and the 8.25 cm diameter corers. The largest diameter corer (12.5 cm) was not used due to lack of time.

D. Laboratory Studies

1. Patch size, distribution, and composition

A series of tests were made to examine the attributes of patches in controlled conditions, in order to describe the static or instantaneous properties of patches, rather than the dynamics of patch formation. The LP (laboratory project) series was used to examine the characteristics of patches formed in the absence of selected stimuli which were felt to potentially cause or influence patchiness in Eohaustorius brevicuspis in the field.

The series of usable trials begins with the LP3 trial, as the LP1 and LP2 trials were conducted in containers which were too small. The LP3 trial and subsequent trials were conducted using a plywood box measuring 53 cm by 30 cm by 30 cm deep on the inside. The box was filled in each trial to a depth of 20 cm with sand taken from the Lost Creek site,

from the center of the distribution of E. brevicuspis at this location. This tidal elevation also corresponded to the lower limits of the abundant polychaete Euzonus mucronata. All sand in the LP series trials was sieved free of larger debris with a 0.5 mm sieve, and in later trials had been resieved and reused up to five times. After filling the box with drained sand, the sand was vigorously mixed with a stream of sea water for at least five minutes to further ensure homogeneity. A baffled water flow of approximately 2.5 liters per minute was then established into the box from the laboratory seawater system. The outlet for the water was over one end of the box, which was slightly lower, creating a directional flow along the length of the box. No attempt was made to provide additional water circulation through the deeper sand.

Amphipods or mixed macrofauna were collected at Lost Creek, sieved, and held for 24 hours before placement in the container. By picking up several individuals with a fine paintbrush and dipping the brush into the overlying water at regular intervals, placement was made approximately uniform. Water circulation was suspended until the amphipods were burrowed into the sand. Prior to burrowing, most individuals swam for a few seconds to several minutes, so the procedure for placing individuals in the box probably did not cause an artificial patchiness.

All trials were terminated after approximately 72 hours. An aluminum sheet was inserted into the sand near one end of the box, sand beyond that point scooped out, and the box tilted to drain the water past the metal plate. Draining required about five minutes, although after the first minute most of the sand was well-drained. Repeated observations that E. brevicuspis is unable to move through well-drained

sand have been made. This procedure was probably sufficient to preserve the pattern of distribution of individuals which was present at the time of termination of the trial.

The sand in the box was then partitioned and sieved during the next 24 hours. The box was placed on one end and the sand nearest the draining end discarded. Layers of sand two centimeters thick were then cut from the box; in the normal position these would be two cm thick vertical walls across the width of the box. Each layer was cut into blocks two centimeters wide and 6.6 centimeters long. When viewed from above, the box of sand was sectioned into two by two cm squares horizontally, and into three layers 6.6 cm deep. This permitted fine resolution of distributions horizontally, and a crude estimate of vertical distributions. A similar method was used by Usher (1971), for the study of the microdistribution of soil arthropods. Each block of Usher's samples consisted of 48 units, in an array of four units by four units, with three layers by depth. In the LP trials, there were 12 by 16 units in the horizontal direction, and three layers, for a total of 192 units per array.

a) LP3: The first usable trial of the series was begun on 8/15/77 and terminated 8/18/77. A volume of sand 53 cm by 30 cm by 20 cm, equal in size and shape to the interior of the box used in the laboratory was sieved on the beach at Lost Creek. The amphipods and all other macrofauna except the polychaete Euzonus mucronata were placed in the laboratory box. The purpose of this trial was to test for possible effects of Euzonus on patchiness, because its mucus-lined burrows might provide sufficient spatial heterogeneity to influence the distribution of E. brevicuspis.

b) LP4: In this trial, begun on 8/21/77, only the Eohaustorius brevicuspis were placed in the box. The collection procedure was the same as for LP3, using the natural density found in the field. Aggregation in this trial would indicate that aggregates form in the absence of known physical heterogeneity, other macrofauna, and most of the normal physical processes (e.g. wave action) of the open coast beaches.

c) LP5: This trial was begun on 8/31/77. All macrofauna except Euzonus mucronata and the isopod Cirolana harfordi were placed in the container, in order to obtain information on the importance of Cirolana as a factor in aggregation. Even if Eohaustorius aggregated in the absence of Cirolana there would be a potential effect of Cirolana on the degree or nature of patchiness, if it was a predator of E. brevicuspis.

d) LP6: The LP6 trial, begun on 10/16/77, was a replicate of the LP4 trial and was intended to confirm the results of the LP4 trial. In addition, as in the LP5 trial, all individuals recovered at the end of the experiment were retained in vials coded for the exact position of the unit, and all individuals were later measured and sexed.

e) LP7: The LP7 trial was begun on 6/15/78. The intent was to test the persistence of patches over a single tidal cycle or portion of a cycle. An area of maximum density of Eohaustorius brevicuspis was selected at the Lost Creek site, and a volume of sand of the same dimensions as the laboratory box was collected and returned to the laboratory for sieving. All macrofauna were placed in the test container which was drained on 6/18/78. The sand was sectioned as before, and the amphipods recovered from each section were kept alive in separate containers. This phase of the LP7 trial provided a test of the attributes of patches formed in the laboratory at a very high density.

The amphipods from a contiguous group of blocks with the greatest density were placed together in seawater with Neutral Red stain for 72 hours. The remaining individuals were pooled and retained in a large bowl without sand for this period. On 6/22/78, all surviving amphipods were placed in the laboratory box. Only half of the amphipods originally recovered survived the 72-hour period, although in other cases E. brevicuspis survived similar periods without sand with lower mortality. The undyed amphipods were replaced in the box in the usual manner. Dyed amphipods were released within a tube 6.35 cm in diameter inserted into the sand in the center of the box. The amphipods were allowed time to burrow completely into the sand before the tube was carefully removed. The time of replacement of the amphipods in the box was coincident with the time of high tide at Lost Creek. At the time of the succeeding low tide, approximately six hours later, the box was again drained and the positions of dyed and undyed individuals noted separately. If the dyed amphipods were found at depth in the sand, but at approximately the same horizontal position as originally placed, downward migration probably involves primarily vertical movement rather than a slanting burrowing pattern. This would indicate that patches could potentially remain as discrete units through a tidal cycle by simply adding a component of vertical movement to the normal pattern of movement. It would be more difficult to suppose that patches could remain integral if vertical movement were at an angle through the sand.

2. Tidal rhythmicity

A single test of the possibility of tidal rhythmicity was made. The PD (patch dynamics) trial examined in greater detail the vertical positioning of the population in the laboratory, some indication of which had come from the LP series. In the LP trials, it was noted that the depth of the layer in which the maximum density of amphipods occurred was related to the stage of the tide on the beaches. When the box was drained at a time corresponding to a rising or falling tide, the greatest density was found in the middle layer (LP4 and LP6). When drained at the time of low tide, the greatest density was found at the bottom (LP5), and at the time of high tide, the greatest density was found at the top of the container (LP3).

On 4/18/78, a volume of sand 48 inches by 24 inches by 10 inches deep was sieved in situ at Lost Creek, in the region of apparent greatest density of E. brevicuspis. An identical volume of sieved sand from Lost Creek was placed in a seawater tank of the same dimensions. All macrofauna found by sieving were placed in the sand in the tank. Seawater circulation was provided by two hoses which eliminated any quiet areas in the water overlying the sand in the tank. After 27 hours, a sampling series was begun, coincident with the time of high tide on the open beach. Four cores of 3.2 cm diameter were taken at randomly selected positions in the tank, corking the coring tube to withdraw a nearly intact core without draining water from the sand in the tank. The water level above the sand was lowered to near the sand surface to avoid water overlying the cores in the tubes. The drained cores were immediately sectioned into seven 2.5 cm sections, and the sections stored for sieving on the following day. Sampling times were at 1015, 0115, 0400, 0745, and 1030 hours on the

19th and 20th of April. On retrieving the cores, the lowest 2 cm of the core usually washed out, so that the bottom of the sand was not sampled.

3. Predation by Cirolana on Eohaustorius
brevicuspis

Bosworth (1976) discussed the possibility that Cirolana harfordi could be a predator on E. brevicuspis. I observed Cirolana attacking and eating adult E. brevicuspis in shallow bowls of seawater without sand present. The time for one adult Cirolana to eat one Eohaustorius adult was about five minutes, and the escape rate in the bowls was negligible. Up to four Cirolana were observed attacking a single prey individual. There appeared to be some added attraction to prey which had already been damaged.

To test the maximum rate at which Cirolana could eat Eohaustorius individuals, without regard to size, eight bowls 18 cm in diameter were filled to a depth of five centimeters with clean sand. A random size assortment of ten E. brevicuspis individuals were placed in each bowl. Two adult Cirolana were placed in each bowl at 1530 hours on 9/9/77. After 45 hours, the contents of the bowls were sieved. A similar set of ten bowls with E. brevicuspis but without Cirolana were maintained for the same period. Damaged bodies were counted as absent or preyed upon, while undamaged but dead amphipods were counted as present. The damage done in feeding by Cirolana is thorough and unmistakable compared to death from other causes.

III. OBSERVATIONS AND RESULTS

A. Field Sampling

1. Preliminary sampling

The results of the NE and LN sampling indicated that patchiness was present at scales of a few centimeters and on the order of one to two meters. Distribution maps of the NE sample arrays are shown in Figure One. The graph of the composite Morisita's I_δ calculated for each block size, versus the block size, is shown in Figure Two. The graph peaks at the two by two unit block size, or five centimeters square. The distribution maps show that blocks of four units contain up to fifteen amphipods where they are dense within the array of cores, and as few as zero or one where sparse. Although the Morisita index is less sensitive to gaps than to areas of high density, it is possible that "patches" of this species could be either areas of higher density, or gaps in the distribution of individuals. Gaps such as this could be caused by the patchy effects of shorebird predation. Laboratory studies were designed to test this possibility.

The plot of the density per core versus the position in the LN1 line of cores is shown in Figure Three. A regular fluctuation appeared to occur in the density per core. Analysis by the Kershaw modification of the Grieg-Smith method of pattern analysis was attempted. The shortness of the line of cores and the regular fluctuation in density permitted a difference in starting point of only one core to produce diametrically opposed conclusions.

The LN2 series of cores was taken to provide a longer line of cores which could be effectively analyzed by the Kershaw method. The graph of the density per core versus core position is shown in Figure Four. The mean square to mean ratios (Table One) indicate that the greatest variation occurred between blocks of one core and between blocks of sixteen cores. This indicates patchiness at scales of 15 cm and 240 cm. All scales except the largest, including a range from 15 cm to 240 cm, were significantly non-random. F-ratios of successive mean squares indicated that the greatest change in the mean square occurred between 15 cm and 30 cm scales, and the 120 cm and 240 cm scales. The P-value of these F-ratios (probability of a type 1 error) was between .9 and .95. For so few degrees of freedom (Table One), however, the F test is not robust, and little reliance can be placed on exact significance levels. Tentatively, the LN2 sample analysis indicates patchiness over distance of about 15 cm and 240 cm. The relationship, if any, between the two scales is not obvious. Since known heterogeneity of the beach does not occur at distances of 15 cm, but does occur on the order of 2-3 m, further investigation concentrated on the smaller scale. The smaller scale was also more suitable for laboratory investigation than the larger.

2. Sampling Program

The PS series of samples was designed to investigate the small-scale distribution of Eohaustorius brevicuspis in the field using the Morisita (1962) and Iwao (1973) methods. Figures Five through Eight show the plots of Morisita's I_g and Iwao's ρ versus the core diameter for PS1 through PS4, respectively.

a. Patchiness scale: Peaks in either index plotted against the core diameter indicate the approximate scale or scales of patchiness. Most of the graphs for either index have two peak values. The peaks occur most frequently at core diameters of 3.2 cm and 6.35 cm. The frequency of peaks for each index is:

core diameter (cm)	2.4	3.2	4.5	6.35	8.25
I_{δ}	3	4	1	5	2
ρ	2	5	2	4	3

The pattern of peaks occurring at the core sizes of 3.2 and 6.35 cm suggesting two scales of measured patchiness, could result from patches of two dominant sizes. Since the larger diameter is twice the smaller, it is also possible that large-diameter cores are sampling adjacent patches on occasion. The cores are two-dimensional representations of three-dimensional density distributions, within the sand, and it is possible that some patches are separated vertically but are fused when projected to two dimensions.

b. Distribution of patches: Uniform distributions of patches may be indicated by values of Iwao's ρ index near zero for core sizes just larger than the indicated patch size. This occurs in three strata in PS1-PS4; in an additional two strata the value of ρ is -1.0 for cores just after the indicated patch size. Negative values would not be expected from a uniform distribution pattern of patches.

c. Distribution within patches: Both Morisita's and Iwao's indices are potential indicators of uniformity in the distribution of individuals within patches. The expected value of I_{δ} would be near one for small cores, while the expected value of ρ would be near zero.

I_0 values were low for every stratum in PS1-PS4 for small cores, except when a peak value occurred at the smallest core size (3 of 15 strata). This strongly suggests uniform intra-patch distribution patterns.

Iwao's ρ for small core sizes was always 1.0 or greater, but in virtually every stratum the index value for larger cores was greater than that for the smallest core. The pattern of initially low values is consistent with that expected for uniform intra-patch distributions, although the values observed are higher than expected.

d. Patch size at low density: A linear regression of Lloyd's mean crowding index versus the mean density per core was used to estimate the number of individuals per patch at relatively low densities. Least squares regression was used, although the assumption that the independent variable was measured without error may have been violated for the mean density. The regression was calculated separately for each core size used in all four of the PS samples. To provide a range of mean densities, each stratum was considered a separate population which varied in aggregative properties only with density. Obviously, tidal height or numerous other differences could alter the nature of aggregation between strata, so this analysis is only exploratory.

The regression parameters for five core diameters are:

<u>core size</u>	<u>a</u>	<u>b</u>	<u>r²</u>	n = 9
2.4 cm	0.18	1.47	.92	
3.2	-1.79	2.65	.90	
4.5	-2.65	2.29	.92	
6.35	-3.34	2.00	.78	
8.25	-1.15	1.54	.91	

All regressions were significant at the 99% level or greater. Iwao (1968, 1973) stated that the intercept should equal -1.0 when the distribution is uniform. If aggregates are uniformly separated and individuals are distributed uniformly within aggregates, then it may be possible to have negative intercepts less than -1.0. The low intercept values for the PS data may indicate such a distribution, or may be the result of differences in the properties of aggregation in different strata. No conclusions can be made from the linear regressions in this study. A non-linear regression model may have been more revealing.

3. Generality of field results

The PS samples taken at Driftwood State Park (PS4) were analyzed in the same manner as the samples taken at Lost Creek State Park (PS1-3), and have been included in evaluations of attributes of patchiness in the field. Comparison of the graphs of Morisita's I_g and Iwao's ρ for PS4 to those for PS1 through PS3 shows no apparent differences between the attributes of patchiness in the two locations.

B. Laboratory Studies

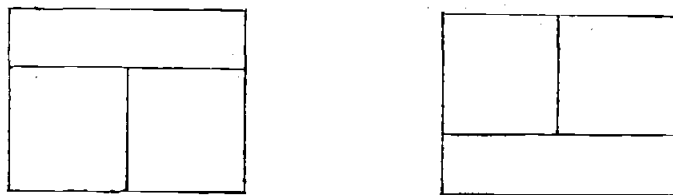
1. Patch Size

Four trials of the LP series have been analyzed by the Grieg-Smith method, which uses a mean-square estimate of the variance to evaluate the size of patches sampled by a grid of contiguous cores or quadrats. When the grid is partitioned into blocks which are the same size as the patches, the variance between blocks is greatest. The usual chi-square tests are not completely valid when the assumption is that the distribution will be

non-random, and patterns in the variance versus block size graphs are more often used to evaluate patch size than the exact magnitude of the variance. A simple F-ratio test can be used to test whether an increase in variance from one block size to the next larger is significant, but again the test is not strictly valid.

A rectangular array was used to map the distribution pattern of Eohaustorius brevicuspis in the LP series. The array was 12 units by 16 units horizontally, and was sectioned into three layers. Each unit was about 2 cm by 2 cm, and each layer was approximately 6.6 cm thick. Layers were analyzed by the Grieg-Smith method separately, then combined to produce an areal distribution map which was comparable to the two-dimensional field sampling. The areal maps were also analyzed in the same manner.

A modified procedure was used to evaluate the rectangular array, since the original method was designed for a grid of size 2^j units. Only two 8x8 adjacent, non-overlapping subsets can be defined in the 12x16 grid at one time. There are two possible ways to define blocks of 8x8 units, as shown below:



Rather than arbitrarily selecting one arrangement to estimate the mean square variance for 8x8 blocks within 8x16 blocks, both arrangements were used. Graphs of the mean square:mean ratio versus block size (Figures Nine through Twelve) therefore include two alternative lines for block sizes 4x8 and 8x8 units (8x16 cm and 16x16 cm). For block sizes smaller than 8x8 units, the entire array was used to estimate mean square variance.

The frequency of peak variances at each block size is:

block size (cm)	2x2	2x4	4x4	4x8	8x8	8x16	16x16
layer maps	0	0	1	2	1	6	3
areal maps	0	0	1	1	1	1	2

In every case (layer maps or areal maps) a peak variance occurs at the larger block sizes, especially at the 8 cm by 16 cm size. In some cases a peak value also occurred at one of the small block sizes, but in only one case (bottom layer of LP5) was this peak of the same magnitude as the peak variance at the larger block size. The analysis indicates that, while significant aggregation was generally found at more than one block size, the greatest mean squares and strongest indication of aggregation occurred at the 8x8 cm or 8x16 cm block size. This presumably represents the approximate size of patches in the experimental container. Since the mean squares did not remain at the high level in most cases, it is possible that patches tended to be distributed uniformly in the box.

The LP series data were also analyzed for patch sizes using the method proposed by Goodall (1974), in which random pairs of units are drawn from a grid of units at varying distances between units. The pooled estimate of the variance between paired units should be greatest when the distance between units is equal to the diameter of patches. The pooled variances are plotted against the distance between paired units in Figures 13 through 17.

Adjusted variances were used to reduce the chance of a single greatly disparate pair of units producing a peak in the pooled variance. The pair of units with the greatest variance were dropped from the pooled variances for each inter-pair distance. It is assumed that when the inter-pair distance equals the patch size, more than one pair of units should have

high variances. Dropping only the largest variance should eliminate spurious peaks in the pooled variance and reduce all pooled variances slightly.

Bartlett's (1964) test permits comparison of a group of independent variances, under the null hypothesis that each variance estimates the same population variance. For the LP data, acceptance of the null hypothesis would mean that the variance between pairs estimated for different spacings were not significantly heterogeneous, and that peaks in the variance:spacing graphs were meaningless.

The results of Bartlett's test are given in Table Eight, for both the original pooled variances and for the adjusted variances. The original variances are significantly heterogeneous for all but one grid when layers are considered separately, but are not heterogeneous in the case of areal projections. The adjusted variances had higher significance levels, and all but one areal projection were also significantly heterogeneous. The adjustment apparently increases the resolution of differences between the variances estimated at different spacings, by eliminating a considerable part of the random error typical of variance estimates with small sample sizes.

The frequency distribution of peak values in adjusted variances among spacings is:

distance between unit centers (cm)	2	4	6	8	10	12	14	16
number of peaks for layers	3	2	4	2	2	5	2	3
for areal projections	0	0	2	2	1	1	1	1

It is apparent that patch scales as measured by the Goodall method varied widely but were more frequently found at 6 cm and 12 cm (inter-pair distance from center to center). Detailed comparison of the graphs to the

patches outlined for the LP series (see section I-B/6a) indicates that much of the variability in location of peaks can be attributed to differences in distribution patterns between grids rather than errors in the method.

a. i. LP3 top layer: Small clumps of one unit in size, and a large group of about 6 units diameter were correctly indicated.

ii. LP3 middle layer: Groups of three units in diameter were correctly indicated but the method was only approximately correct in indicating the six-unit size.

iii. LP3 bottom layer: No adjusted variances were available.

iv. LP3 areal map: Sizes of five and seven units were correctly indicated, but no indication was given of smaller groups present.

b. i. LP4 top layer: The small patches of 2 units diameters were suggested, and the collection of these in an area of eight units was also indicated. The method does not distinguish between this double-clumped pattern and the presence of two sizes of patches (as in LP3 top layer).

ii. LP4 middle layer: Patchiness on the order of six units diameter was indicated in the graph, but not by the distribution map. This may have resulted from the close spacing of patches.

iii. LP4 bottom layer: The patches of three units size were indicated, but patches of six units in diameter were also indicated in the graph. Again, the closeness of small patches may have resulted in spurious measurement of larger patches.

iv. LP4 areal map: Two sizes of patches were present and indicated by the graph.

c. i. LP5 top layer: The graph indicated patchiness on the order of four and six units diameter, which contradicts the distribution map evidence.

ii. LP5 middle layer: The graph indicated patchiness at five and seven units; again, this is contrary to the distribution map patches.

iii. LP5 bottom layer: The graph and distribution map patches were in agreement, with patches at two and four units diameters.

iv. LP5 areal map: If the critical density is set at four individuals per unit, the graph and distribution map patches were not in agreement. The graph would reflect the patches outlined if the critical density were set at two individuals per unit.

d. i. LP6 top layer: Small patches of one unit size were indicated by the graphical method. The graphs also suggested patches of seven units diameter, which overestimated the size of the single larger-area patch present.

ii. LP6 middle layer: The graphical method indicated two patch dimensions. The outlined patches are of approximately the same sizes, with small patches clumped together.

iii. LP6 bottom layer: The graphical method and the outlined patches were in agreement.

iv. LP6 areal map: The graph indicated patches on the order of the size of the outlined patches, but does not detect the presence of a few small patches.

In general, the Goodall method appears to reflect the patches which are defined by contouring density on the distribution maps, but the graphs could easily be over-interpreted. In several cases, the patch dimensions indicated by the graphs reflected some patches but not others. The method would be most suitable for distributions in which all patches of high (or low) density are about the same size.

2. Distribution of patches

Thompson (1958) has shown that the mean square estimates of the variances within blocks in a Grieg-Smith hierarchical analysis of variance will increase with the block size if the distribution of patches is random. The mean squares will peak and decrease after the block size exceeds the patch size only if the distribution of patches is uniform. Graphs in the present study were usually of the latter type. It can be inferred that the distribution of patches of E. brevicuspis in the laboratory situation is more uniform than would be expected under a random distribution mode.

3. Distribution within patches

The proposed new method of detecting uniformity in within-patch distributions was applied to patches larger than one unit area. The statistic χ^2_p for all patches of two or more units area in LP3-LP6 was 29.22 (d.f. 84), which deviates from the random expectation in the direction of uniform distribution (99.5% level). The values for patches within each of the layers of LP3 through LP6 are listed in Table Nine. For most of the layers taken separately, the χ^2_p values are not significantly different from random expectation. However, the statistic is near significance at the 95% level in half the layers, and is very highly significant in four cases. It would appear that in general, the distribution of individuals within patches tends to uniformity, although this may not be obvious when only a few patches are considered.

4. Patch composition

a. Correlations analysis

Patches in the LP6 distribution maps were defined as previously described. Data on the numbers and sizes of males and females per unit were used to estimate:

MSM: the mean size of males within a patch,

MSF: the mean size of females within a patch,

MSALL: the mean size of all individuals in a patch,

VMSALL: the variance of MSALL for each patch,

AREA: the area of each patch in two cm by two cm units,

MALES: the number of males in a patch,

FEMALES: the number of females in a patch,

PSIZE: MALES + FEMALES,

DENSITY: PSIZE/AREA.

Patches in which only one sex was present were excluded. These were invariably of one unit area and contained only two individuals. One additional patch was excluded, consisting of one very small male and one very large female. The resulting high variance of the mean size, which appeared due to chance only, had considerable influence on the correlations analysis.

Spearman's rank correlation coefficient was calculated for all correlations between the above variables of patch composition. Many of the correlations are between related variables, such as PSIZE and MALES. These can be regarded as significant only if the correlation is opposite in sign to that expected. The correlations are listed in Table Eleven. The correlations which were significant at the 95% level indicated that:

i. The area of patches and the number of individuals in patches are very highly correlated. Large-area patches contain more individuals.

ii. The area and density of patches are not correlated. The density within patches varies independently of the area of the patch. It may be that the density within patches is a constant (within sampling error limits) for patches of different size.

iii. Density is correlated with the number of individuals in the patch, possibly only because of the definition of density used. It is possible that the few cases in which patches had unusually high densities (all in larger patches) produced the significant correlation.

iv. Both the numbers of males and the numbers of females increase in larger patches. Apparently males and females do not segregate into patches of different size or density; the factors determining patch size probably affect both sexes equally.

v. The mean size of males increases with the mean size of females. This may be a consequence of the distribution of sizes with depth in the LP6 trial, as discussed in section III-B/9. Smaller individuals were located nearer the surface of the sand than large individuals. Males and females would be larger in patches located deeper in the sand.

vi. The variance of the mean size of individuals of both sexes was positively correlated with the area and number of males and females in patches. All the latter variables are expressions of larger patch size. In larger patches there is a greater probability of the few very small and very large individuals occurring together. The average variance in larger patches would be higher than that expected for most small patches.

b. Principal components analysis

The variables measured for patches defined in the LP6 distribution maps were evaluated by principal components analysis. Some patches were excluded from the data table, as described for the correlations analysis. Variables were standardized by subtracting the mean value and dividing by the standard deviation. The correlations between the principal components and the standardized variables are listed in Table Twelve. These correlations indicate the relative contribution of each variable to each principal component.

The first two principal components contain 78.4% of the total variance of the standardized data table. The third and fourth components contain 10.1% and 6.9%, respectively. The first four components together contain 95.4% of the information in the data table, and were considered sufficient to describe the data.

i. Principal component one: The contributing variables are those related to the number of individuals per patch and the area of patches. Inclusion of PSIZE and AREA in the same component implies that they are correlated. The variables VMSALL and DENSITY are correlated to the first component to a lesser degree. At least some large patches appear to have high density and a greater variation in the size of individuals.

ii. Principal component two: The second component expresses the variation in the mean size of individuals. The mean sizes of males and females are correlated. Size of individuals is unrelated to other patch composition variables measured.

iii. Principal component three: The density within patches has a large component of variability which occurs independently of other measured patch composition variables.

iv. Principal component four: The variance of mean size of individuals has a component of variation which is independent of other measured patch composition variables.

The conclusions reached through principal components analysis are generally the same as those from the correlations analysis. However, the correlation of DENSITY to PSIZE but not to the variable AREA was not indicated by the principal components analysis.

5. Patch size and density

Simple linear regression was used to examine the relationship between patch size and the overall density. Each layer was treated as a sample for which the total number present was exactly known, and the average patch area, number per patch, number of patches, variance of the patch area, and variance of the number per patch were estimated. These data are listed in Table Thirteen. The use of layers as separate populations is justified only if the individuals forming patches respond to the density within the layer and not to that in other layers. This may be approximately correct if the individuals respond to the density within a limited range, or if they tend to travel horizontally but not vertically. In the former case, one would expect that the response to density would vary from one end of the LP container to the other, if the density within the layer varies. This regression method should be regarded only as a rough test at best.

The observations on each variable for twelve layers (LP3 through LP6) were plotted against the inverse cumulative standard normal distribution.

A linear plot is strong evidence that the variable follows an approximately normal distribution and parametric methods may be applied, even though the sample size is small. Plots for the mean area of patches and its variance, the number of patches per layer, and the layer density were nearly linear. The plots for the mean number of individuals per patch and the associated variance deviated from linearity at large values of the patch size or variance. The plot was considered sufficiently near to linear to apply least squares regression. The regression parameters were:

<u>dependent variable</u>	<u>intercept</u>	<u>slope</u>	<u>correlation r^2</u>
PSIZE	1.74	.039	.82
s(PSIZE)	-1.89	.066	.79
AREA	1.64	.005	.47
s(AREA)	0.84	.009	.48
NUMBER OF PATCHES	8.02	.032	.41

All correlations were significant at the 95% level or greater. For comparison, Spearman's non-parametric correlation coefficient was also calculated.

	<u>DENSITY</u>	<u>S (PSIZE)</u>	<u>AREA</u>	<u>S (AREA)</u>	<u>#PATCHES</u>
PSIZE	.706	.916	.942	.881	.218
S (PSIZE)	.692		.910	.895	.183
AREA	.721			.949	.225
S (AREA)	.580				.028

All correlations other than those involving the number of patches in a layer are significant at the 95% level.

Patches were larger in area and contained more individuals when the layer density was higher. The number of individuals per patch was more strongly correlated with density than was the mean area of patches, using parametric correlation. The non-parametric method used indicated that both are equally correlated with layer density. At higher layer density, the variability of either the area or the number per patch was greater.

Over the range of densities found in the LP series, predicted values of the variables are:

<u>DENSITY</u>	<u>PATCH AREA</u>	<u># PATCH</u>	<u># OF PATCHES</u>
60/layer	1.94	4.08	9.94
200/layer	2.64	9.54	14.42
400/layer	3.64	17.34	20.83

For a 666% increase in layer density, the patch area and the number of patches approximately doubled, while the number per patch increased 400%. This necessarily implies that at least some patches have higher per-unit density in layers with high densities.

The predicted patch size at zero density is a rough estimate of Iwao's (1968) concept of the minimal patch size $\bar{M}_c^* + 1$ (Section IIA/3). A minimal patch size greater than zero, as found here, indicates that the basic form of interaction between individuals is aggregation.

6. Stability and persistence of patches during downward migration

The distribution maps for the positions of dyed amphipods as originally placed and when recovered are shown in Figure Twenty-three. Twenty-eight

of the dyed amphipods were found at some depth below the 6.3 cm diameter area of the surface where they were released. Sixteen were found in the top 6.6 cm deep layer, having travelled downward no further than that distance in the 6 hr. test period. Fourteen were found in the middle layer, having travelled downward between 6.6 and 13.2 cm in the 6 hours. No amphipods were recovered from the bottom layer. Only two of the 30 dyed amphipods moved both vertically downward and to the side, and were no longer immediately below the area of placement. Apparently, tidal migration occurs through addition of a component of vertical motion to the normal motion when within patches. A patch could remain integral through at least one low tide period, since vertical motion does not appear to be primarily at an angle. It is not certain whether the patch of dyed amphipods would have remained as a single patch over a longer period although they remained in close proximity over six hours.

7. Tidal migration

The possibility that vertical migration in the sand occurred as an endogenous tidal periodicity was examined in the Patch Dynamics (PD) trial. The results of the PD trial are shown in Table Fifteen. At the time of high tide, 10 individuals were collected in four cores, 9 in the upper half of the sand. At the time of the falling tide, 4 individuals were found, and at low tide only one was recovered. Any amphipods near the bottom of the tank escaped because of washout of sand from the bottom 2-3 cm of the cores. During the rising tide, 13 individuals were found in the upper half of the sand. At the second high tide, 18 amphipods were recovered, 14 of which were in the upper half of the sand. In no case was there a concentration of individuals in the lower part of the

sand which could be sampled, indicating that migration through the lower part of the sand is rapid. The possibility exists that during tidal migration the top and the bottom positions may be occupied for a disproportionately longer time, and the migration may be rapid.

The data are interpreted here as indicating tidal migration. The possibility cannot be eliminated that the low numbers of individuals recovered at low tide was solely due to a patchy distribution.

8. Predation by Cirolana on Eohaustorius brevicuspis

At the end of the experiment, all eight of the bowls without Cirolana contained ten amphipods, either living or dead, but all undamaged. In the experimental bowls containing two adult Cirolana the numbers of living or undamaged E. brevicuspis were: 8, 9, 9, 9, 10, 10, 10, 10. The Mann-Whitney U-test of the difference in median values was applied. The test indicated that the number of amphipods damaged or missing in bowls with Cirolana was significantly greater than that in the control group (Pr less than .005). The approximate rate of predation of mature Cirolana on a mixed population of Eohaustorius brevicuspis is 0.167 Eohaustorius per Cirolana per day. This should be a maximum estimate because the predation rate for juvenile Cirolana should be less than for adults, and during part of the tidal cycle Cirolana and Eohaustorius are apparently not present at the same depth in the sand.

At an average density of 200 Cirolana/m², if this maximum rate were maintained for one-half the tidal cycle (during high tide) over one year, the total mortality due to predation would be on the order of 6,000

Eohaustorius per m². This is on the order of the total fecundity of E. brevicuspis (Bosworth, 1976). Predation by Cirolana could be a major source of mortality, accounting for nearly all deaths in the population.

9. Sizes of individuals by layer in LP5 and LP6.

The sex and size of all individuals recovered in LP5 and LP6 were recorded in conjunction with examination of the composition of patches. The mean sizes and associated variances of males and females in each of the layers of the LP5 and LP6 trials were:

<u>level</u>	<u>Males</u>		<u>Females</u>	
	<u>size</u>	<u>variance</u>	<u>size</u>	<u>variance</u>
LP5 top	4.60	.698	4.97	.856
LP5 middle	4.95	.730	4.06	.857
LP5 bottom	5.09	.930	5.34	.855
LP6 top	5.16	1.13	5.26	1.88
LP6 middle	5.50	1.56	5.71	1.60
LP6 bottom	6.43	1.77	6.41	1.60

T-tests were used to compare the sizes of individuals in different layers for both males and females. For such multiple comparisons, the total Type One error rate is set at $\alpha = 0.05$. The minimum significance level for pairwise comparison is $\alpha = 0.0167$ (98% level). The test statistic values, associated degrees of freedom, and significance level were:

<u>LP5</u>	<u>t(males)</u>	<u>df</u>	<u>%</u>	<u>t(females)</u>	<u>df</u>	<u>%</u>
top-middle	1.51	51	90	0.392	63	65
middle-bottom	0.66	105	70	1.61	104	90
top-bottom	2.36	106	99	1.79	127	95
<u>LP6</u>						
top-middle	1.57	166	90	1.74	136	90
middle-bottom	4.58	181	99	3.53	169	99
top-bottom	5.04	95	99	4.16	97	99

In the LP6 study, there was a significant difference in the mean sizes of both males and females between the top and the bottom layers. The mean size of males also differed significantly between top and bottom layers in the LP5 study. Since the layer in which the majority of individuals was located differed between the two trials, it is likely that the gradient in size observed for the trials would be a constant feature of the distribution of the species. Similar distributions have been observed on one occasion in field sampling, in which crude shovel separation of depth layers showed a concentration of juveniles near the surface. Such differences, if present in the field, are usually too slight to observe readily with the naked eye.

IV. SUMMARY

1. Patch size: Patchiness was found at several scales of horizontal distance. Field sampling indicated patchiness over distances of two meters, for which the higher-density areas were about three times as dense as the lower-density areas. Patchiness over distances of 15 cm was also found in field sampling, and confirmed in laboratory studies under controlled conditions. These studies indicated that small-scale patchiness represented aggregates of individuals surrounded by low-density areas. The number per aggregate depended on the overall density of Eohaustorius brevicuspis. Field and laboratory data also suggested aggregates of smaller size, especially three and six centimeters in diameter. These were found under the same conditions as the 15 cm patches.

2. Distribution of patches: One analytical method indicated that patches under laboratory conditions may tend to be uniformly separated. Field sampling data proved inconclusive concerning the distribution of patches.

3. Distribution within patches: Analysis of both field and laboratory data indicated that the distribution of individuals within aggregates tended to be uniform. The chi-squared method indicated that the deviation from random intra-patch distribution was significant at the 99.5% level or greater.

4. Patch formation: The amphipods formed patches in the laboratory in the absence of predators, competing species, or observable environmental heterogeneity.

5. Patch dynamics: Aggregation occurs at all stages of the tidal cycle, although there is vertical migration with the tide. Migration appears

to involve the addition of a vertical component of motion to the normal movement pattern, suggesting that a given aggregate need not disperse when the tide changes.

6. Response to density: In laboratory experiments, higher density at a given depth in the sand was correlated with larger patch areas, more individuals per patch, and more patches. Over the range of "local" densities in the series of laboratory tests, the area of patches and the number of patches doubled, while the number of individuals per patch quadrupled. Large patches were found at low densities, but the largest patches were found under the highest densities. The variation in the number of individuals per patch increased with density.

7. Patch composition: Males and females appear to contribute equally to patches and are not segregated into different patches. Individuals of all sizes are found in patches. There is no aggregation by size although patches at greater depth in the sand have larger individuals than those near the surface.

8. Minimal patch size: Laboratory data indicated that the number of individuals in a patch at typical low densities would be about four. Extrapolated to near-zero densities, the number per patch would be about two.

9. Predation by Cirolana harfordi on Eohaustorius brevicuspis: A simple test of the potential predation rate by Cirolana indicated that under ideal conditions this isopod could account for a large proportion of deaths in E. brevicuspis. The estimate represents a maximal rate of predation.

10. Generality of results: The Driftwood State Park field sampling data indicated that measured attributes of patchiness were very similar to

those of the Lost Creek population. It is likely that the attributes measured for the Lost Creek population are common to other populations of E. brevicuspis on open coast fine sand beaches.

V. DISCUSSION

A. Methods

The methods used in this study for the determination of attributes of patchiness in Eohaustorius brevicuspis have seldom been applied to marine species. Contiguous-quadrat sampling was used in the studies of Jumars (1975), Jackson (1968), Angel and Angel (1967), Jumars et al (1977), and Gage and Coghill (1977) to examine the distribution patterns of organisms over relatively short distances. Other types of systematic sampling have been applied to small-scale distributional patterns by Hogue (1977), Thistle (1978), and Heip (1975, 1976). No published work has been found in which a range of quadrat sizes was used to evaluate the dispersion patterns of benthic species in detail. This is unsurprising, since sampling with cores of different sizes would be prohibitively expensive in most benthic marine environments. A comparison of these methods and their relative effectiveness in the intertidal seems appropriate.

Application of variable core-size methods has some severe limitations. In this study, a maximum of seven sizes were used. A relatively small sample size of ten units per core size, for three strata at two-foot tidal elevation intervals resulted in 210 cores to be taken, preserved, and counted. It was possible to take this number of cores during a single low tide, provided that two or more people were available, all equipment was carefully labelled in advance, and the locations of random positions for sampling predetermined. It was necessary to map out sampling positions in advance to avoid delays in beginning the actual sampling. One person would mark all positions in the sampling area by numbers designating the core size. Each person taking samples would then select a single core

size and sample only in the positions marked for that corer. This method proved invaluable in saving time and reducing confusion.

The large number of cores per sampling restricted the possible sample size per core size, increasing the chance of random errors in estimating indices of dispersion. As a result, interpretation of graphs of these indices depended to some extent on consistency of patterns in the graphs.

The Morisita and Iwao indices were both suitable for detecting the typical scale of patchiness in the field. The two methods were generally in agreement on the probable patch size and similar properties of aggregation appear to have been measured. Uniform distributions within patches were detected by both methods. The distribution of the patches could not be determined by either method. The expected values of regression parameters described by Iwao (1968) do not account for the large negative values of the regression intercept found in this study.

A disadvantage of the Morisita and Iwao methods is that the significance of peaks cannot be tested, although Morisita's index can be tested for deviations from random expectation. Further disadvantages of Morisita's index method are that the ratio of the areas of successive core sizes must be constant, and that the sample size must be constant for all core sizes. These restrictions place some limitations on the ability to resolve the patch size and on the design of the sampling program.

The contiguous-core sampling methods were especially suitable for detecting variations in density over larger distances. Both the sampling procedure and the sorting of cores were rapid and required little advance preparation. Hierarchical analysis of variance as described by Kershaw (1957) is simple, and the detailed Poisson-expectation limits given by Grieg-Smith (1961) can be used to distinguish significant peaks from random

variations. The major disadvantage of this method is that extension of the analysis to the next larger distance scale requires doubling of the sample size, which can be formidable for larger scales. Like the Morisita index method, this method can only be used to examine scales which double in size at each step. Larger scales of patchiness are examined with few degrees of freedom. The method cannot be used to obtain any information on the distribution of individuals within patches or the distribution of patches.

Several methods of analysis were applied to distribution maps of laboratory populations. The detailed pattern of distribution could not be entirely described using these methods. Patches of higher density were outlined using a modified contouring procedure. In some cases, the boundaries of high-density areas could not be adequately resolved with the grid used, and arbitrary objective decision rules were applied. It was possible, at least, to define patches such that the overall distribution pattern was significantly aggregated. The mean density was not suitable for use as a criterion for patch margins. The mean density was often less than one amphipod per unit, because of a large number of zero counts.

Goodall (1974) described the use of random pairs of units at varying distances to obtain independent estimates of the variance between pairs at different distances with intermediate sample sizes at every distance. In the present study, a grid of 192 units was used, and this resulted in a sample size of about 12 pairs per distance between pairs. This sample size was small enough to allow random error to seriously bias results, though much of the random error could be eliminated by dropping the pair with the highest variance for each distance. In this method the position of paired units is not utilized and therefore double-clumped patterns and

the presence of two distinct patch sizes cannot be distinguished. This characteristic is common to most other methods of detecting patch sizes. A final criticism is that manual selection of random pairs is tedious, requiring about two hours per 192-unit grid. The program for computer analysis offered by Goodall (1974) is highly recommended.

The Grieg-Smith hierarchical analysis of variance applied to the same distribution maps was suitable for determining larger patches, but was insensitive to the presence of smaller-area patches. As with the use of the Goodall method, double-clumped patterns of distribution could not be distinguished from variable patch sizes, and the distribution within patches was not examined.

The proposed dispersion chi-squared method has not been rigorously developed, and conclusions based on it are tentative. However, the method at present is very simple in application, and unambiguous information on the distribution of individuals within patches is obtained. Other methods which were used in this study are influenced by several aspects of distribution patterns. The intra-patch dispersion chi-square is influenced only by the error inherent in the sampling procedure, and the arbitrary nature of the procedure for defining patch boundaries.

Both principal components analysis and correlations analysis were applied to the patch composition data. The principal components were somewhat more easily interpreted, while the correlations analysis revealed some aspects of association between variables that were not clear in the former analysis. Both, of course, are dependent on the definitions of patches in the distribution maps.

From the combined analyses of field and laboratory data, it was possible to come to some general conclusions on the approximate size of

patches, the distribution of individuals within patches, and the composition of patches. Inconclusive or contradictory results were obtained when the distribution of patches was analyzed.

B. Patchiness

The primary goal in this study was the characterization of the patchy distribution of Eohaustorius brevicuspis, in order to provide a foundation for detailed examination of the function of aggregation in a uniform environment.

Patches of E. brevicuspis are aggregates of individuals which form in the absence of proximate stimuli such as environmental heterogeneity, predators, competitors, or other macrofauna. The area occupied by a patch varies, but diameters of three, six, and fifteen centimeters occur more often than others. Larger-scale variations in density occur over distances of one to two meters in the field. Within small patches typical density is about one individual per square centimeter.

Individuals of either sex or of any size are found in any patch. No age or size class segregates into separate patches, although patches near the surface have smaller individuals than those deeper in the sand.

The distribution of individuals within patches tends to be uniform. In the laboratory experiment with the highest density, the high-density areas were very uniformly occupied. This dispersion pattern could be explained by a model of patch formation which includes attraction between individuals at low density, and repulsion at sufficiently high density. Individuals would tend to aggregate, but patches would be internally uniform due to the balancing effects of repulsion. Since intra-patch densities are uniform over a range of overall densities, the threshold

density between the attraction and repulsion of individuals must vary with density. If the threshold were fixed, aggregation would be succeeded by uniform distributions at high densities.

The distribution pattern of patches may be uniform, although the evidence is inconclusive. Iwao (1972) suggested that uniformity in patch distribution may be indicated if patches are randomly distributed but do not overlap. This would be expected if there was a maximal patch size which was optimal for a given overall density. In connection with this, laboratory data indicated that at higher overall density, patches were more numerous, but the number of individuals per patch increased faster than the area of patches. This would seem to indicate that the maintenance of a maximal patch area was more important than the maintenance of the density within patches.

Aggregation could have beneficial effects through environmental modification. The circulation of water through the sand may be increased by aggregation. Several feeding mechanisms are possible for a filter-feeding amphipod. Currents may be created which bring particles to the mouthparts from behind or in front of the body. If feeding occurs while travelling through the sand, forward-directed currents may loosen the sand and make burrowing easier. A dense aggregate of individuals could increase this effect by feeding simultaneously. Water circulation could also be increased by simultaneous feeding if feeding occurs while stationary. In either case, some limitation on patch size, and uniform spacing within patches, would be expected for maximal efficiency. Various models of the relationship of aggregation to feeding are possible. For example, if feeding occurs while stationary, aggregates might be transitory phenomena. Chance encounters could induce individuals to stop traveling and begin

feeding. Additional individuals could be attracted by chemical gradients resulting from food particle breakage, or by water flow patterns. While these hypothesized interactions are oversimplified, it is clear that feeding behavior would be of fundamental importance in understanding the causes and effects of aggregation.

In the laboratory, vertical migration with the tide appeared to occur without obvious stimuli. The purpose of such an endogenous rhythm may be to reduce the risks of living in a high-energy environment. Downward migration during the falling tide reduces the chance of being washed into the surf, which would increase the chance of predation and exposure to turbulence. During low tide remaining at depth also removes E. brevicuspis from surface heating or cooling while the beach sands are exposed. On return to the surface, a fresh supply of food would be available. Since amphipods this small appear to be immobilized at low tide, they probably do not feed during this interval.

Judging from laboratory experiments, the gradient of size of individuals with depth in the sand appears to be constant through the tidal cycle. Bosworth (1976) observed that the period of maximum release of juveniles coincided with the time of winter storms. He hypothesized that this may increase dispersal of juveniles by timing their release with maximum wave disturbance of the sand. The probability of dispersal would be increased if the juveniles remained near the surface of the sand. It would be difficult to account for the origin of such a trait without resort to group selection arguments, since a direct consequence of wave dispersal is increased mortality.

It is unlikely that the size gradient can be attributed to a gradient in sediment size, which could limit juveniles to finer sand at the surface.

The laboratory experiments utilized thoroughly mixed sand, and the open coast beach sand is well mixed and typically well-sorted (Bosworth, 1976).

Adults probably burrow more rapidly than juveniles. If all individuals started from near the sand surface, adults would burrow further down than juveniles during downward tidal migration. A size gradient would result. Juveniles may be released from the marsupium at high tide, near the surface. This would account for the initial near-surface distribution required for this hypothetical mechanism.

Aggregation, though not a proximate response to predation, may be instrumental in decreasing the risk of predation by means similar to those proposed for schooling fish or bird flocks. Again, it is difficult to explain the evolution of aggregation in this species for this purpose without resorting to group or kin selection. It does not seem likely that aggregates are groups of related members. The migration rate between patches is probably too high to make group selection possible.

Eohaustorius brevicuspis has a small ambit, in that the scale of patchiness is considerably less than observable scales of environmental heterogeneity. The species is therefore coarse-grained. Jumars et al (1977) found that Dogielinotus loquax, an amphipod found in the same elevation range as E. brevicuspis, is probably aggregated at scales similar to the ambit of individuals. Jumars (1975) has proposed that communities in which most species have small ambits are more likely to be grain-specialized, and therefore are potentially more diverse than communities of fine-grained species. Although the diversity of the open coast sand beach communities is low relative to, for example, rocky shores, it is possible that it is higher than it would be if species were not aggregated.

An examination of the distribution pattern of other sand-beach macrofauna would determine whether the majority of species were small-ambit, coarse-grained species.

Information of the type presented in this study on the other major species of the sand beach community would be necessary to generalize about the consequences and function of aggregation in uniform environments. Detailed information on the dispersion patterns of species would permit clearly defined hypotheses concerning their function and influence at the community level as well. Topics suitable for further investigation which have already been mentioned are the effects of aggregation on the predation rate, the relationship of aggregation to feeding, and the relative diversity of uniform environment in which aggregation is present or absent. Others might include the effects of aggregation of macrofauna on meiofaunal species and the converse, and the effects of species-specific aggregation on competition between sympatric congeners such as the Eohaustorius group.

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APPENDIX : FIGURES

Figure 1. Distribution maps of contiguous-core arrays in the NE sample, Lost Creek beach, 11/20-21/76.

1	0	4	1	1
4	1	1	0	0
5	2	1	0	0
2	0	3	2	2
1	2	2	2	2
3	5	1	1	0

NE - 1 total = 49

1	1	3	3	0
0	2	0	1	0
1	3	2	2	1
0	3	1	0	1
1	1	0	1	0
0	1	1	1	0

NE - 2 total = 31

3	2	5	5	2
0	4	1	1	4
0	3	0	2	0
1	0	2	2	2
0	0	1	0	1
0	0	0	3	2

NE - 3 total = 46

1	0	1	3	2
1	1	0	0	1
2	1	0	2	4
0	1	2	1	1
0	0	3	6	4
3	2	3	3	2

NE - 4 total = 53

4	3	0	3	3
3	4	2	3	0
0	0	0	0	1
2	4	1	0	1
1	0	2	3	0
1	0	0	4	5

NE - 5 total = 48

Figure 1

Figure 2. Graph of composite Morisita's I_δ index versus block size for NE sample, Lost Creek beach, 11/20-21/76.

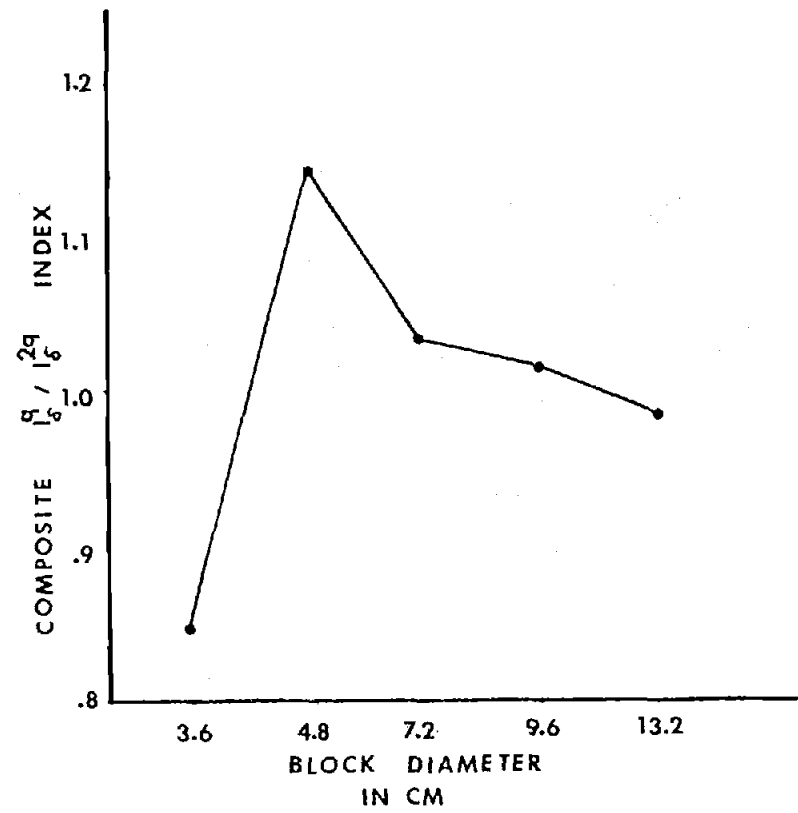


Figure 2

Figure 3. Plot of per-core density versus the position of core for LN1 sample, Lost Creek beach, 11/20/76.

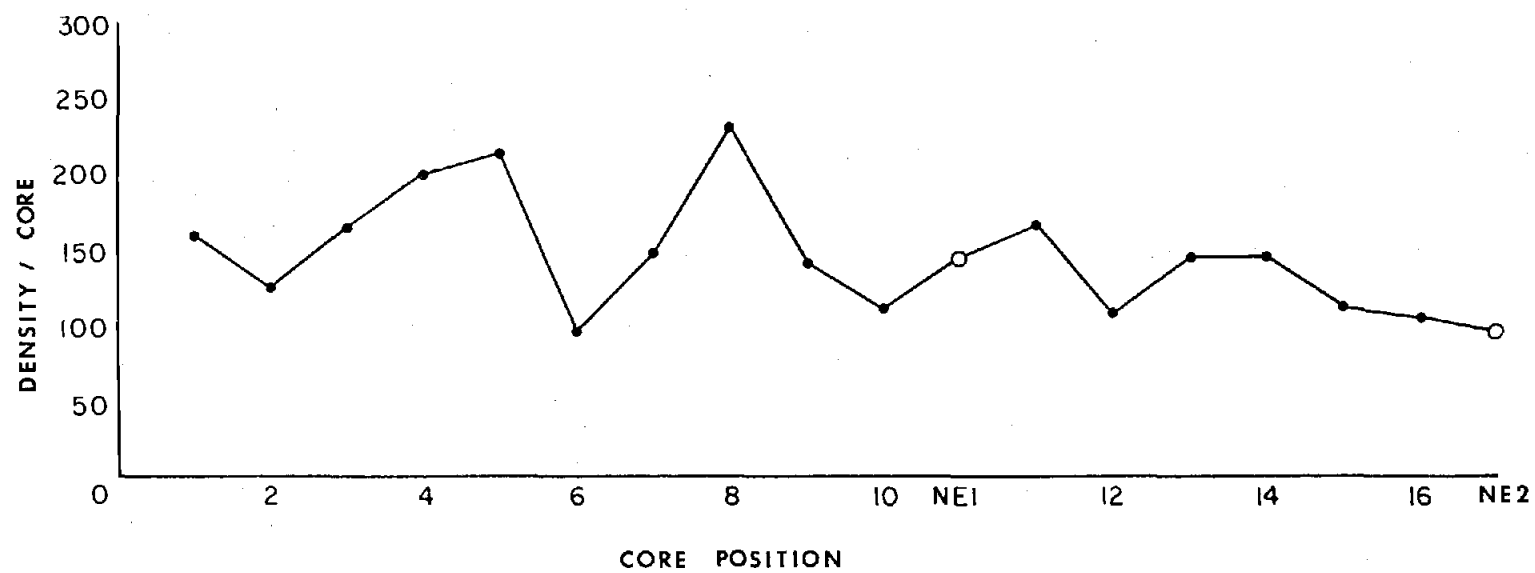


FIGURE 3

Figure 4. Plot of per-core density versus the position of core for LN2 sample, Lost Creek beach, 12/4/76.

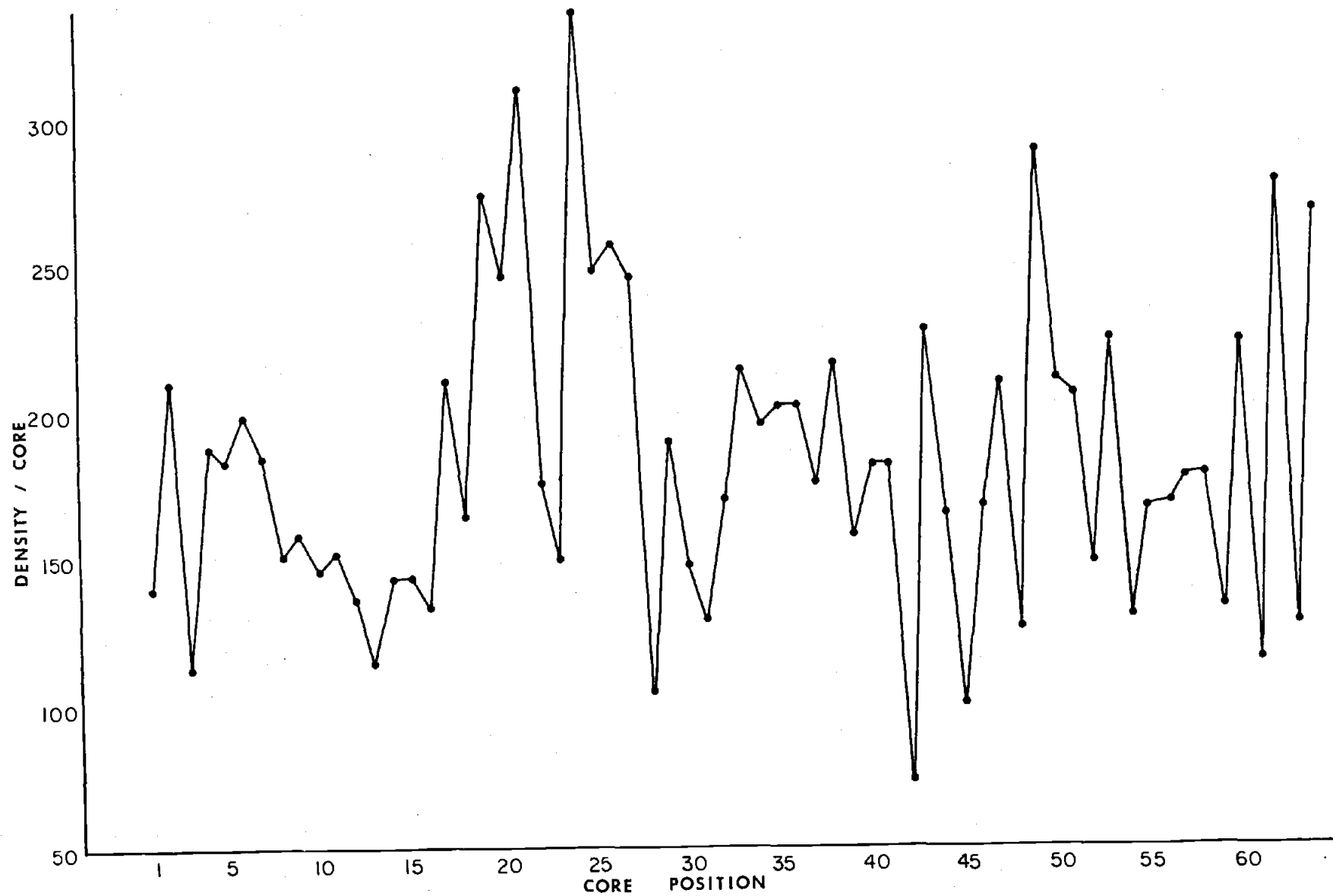


FIGURE 4

Figure 5. Graphs of Morisita's I_{δ} index, and Iwao's ρ index versus core size for PSl samples, Lost Creek beach, 1/29/77. Dashed line is Morisita's index.

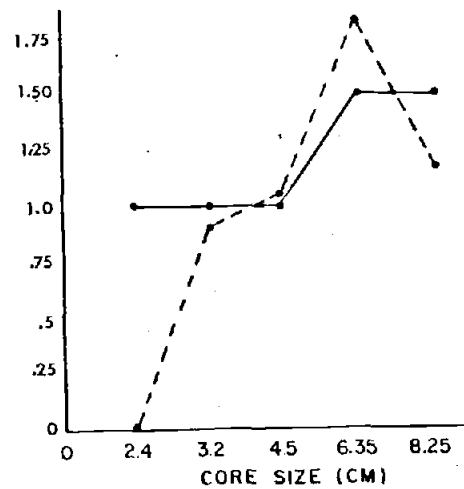
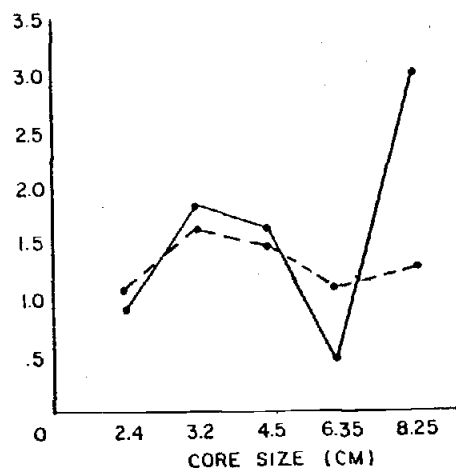
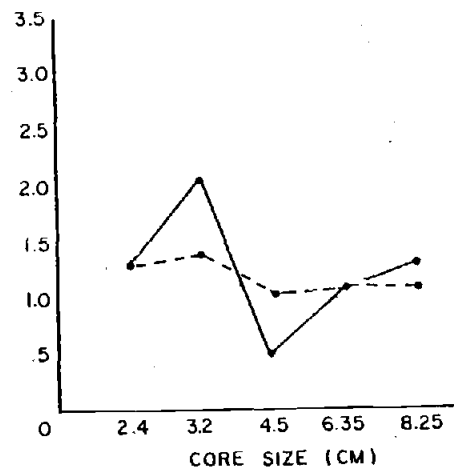
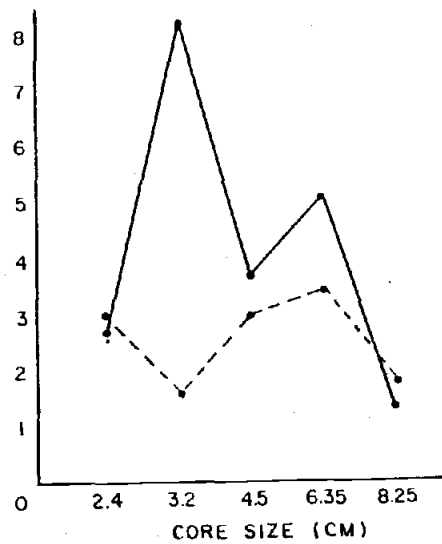


Figure 6. Graph of Morisita's I_δ index and Iwao's ρ index versus core size for PS2 samples, Lost Creek beach, 6/5-6/77. Dashed line is Morisita's index.

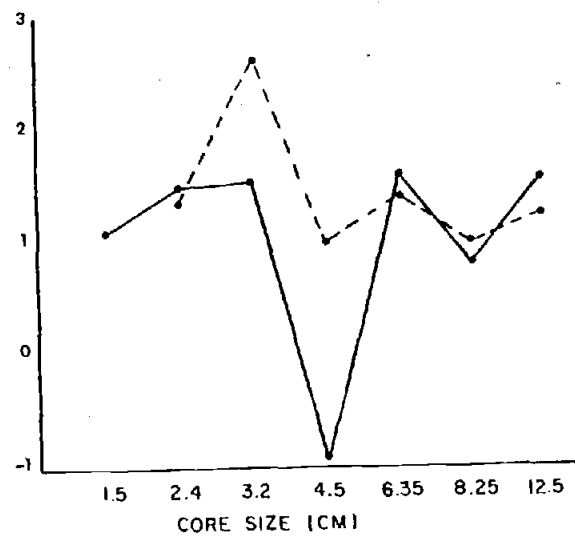
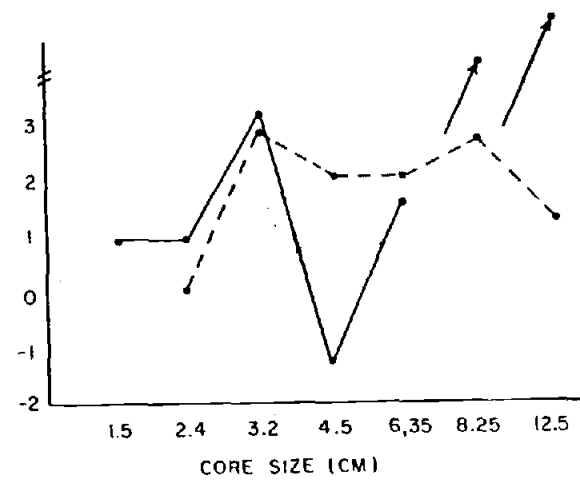
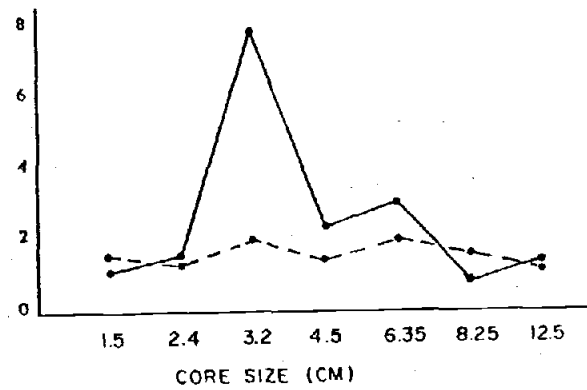


Figure 7. Graph of Morisita's I_g index and Iwao's ρ index versus core size for PS3 samples, Lost Creek beach, 12/22/77. Dashed line is Morisita's index.

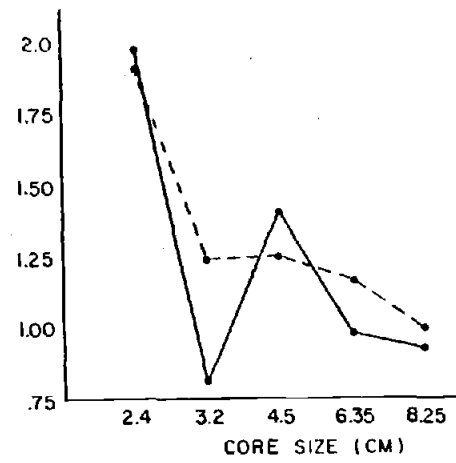


Figure 8. Graph of Morisita's I_δ index and Iwao's ρ index versus core size for PS4 samples, Driftwood State Park, 7/11/78. Dashed line is Morisita's index.

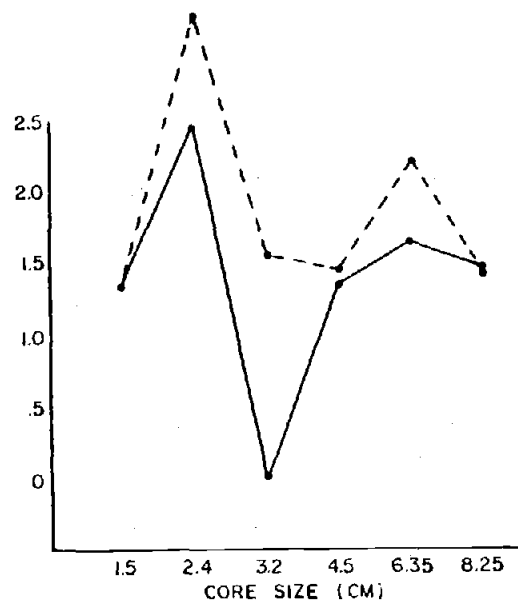


Figure 9. Graphs of mean square to mean density ratio versus block size for LP3 trial, 8/15-18/77.

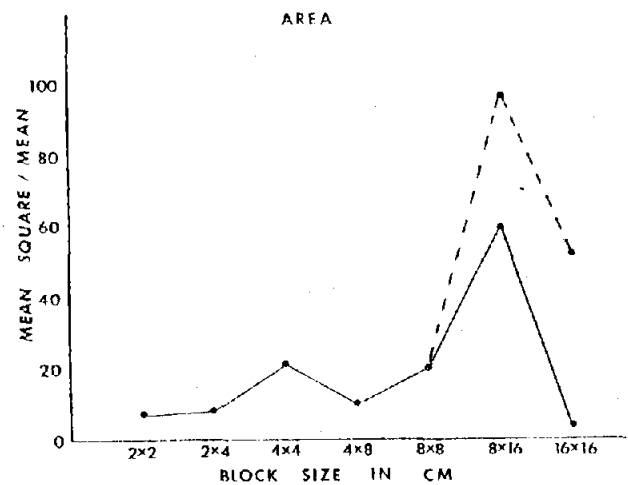
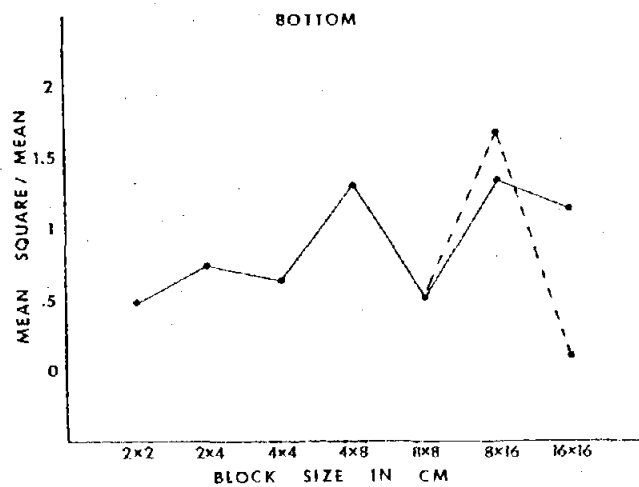
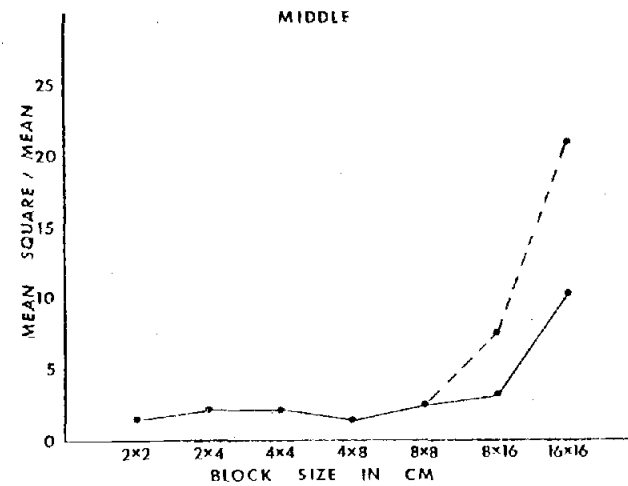
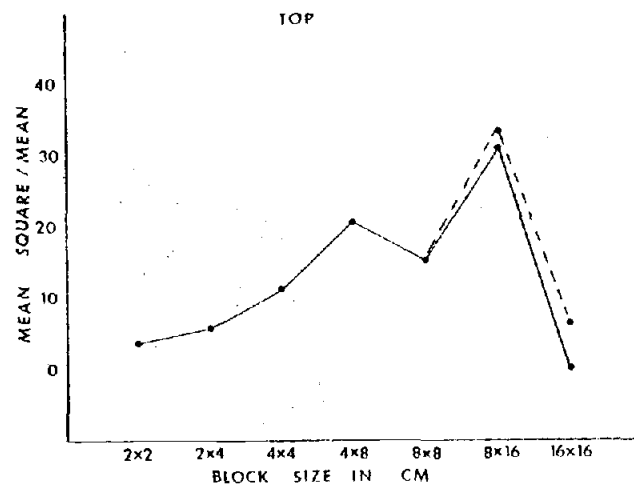


Figure 9

Figure 10. Graph of mean square to mean density ratio versus block size for LP4, 8/21-24/77.

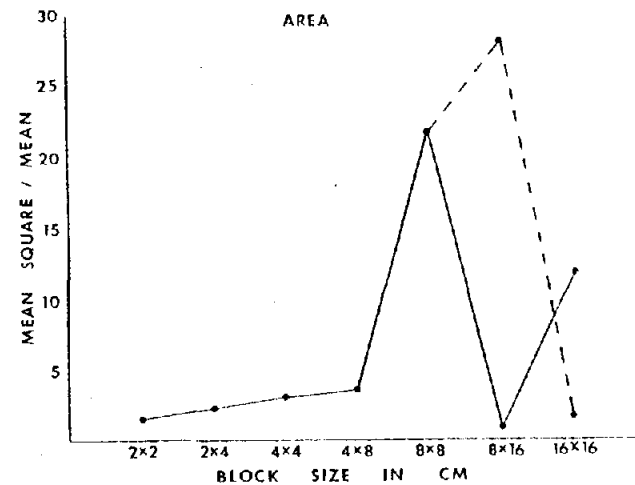
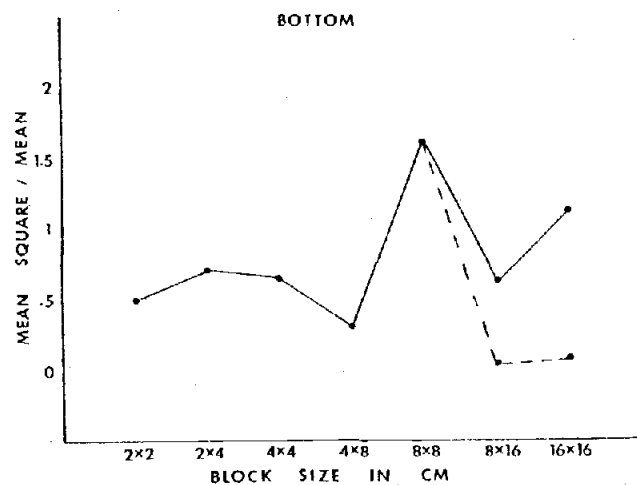
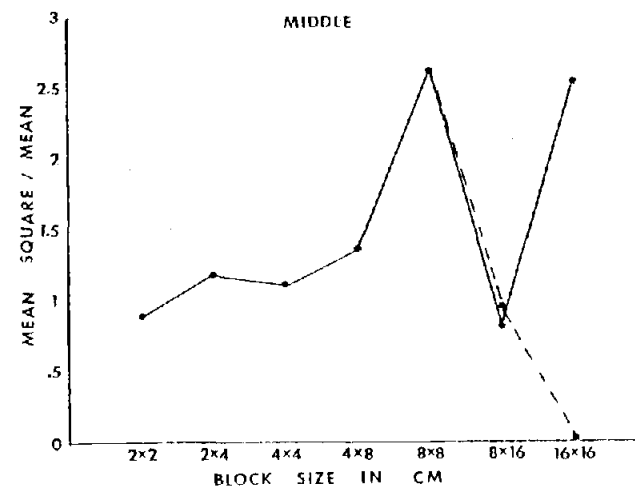
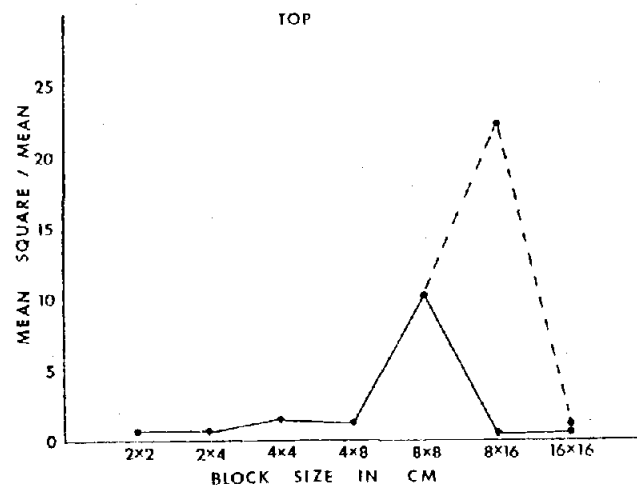


Figure 10

Figure 11. Graph of mean square to mean density ratio versus block size for LP5, 8/31-9/3/77.

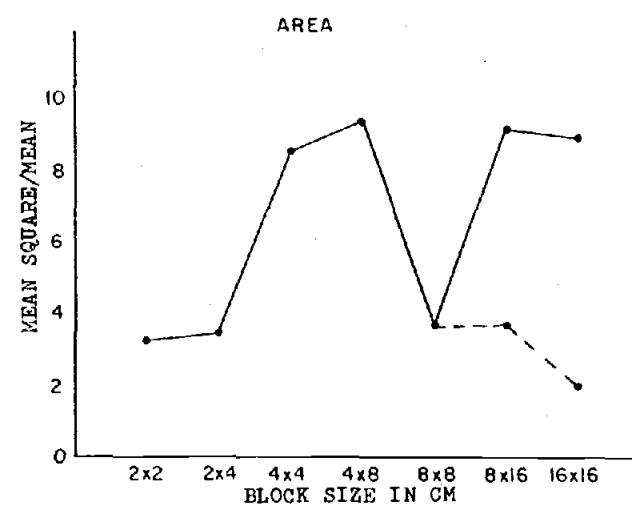
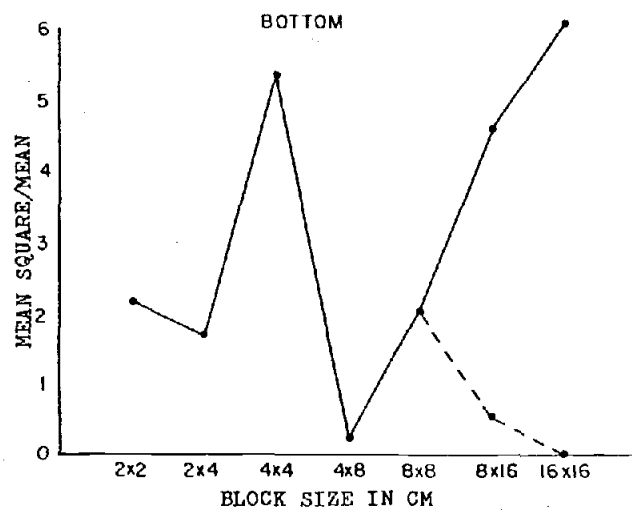
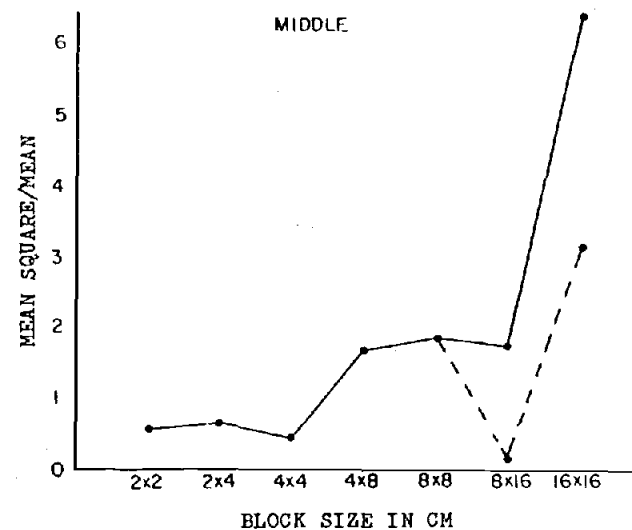
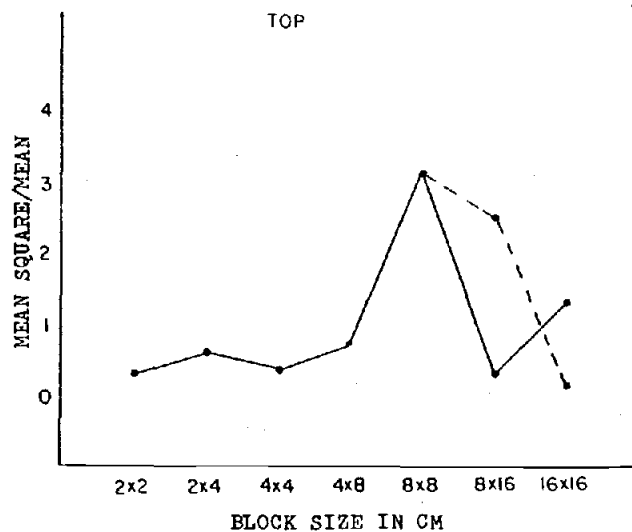


Figure 11

Figure 12. Graph of mean square to mean density ratio versus block size for LP6, 10/16-19/77.

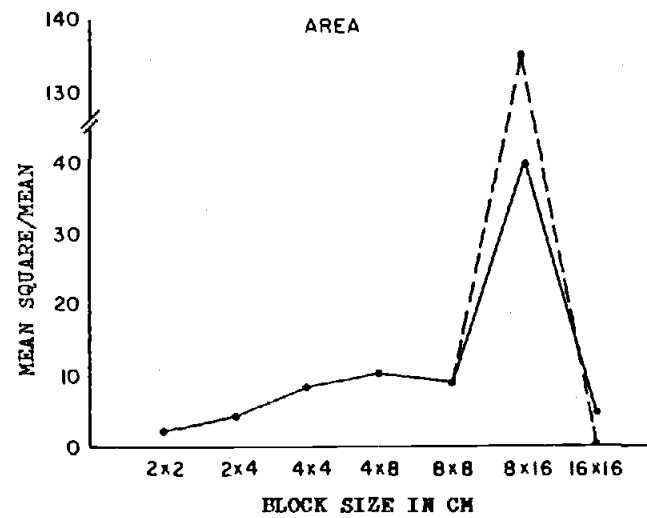
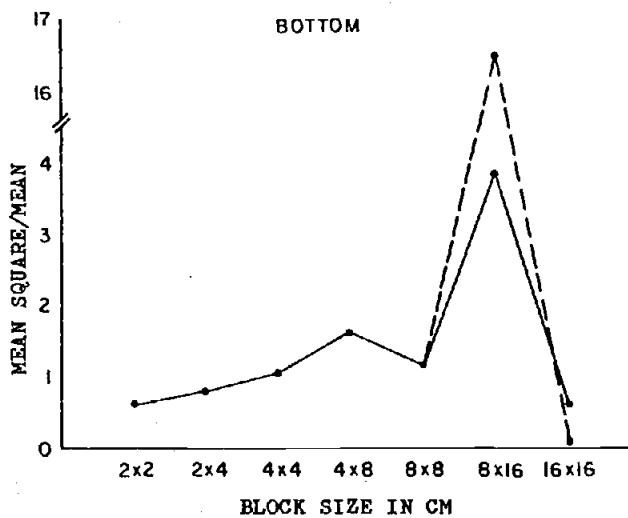
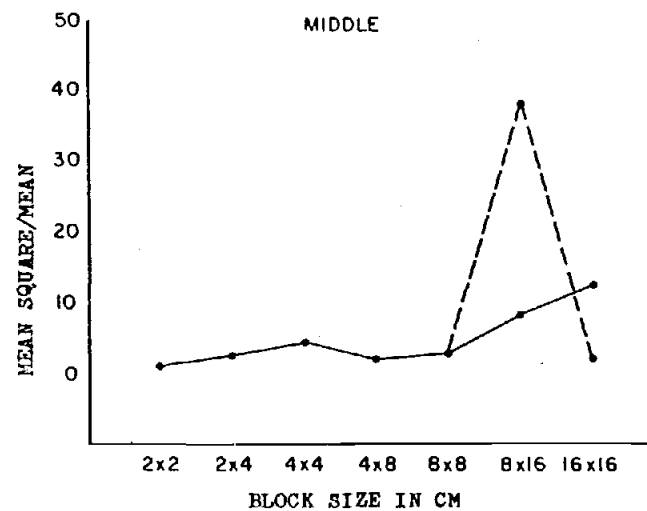
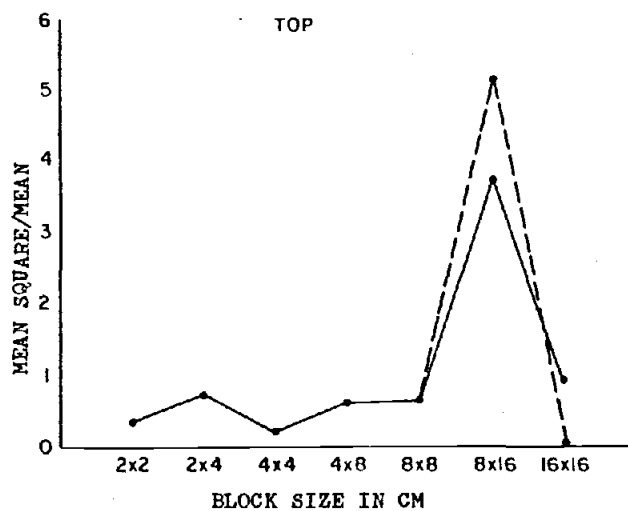


Figure 12

Figure 13. Graph of pooled variance between paired units versus the distance between pairs, for LP3, 8/15-18/77. Dashed line is adjusted variances.

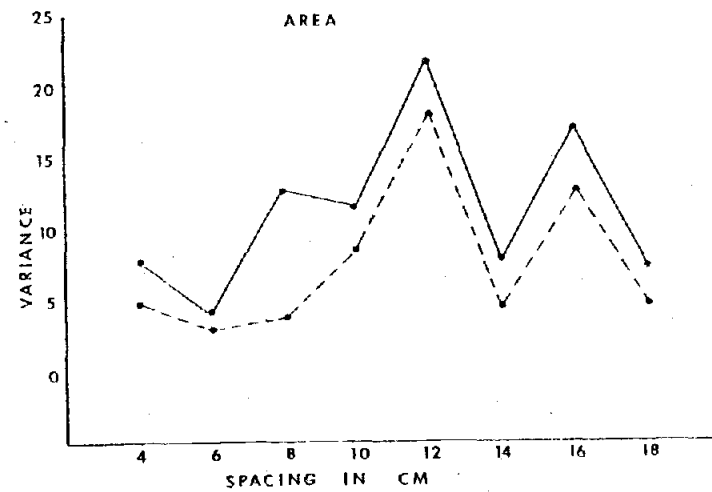
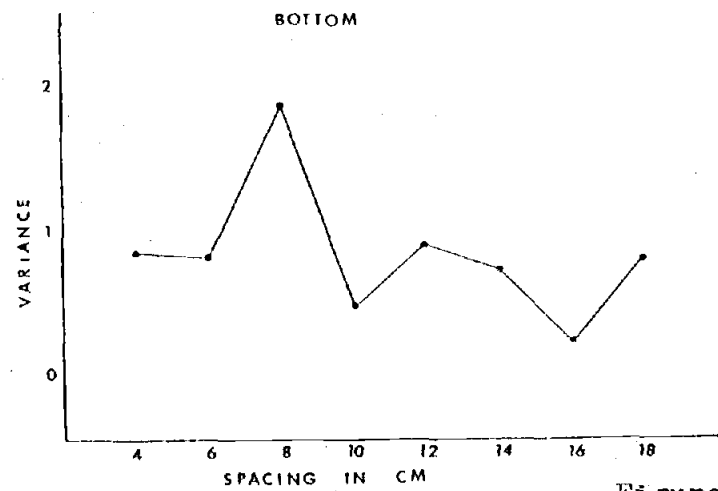
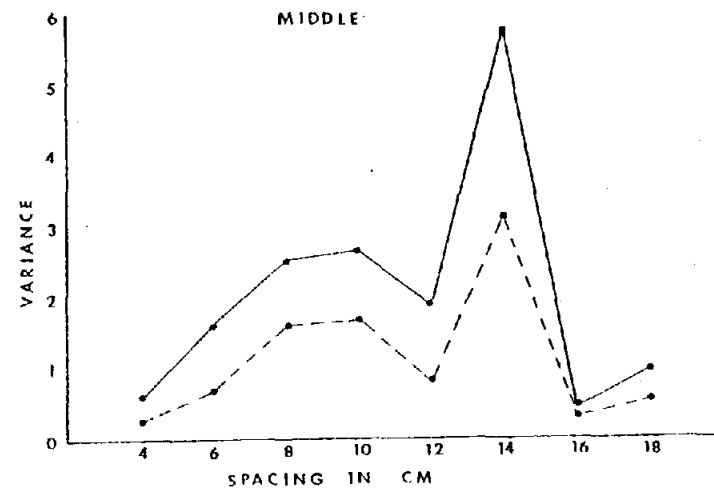
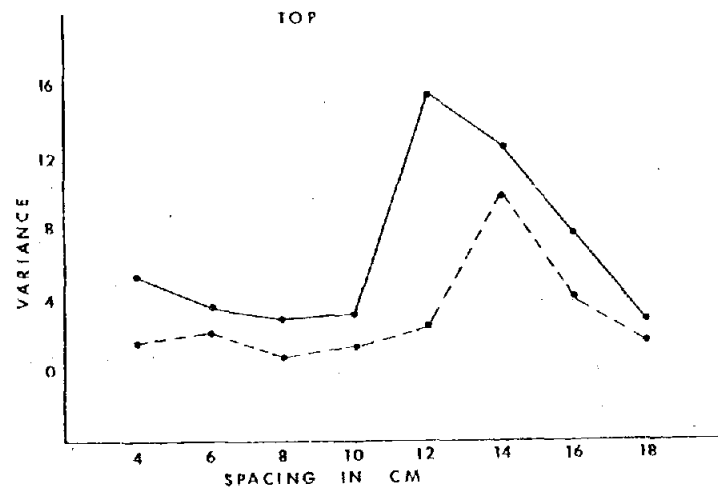


Figure 13

Figure 14. Graph of pooled variance between paired units versus the distance between pairs for LP4, 8/21-24/77. Dashed line is adjusted variance.

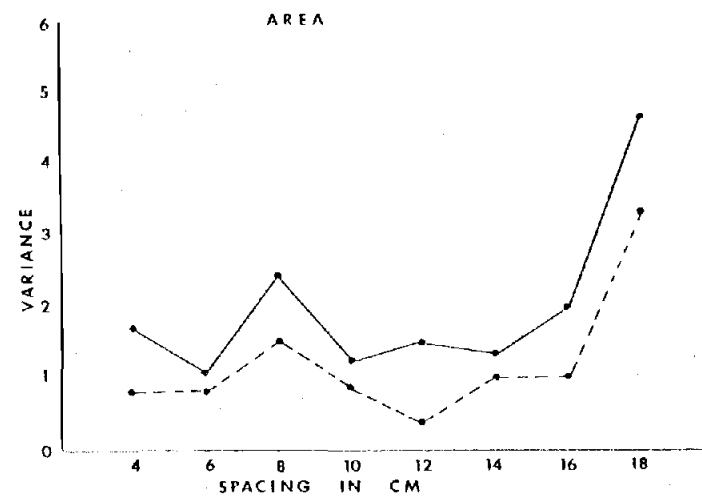
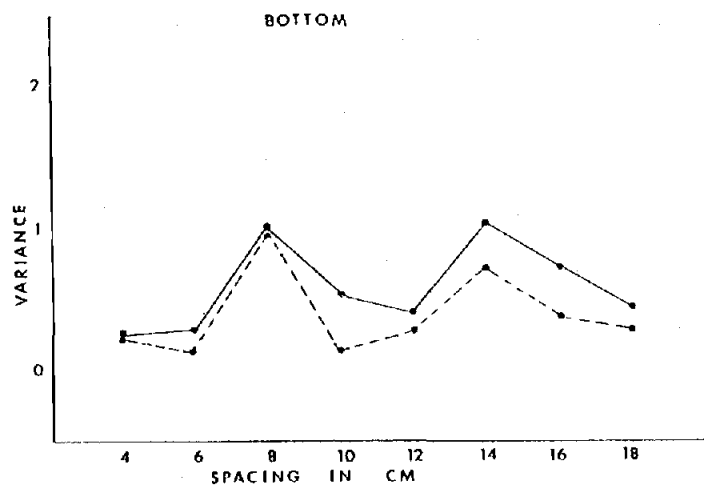
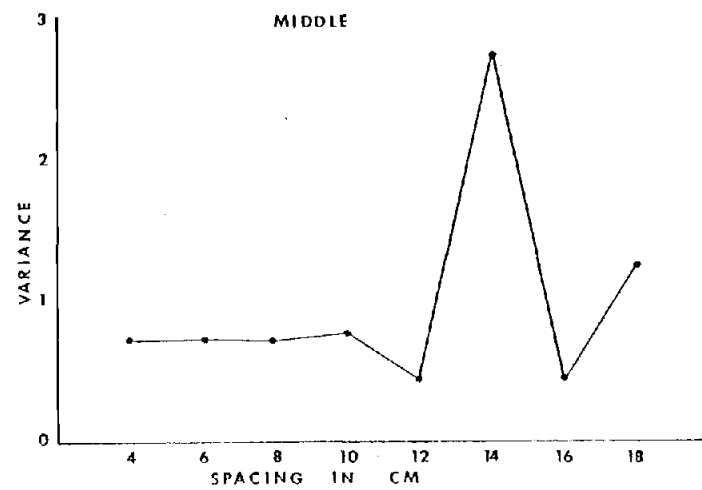
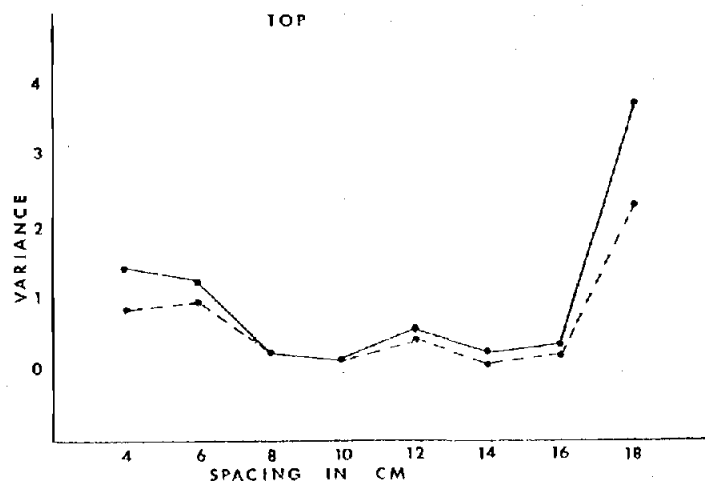


Figure 14

Figure 15. Graph of pooled variance between paired units versus the distance between pairs, for LP5, 8/31-9/3/77. Dashed line is adjusted variance.

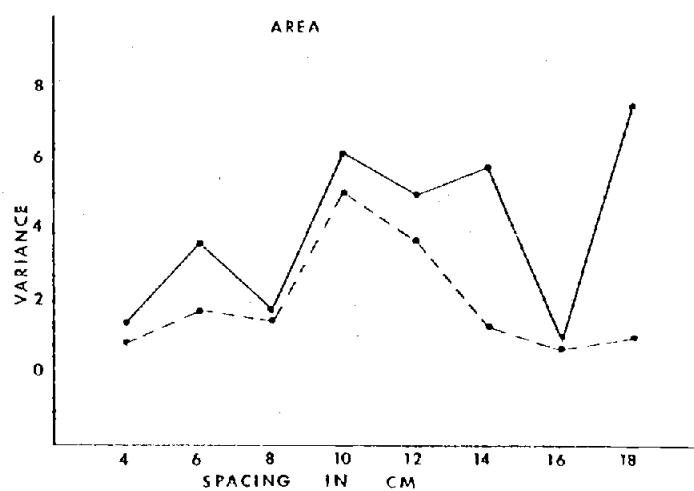
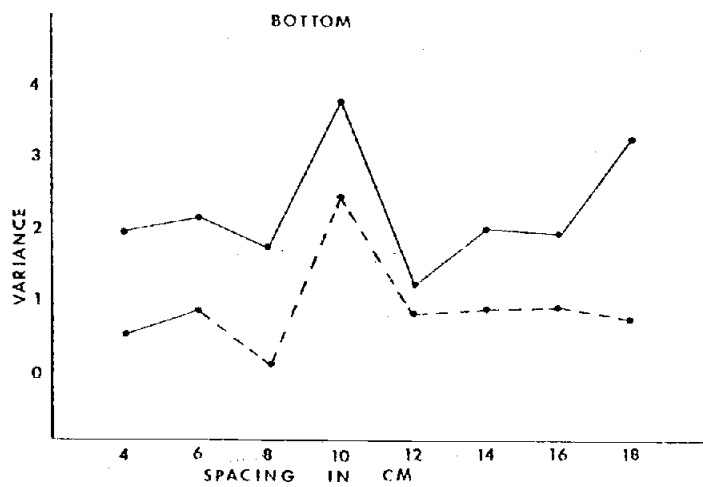
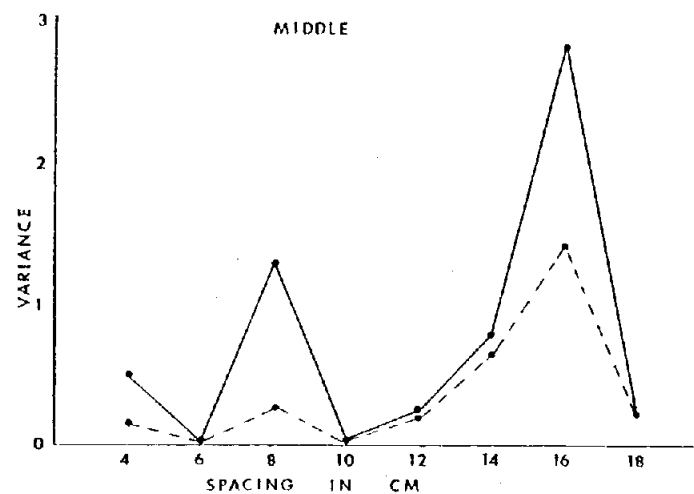
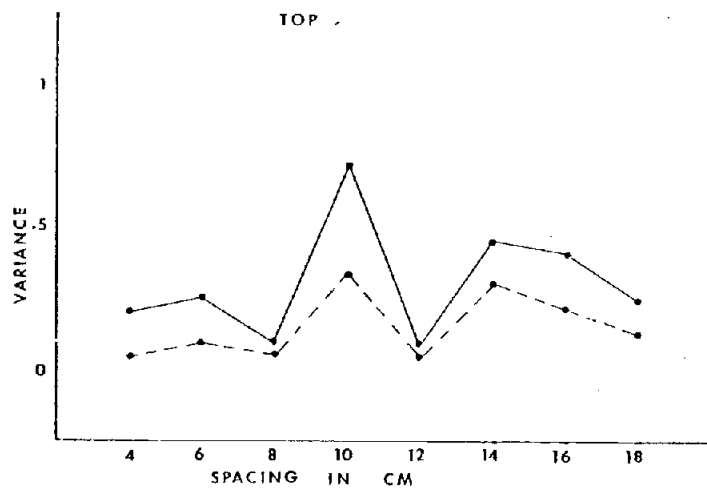


Figure 15

Figure 16. Graph of pooled variance between paired units versus distance between pairs, for LP6, 10/16-19/77. Dashed line is adjusted variance.

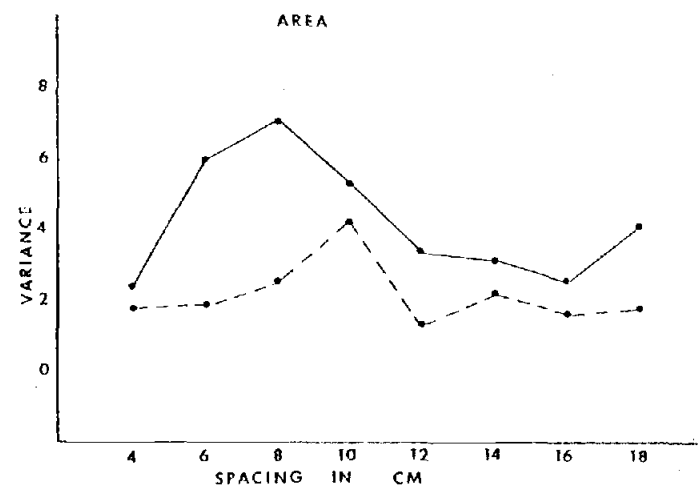
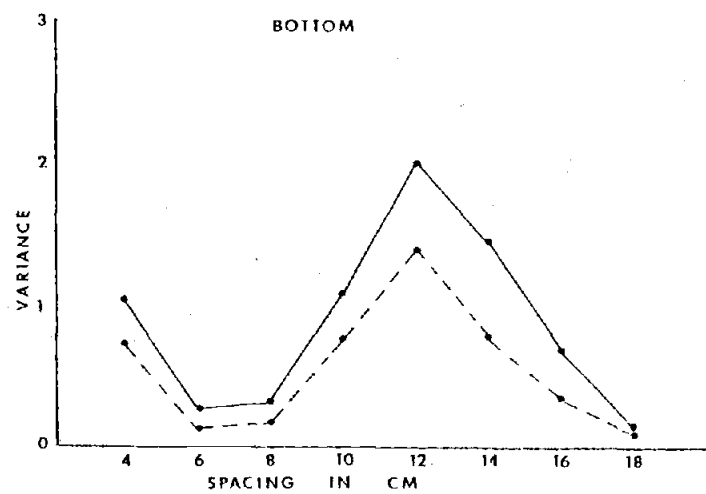
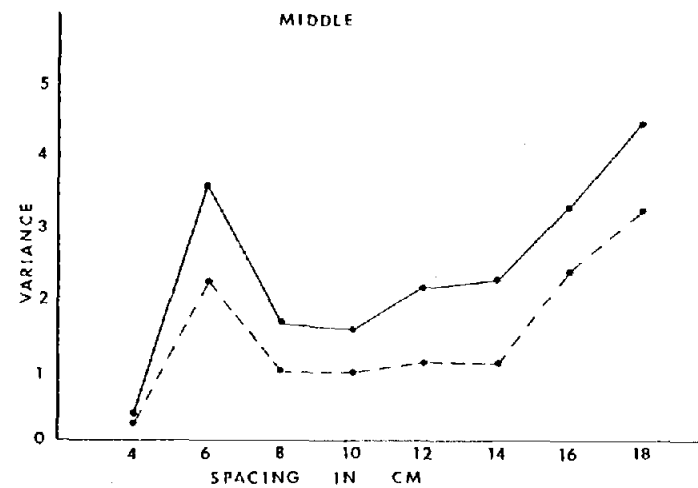
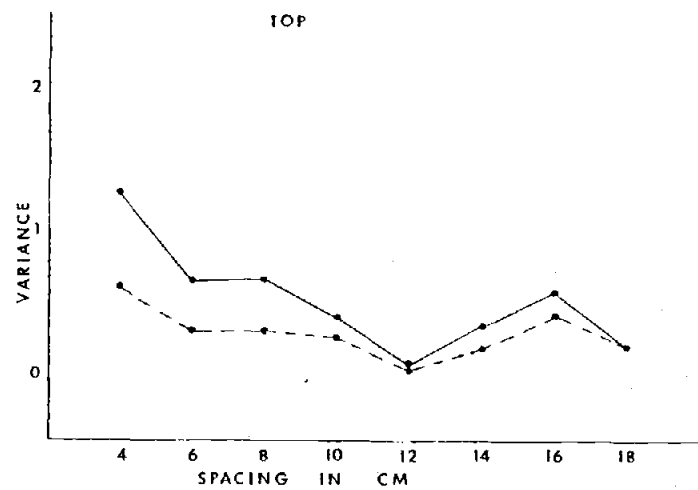


Figure 16

Figure 17. Graph of pooled variance between paired units versus distance between pairs, for LP7, 6/15-18/78. Dashed line is adjusted variance.

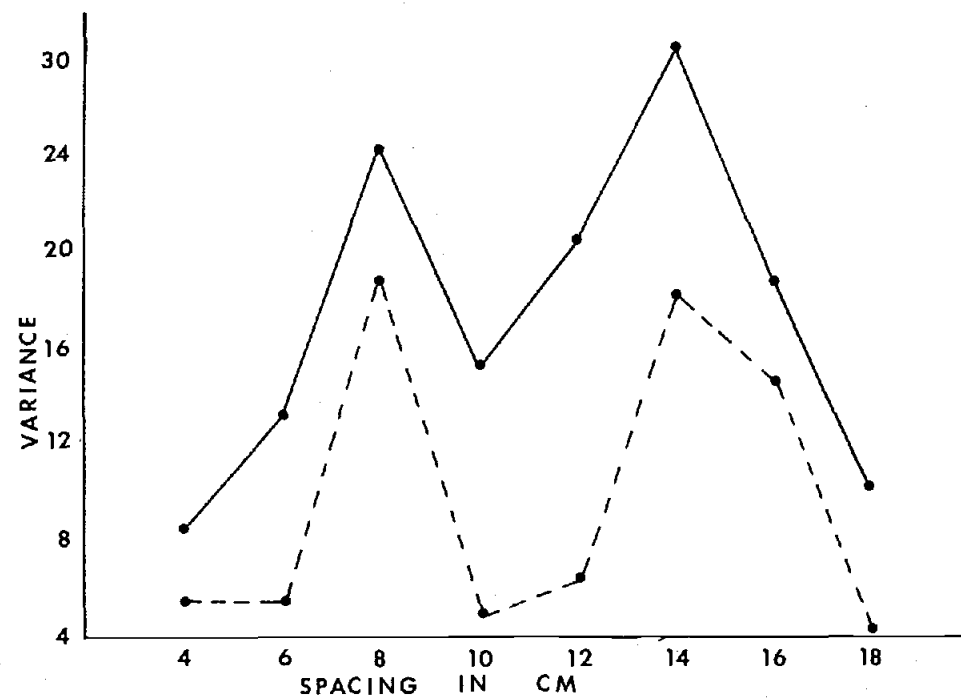


Figure 17

Figure 18. Distribution map by layers for LP3, 8/15/18/77, showing patches outlined by decision rules.

TOP.

0	4	1	3	1	0	0	0	0	0	1	2	0	1	0	0
0	0	0	2	1	0	3	0	2	4	0	1	2	0	0	2
1	3	0	0	0	0	0	1	2	2	1	2	17	10	0	4
3	2	1	1	8	2	3	2	1	2	1	7	5	7	0	0
1	0	2	3	6	1	3	7	4	2	2	2	6	4	0	1
3	2	2	0	0	5	5	7	1	0	0	2	3	1	3	2
4	1	2	5	1	2	1	8	3	1	2	0	0	0	4	2
1	0	5	5	0	10	5	8	6	9	6	1	0	0	1	2
0	1	0	1	4	4	4	5	3	1	0	8	0	1	1	0
0	0	1	0	0	0	9	3	6	11	7	1	0	0	0	2
0	0	2	0	0	0	1	1	0	0	0	0	0	0	2	1
2	2	0	0	1	0	1	0	1	1	0	0	0	1	4	0

BOTTOM

0	0	0	0	0	0	0	0	0	0	5	2	0	0	0	3	0
0	0	0	0	0	0	0	2	0	0	1	1	4	3	0	0	0
0	0	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0
2	0	0	0	0	0	1	0	0	0	0	0	0	0	2	1	0
0	0	0	0	0	0	0	1	3	3	1	0	0	0	0	2	0
2	2	0	0	0	0	0	0	4	1	0	0	0	0	0	0	1
0	2	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0

MIDDLE

6	2	2	1	0	4	0	0	0	0	2	2	1	1	2	0
0	0	0	0	1	1	1	0	0	3	5	2	1	1	1	2
1	0	0	1	0	1	0	3	1	0	2	1	1	1	1	0
4	1	1	0	1	2	5	1	0	0	0	0	2	2	1	0
1	1	0	0	2	0	0	2	0	1	0	0	1	1	0	1
3	5	3	3	0	1	0	3	0	0	1	0	0	0	0	0
1	3	2	9	5	0	0	1	3	0	0	0	0	0	0	0
1	2	1	0	0	2	0	0	0	3	3	1	3	1	0	0
0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0
1	4	2	0	1	0	0	1	0	0	0	0	0	0	1	0
0	0	0	0	0	0	1	4	0	0	0	0	1	0	0	1
0	1	0	0	0	0	5	0	0	0	1	0	0	0	0	0

AREA

6	6	3	4	1	4	0	0	0	5	5	4	1	2	5	0
0	0	0	2	2	1	6	0	2	8	6	7	6	1	1	4
2	3	0	1	0	4	0	4	3	3	3	3	18	11	1	4
9	3	2	1	9	4	9	3	1	2	1	7	9	10	1	0
2	1	2	3	8	1	3	10	7	6	4	2	7	5	2	2
8	9	5	3	0	6	5	14	2	0	1	2	3	1	3	3
5	6	6	15	6	2	1	9	7	1	2	0	0	0	4	2
2	2	6	5	1	12	5	8	6	12	9	2	3	1	1	2
0	1	0	1	5	4	7	5	3	1	0	8	0	1	1	0
1	4	3	0	1	0	9	4	6	11	7	1	0	0	1	2
0	0	2	0	0	0	2	6	0	1	0	0	1	0	2	2
2	3	0	0	1	0	6	2	1	1	2	0	0	1	4	0

FIGURE 18

Figure 19. Distribution map by layers for LP4, 8/21-24/77, showing patches outlined by decision rules.

TOP

0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	1	0	1	0	0	0	0	1	1	1	1	0	0	1	0
0	1	0	1	1	0	0	0	0	1	1	2	1	0	0	0
0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	1	2	3	1	0	0	0
0	0	2	1	0	1	4	2	3	2	1	1	2	2	0	0
0	0	0	1	2	3	1	4	1	0	2	3	0	1	3	0
0	0	0	0	1	4	4	1	1	2	4	5	1	0	0	1
1	0	0	0	3	3	6	1	3	0	7	3	0	1	1	0

MIDDLE

0	0	0	1	1	0	2	3	3	0	3	2	2	3	0	0
1	0	1	0	0	1	1	1	1	1	1	0	0	0	0	0
0	0	0	0	1	0	2	1	1	3	1	1	2	0	2	0
0	1	0	1	3	0	2	3	1	2	0	1	3	1	3	0
0	0	0	0	0	0	0	2	0	1	1	1	2	0	0	1
0	1	0	0	0	1	3	2	0	1	0	0	2	2	1	1
0	0	3	0	2	2	2	0	2	1	2	0	1	0	0	0
0	0	0	1	0	1	1	0	0	1	4	0	1	1	0	2
0	0	0	0	0	1	1	1	0	0	1	3	2	0	4	1
0	0	1	1	1	1	1	0	1	1	0	0	2	0	1	0
0	1	1	0	4	0	1	1	0	1	1	0	1	1	1	1
0	1	1	5	0	1	2	5	0	2	0	0	0	0	0	0

BOTTOM

0	0	0	0	2	0	0	0	0	1	0	1	1	0	1	1
0	0	0	0	1	2	0	0	0	0	0	2	1	0	1	
0	0	0	0	0	1	0	0	0	0	0	1	1	0	2	
0	0	1	0	0	0	2	1	0	1	2	4	0	0	0	2
0	0	1	0	0	0	0	2	1	0	0	2	1	2	2	0
0	0	0	0	1	2	2	1	1	0	0	1	1	0	0	0
0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	1	1	0	0	0	1	0	0	2	0
0	0	1	0	0	0	3	1	0	0	0	3	1	0	1	0
0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1
0	0	0	1	0	0	1	1	0	0	1	0	0	1	1	1
0	0	0	0	4	0	0	0	0	1	0	1	0	1	0	0

AREA

0	0	0	1	3	0	2	3	3	1	3	3	3	3	1	1
1	0	1	1	1	3	1	1	1	1	1	0	2	1	0	1
0	0	0	0	1	0	3	1	1	3	1	2	3	1	2	2
0	2	1	2	3	0	4	4	2	4	2	6	3	1	4	2
0	1	1	1	1	0	0	4	1	2	2	5	4	2	2	1
0	1	0	1	1	3	5	3	1	1	1	1	3	2	1	1
0	0	3	0	2	2	4	1	2	1	2	0	1	0	0	0
0	0	0	2	1	1	2	1	0	2	6	4	2	1	2	2
0	0	3	1	0	2	8	4	3	2	2	7	5	2	5	1
0	0	1	2	4	4	2	4	3	1	2	3	3	1	5	1
0	1	1	1	5	4	6	3	1	3	6	5	1	3	3	2
1	1	1	5	7	4	8	6	3	3	7	4	0	2	1	0

FIGURE 19

Figure 20. Distribution map by layers by LP5, 8/31-9/3/77, showing patches outlined by decision rules.

TOP

0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	2	0	0	1	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
2	2	0	0	0	0	1	1	0	0	0	1	0	0	2
0	0	0	0	1	3	1	1	0	0	0	1	0	0	0
0	1	2	0	0	1	0	0	0	0	0	0	0	0	0
0	1	2	1	0	0	1	0	2	0	0	0	0	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	0	1	2
0	1	0	0	0	0	0	0	0	0	0	0	1	0	2
1	0	4	0	0	0	0	0	0	0	1	0	0	1	2

MIDDLE

0	0	0	0	0	0	0	1	0	1	0	1	0	0	1
1	0	0	0	1	1	0	0	0	0	0	1	0	0	1
0	0	0	0	0	0	0	0	0	0	0	2	1	3	4
1	0	0	0	0	0	0	0	0	0	0	1	2	2	3
1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
0	0	1	0	0	3	0	0	1	0	2	3	0	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	1	0	0	0	2	0
0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	1	0	1	0	0	0	0	0	0	0	1	6	5

BOTTOM

1	2	0	0	0	0	1	0	0	3	4	3	2	1	0
1	1	0	1	1	1	1	0	0	0	3	0	1	1	0
0	1	2	0	0	0	1	1	0	0	2	2	2	5	9
0	1	2	0	0	0	1	1	0	0	4	1	1	1	2
0	1	2	0	0	0	2	0	0	0	0	0	2	1	0
0	0	0	0	0	0	1	2	0	0	0	0	2	2	0
2	1	0	1	1	0	7	5	3	1	3	1	0	1	1
6	2	1	0	0	0	1	0	0	0	0	1	0	1	1
3	0	1	1	0	1	0	1	0	0	0	0	0	0	0
8	0	0	0	0	0	0	1	2	0	1	1	0	0	1
1	0	1	0	0	2	2	0	0	3	0	0	5	1	2
0	1	1	0	0	0	0	3	2	2	5	1	2	1	0

AREA

1	2	0	0	0	0	1	1	0	4	4	4	2	1	1
2	3	0	1	3	3	1	0	0	0	0	4	0	1	2
0	1	2	0	0	0	1	1	0	1	2	4	3	10	13
3	3	2	0	0	0	2	2	0	0	5	4	3	3	7
1	1	2	0	1	3	3	1	0	0	0	2	1	2	1
0	1	0	0	0	0	2	2	0	1	0	1	2	2	0
2	2	3	2	1	3	8	5	6	1	5	4	0	2	2
6	2	2	0	0	0	1	1	0	0	0	0	1	0	1
3	0	1	1	0	1	0	1	0	0	0	1	0	0	0
8	0	0	0	0	1	0	1	2	1	2	1	0	2	2
1	1	1	0	0	2	2	0	0	3	0	0	6	2	2
1	1	6	0	1	0	0	3	2	2	6	1	3	8	7

FIGURE 20

Figure 21. Distribution map by layers for LP6, 10/16-19/77, showing patches outlined by decision rules.

TOP

2	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0
0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	1	1	0	2	0	0	0	0	0
1	0	0	1	0	0	0	1	0	0	2	2	0	0	1	0
1	0	1	3	1	0	0	1	1	3	3	0	2	1	0	0
1	1	0	0	0	1	0	2	4	2	1	0	1	2	1	1
0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0
1	0	0	0	0	2	0	1	0	0	0	1	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	2	0	0	0	0	0	0	0	0	1	0	1	0
1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0

MIDDLE

2	1	0	0	1	0	0	0	1	1	2	0	0	1	1	0
1	3	0	0	0	0	0	0	2	4	1	0	1	2	3	0
0	1	0	0	0	0	0	7	2	5	4	3	2	0	0	2
1	1	0	1	1	2	2	5	1	3	2	1	2	1	2	1
1	1	1	2	3	0	1	2	3	5	1	2	1	3	3	4
1	1	6	2	0	3	3	1	1	1	5	4	1	1	1	3
2	1	3	4	0	1	1	1	1	0	7	9	4	6	0	2
0	1	1	3	1	0	2	2	0	0	0	0	0	3	3	0
0	0	0	0	0	0	3	3	0	1	0	2	0	0	0	0
1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1
0	0	1	1	2	2	0	0	2	0	0	0	0	1	0	0
0	0	0	1	1	2	0	0	0	1	0	0	0	1	0	0

BOTTOM

2	2	1	0	1	0	1	1	0	4	3	1	0	0	0	0
0	1	1	0	1	1	0	0	0	1	1	0	0	0	1	0
1	1	2	2	0	0	0	1	0	1	1	1	1	0	0	1
0	2	0	2	0	1	2	0	0	0	0	0	0	1	1	1
1	2	1	3	1	1	3	2	0	2	2	4	1	2	0	0
0	2	5	2	1	0	2	2	0	2	2	0	3	1	0	2
0	1	0	1	4	1	0	3	2	1	2	2	2	1	0	1
0	0	1	0	0	0	1	1	0	0	1	3	0	0	1	0
0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0
0	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0

AREA

6	3	1	0	2	0	1	2	2	5	5	1	0	1	2	0
1	5	1	0	2	1	0	0	3	6	2	0	1	2	4	0
1	2	2	2	1	0	7	3	5	6	4	3	1	0	2	1
1	3	1	3	1	3	4	6	2	3	4	1	2	2	3	2
3	3	2	6	4	1	4	5	3	7	5	9	2	5	4	4
2	3	12	7	2	3	5	4	2	6	10	4	6	3	1	5
3	3	3	5	4	3	1	6	7	3	10	11	7	9	1	4
0	1	2	3	2	0	3	4	0	0	1	4	0	4	4	0
1	0	0	0	0	2	3	4	0	1	1	5	0	0	0	0
1	2	1	0	1	1	0	1	0	2	1	0	1	0	0	1
1	0	1	3	2	2	0	1	3	0	0	0	1	1	1	0
1	0	2	3	1	2	0	0	0	1	0	0	0	1	0	0

FIGURE 21

Figure 22. Distribution map of high-density LP7 trial, 6/15-18/78.

4	0	0	3	1	4	4	2	5	2	3	7	11	5	3	3
3	0	3	6	6	2	3	8	4	6	5	3	1	3	6	2
3	2	3	1	2	1	4	0	2	8	6	15	9	11	2	1
2	2	7	2	4	2	5	4	3	8	14	14	16	20	12	5
5	1	3	6	18	15	15	15	13	4	19	19	19	12	8	3
8	2	4	7	3	10	6	9	10	22	6	4	6	9	4	3
4	2	1	1	6	9	10	9	13	7	0	6	7	3	11	3
6	0	4	4	9	9	5	22	10	2	7	10	1	4	1	1
1	4	3	4	1	3	4	11	5	2	5	11	1	5	2	0
3	4	4	5	1	2	11	14	4	4	6	20	2	5	1	1
0	3	4	4	2	3	6	8	1	3	3	4	0	1	3	0
0	4	1	2	0	2	6	11	8	6	7	16	5	2	0	4

Figure 22

Figure 23. Distribution map of LP7 on second recovery, showing positions of dyed amphipods. Units under location of original placement are outlined.

Top layer

2	4	0	1	0	1	2	1	1	1	0	0	1	0	0	2
0	2	0	2	2	0	1	1	1	1	0	0	0	1	1	0
2	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0
1	2	2	0	0	0	2	1	0	0	0	0	0	0	0	0
1	0	4	1	0	0	0	0	0	1	0	0	0	1	0	0
0	0	1	0	1	1	0	0	0	0	1	0	1	2	0	0
0	0	0	0	2	0	2	2 ¹	2 ¹	0	0	1	2	2	1	0
0	0	0	0	0	1	7 ⁵	2 ²	3	0	1	2	1	1	0	0
0	1	1	0	1	1 ¹	0	7 ⁵	4 ²	2	0	0	1	1	0	0
1	1	1	1	3	2	1	2	0	0	0	1	0	1	0	1
2	1	1	2	0	5	4	1	2	1	0	1	2	3	0	1
0	0	1	5	0	1	4	4	0	2	1	1	2	0	2	0

Middle layer

0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1
0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0
0	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1 ¹	1	2 ²	0	0	0	0	0	1	0
0	0	0	0	0	0	0	1	4 ¹	0	0	1	0	0	2	1
0	0	0	0	0	0	2	4 ³	2 ²	0	0	0	0	0	0	0
0	0	1	0	0	0	1	2 ²	2 ¹	1	0	1	0	0	0	0
0	1	0	0	0	0	4	0	2	0	0	0	0	2 ¹	0	0

APPENDIX : TABLES

Table 1. Mean square variances for
heirarchal ANOVA of LN2.

<u>Block size(cm)</u>	<u>Sum of squares</u>	<u>d.f.</u>	<u>mean square/mean</u>
15	99553.0	32	17.03 **
30	25128.5	16	8.60 **
60	12832.0	8	8.78 **
120	18286.0	4	25.02 **
240	25632.0	2	70.15 **
480	0.75	1	0.004 ns

** chi-square test significantly different
from random expectation at 99% level

ns not significantly different from random
expectation at 95% level

TABLE 2.

CALCULATED INDICES
FOR PS1 STUDY - LOST CREEK
SITE

<u>STRATUM 12-14 ft</u>		Core diameters (cm)				
Indices	2.40	3.20	4.50	6.35	8.25	
\bar{x}/core	0.50	0.40	1.70	3.30	15.20	
s^2	0.94	0.49	7.79	33.34	205.9	
I	3.00*	1.67ns	3.01**	3.56**	1.75**	
I (q)/I (2q)	--	1.80	0.55	0.85	2.03	
$\frac{\bar{x}_i - \bar{x}_{i-1}}{\bar{x}_i - \bar{x}_{i-1}}$	2.75	8.27	3.70	5.16	1.45	
<u>STRATUM 10-12 ft</u>						
\bar{x}/core	3.10	5.80	11.60	25.1	46.6	
s^2	6.32	21.07	24.27	108.1	392.71	
I	1.31*	1.42**	1.09*	1.12**	1.14**	
I (q)/I (2q)	--	0.92	1.30	0.97	0.98	
$\frac{\bar{x}_i - \bar{x}_{i-1}}{\bar{x}_i - \bar{x}_{i-1}}$	1.29	2.08	0.52	1.14	1.29	
<u>STRATUM 8-10 ft</u>						
\bar{x}/core	0.90	1.90	3.40	6.80	8.70	
s^2	0.99	4.32	9.38	13.49	33.79	
I	1.11ns	1.64**	1.48**	1.13*	1.30**	
I (q)/I (2q)	--	0.68	1.11	1.31	0.87	
$\frac{\bar{x}_i - \bar{x}_{i-1}}{\bar{x}_i - \bar{x}_{i-1}}$	1.00	1.88	1.68	0.44	3.03	
<u>STRATUM 6-8 ft</u>						
\bar{x}/core	0.30	1.00	1.50	4.31	5.84	
s^2	0.23	0.89	1.61	20.90	12.16	
I	0.00ns	0.89ns	1.05ns	1.83**	1.17*	
I (q)/I (2q)	--	0.00	0.85	0.57	1.56	
$\frac{\bar{x}_i - \bar{x}_{i-1}}{\bar{x}_i - \bar{x}_{i-1}}$	1.00	1.00	1.00	1.50	1.50	

* = 95% significance ** = 99% or greater
ns = not significant at 95%

TABLE 3

CALCULATED INDICES
FOR PS2 STUDY - LOST CREEK
SITE

<u>STRATUM 8-10 ft</u>		<u>Core diameters</u>						
<u>Indices</u>	<u>1.52</u>	<u>2.40</u>	<u>3.20</u>	<u>4.50</u>	<u>6.35</u>	<u>8.25</u>	<u>12.5</u>	
\bar{x}/core	0.70	6.10	7.91	21.9	29.8	50.1	159.10	
s^2	0.90	10.30	62.80	167.00	834.61	1254.83	7571.9	
I	1.43ns	1.10ns	1.80**	1.27**	1.83**	1.43**	1.27**	
$I(q)/I(2q)$	--	1.30	0.61	1.42	0.70	1.27	1.13	
$\frac{x_i^* - \bar{x}_{i-1}}{\bar{x}_i - \bar{x}_{i-1}}$	1.00	1.40	7.77	2.18	2.87	0.63	1.24	
<u>STRATUM 6-8 ft</u>								
\bar{x}/core	0.10	0.20	1.90	2.60	11.60	11.94	11.73	
s^2	0.10	0.18	8.76	7.38	162.7	271.1	50.6	
I	--	0.00ns	2.81**	2.05**	2.02**	2.67**	1.26**	
$I(q)/I(2q)$	--	--	0.00	1.37	0.82	0.76	2.12	
$\frac{x_i^* - \bar{x}_{i-1}}{\bar{x}_i - \bar{x}_{i-1}}$	1.00	1.00	3.28	-1.30	1.59	16.5	46.45	
<u>STRATUM 4-6 ft</u>								
\bar{x}/core	0.10	0.93	1.51	1.84	4.51	10.6	22.0	
s^2	0.10	1.20	5.43	1.73	14.1	12.3	169.3	
I	--	1.39ns	2.67**	0.98ns	1.43**	1.01ns	1.28**	
$I(q)/I(2q)$	--	--	0.52	2.72	0.69	1.42	0.79	
$\frac{x_i^* - \bar{x}_{i-1}}{\bar{x}_i - \bar{x}_{i-1}}$	1.00	1.40	1.47	-1.00	1.53	0.76	1.48	

* = 95% significance (test for non-randomness)

** = 99% significance or greater

ns = not significant at 95 %

Table 4a.

CALCULATED INDICES
FOR PS3 STUDY - LOST CREEK
SITE

<u>STRATUM 5.7 - 6.3 ft</u>		<u>Core diameters</u>				
<u>Indices</u>	<u>2.40</u>	<u>3.20</u>	<u>4.50</u>	<u>6.35</u>	<u>8.25</u>	
\bar{x}/core	0.70	2.10	3.20	7.80	18.7	
s^2	1.12	3.21	5.95	19.32	349.7	
I	1.90ns	1.24ns	1.25*	1.17**	0.99ns	
I (q)/I (2q)	--	1.53	0.99	1.07	1.18	
$\frac{x_i^* - x_{i-1}^*}{\bar{x}_i - \bar{x}_{i-1}}$	1.97	0.81	1.40	0.95	0.93	

* = 95% significance (test for non-randomness)

** = 99% significance or greater

ns = not significant at 95%

Table 4b.

CALCULATED INDICES
FOR PS4 STUDY - DRIFTWOOD
STATE PARK SITE

<u>STRATUM 6.3 - 8.3 ft</u>		<u>Core diameters</u>				
<u>Indices</u>	<u>1.52</u>	<u>2.40</u>	<u>3.20</u>	<u>4.50</u>	<u>6.35</u>	<u>8.25</u>
\bar{x}/core	0.60	2.90	3.70	5.00	21.70	45.60
s^2	0.71	22.99	12.01	18.00	653.34	1086.49
I	1.33ns	3.23**	1.56**	1.48**	2.21**	1.45**
I (q)/I (2q)	--	0.41	2.07	1.05	0.67	1.52
$\frac{x_i^* - x_{i-1}^*}{\bar{x}_i - \bar{x}_{i-1}}$	1.35	2.45	0.00	1.34	1.65	1.48

Table 5. Values of mean square/mean density, LP series

Block size	d.f.	LP3			LP4			LP5			LP6		
		top	mid	bot	top	mid	bot	top	mid	bot	top	mid	bot
2 x 2 cm	128	3.75*	1.55*	0.49+	0.64+	0.89	0.51+	0.30+	0.58+	2.17*	0.35+	1.06	0.64+
2 x 4	64	5.70*	2.09*	0.73	0.61+	1.18	0.70	0.60+	0.65+	1.70*	0.71	2.81	0.80
4 x 4	32	11.00*	2.05*	0.63	1.31	1.11	0.65	0.38+	0.44+	5.36*	0.22+	4.29*	1.04
4 x 8	16	20.58*	1.43	1.30	1.28	1.36	0.31+	0.71	1.69	0.22+	0.60	2.32*	1.63
8 x 8	8	15.30*	2.38*	0.52	10.44*	2.60*	1.63	3.18*	1.85	2.06	0.66	2.97*	1.17
upper set													
8 x 16 cm	2	31.29*	3.13	1.33	0.57	0.83	0.63	0.32	1.76	4.58*	3.76*	8.41*	3.85*
16 x 16	1	0.01+	10.13*	1.13	0.63	2.53	1.13	1.32	6.57*	6.13*	0.95	12.50*	0.63
lower set													
8 x 16 cm	2	33.82*	7.45*	1.68	22.58*	0.91	0.04	2.53	0.16	0.53	5.16*	38.03*	16.51*
16 x 16	1	5.28*	21.13*	0.07	1.13	0.00+	0.07	0.13	3.13	0.00+	0.07	2.00	0.07

Areal projection data

2 x 2 cm	128	7.09*	1.68*	3.37*	2.37*
2 x 4	64	8.48*	2.32*	3.51*	4.42*
4 x 4	32	21.10*	3.18*	8.61*	8.11*
4 x 8	16	10.18*	3.69*	9.44*	10.49*
8 x 8	8	20.58*	21.63*	3.72*	9.24*
upper set					
8 x 16 cm	2	60.53*	0.98	9.25*	40.33*
16 x 16	1	4.50	11.88*	9.03*	5.28*
lower set					
8 x 16 cm	2	97.10*	28.13*	3.77*	135.03*
16 x 16	1	51.26*	1.53	2.00	0.28

* = deviates from 95% Poisson expectation- aggregation
+ = deviates from 95% Poisson expectation- uniformity

Table 6a. Values of pooled variance between paired
units for the LP series. Degrees of freedom below.

<u>distance</u>	<u>top</u>	LP3 <u>mid</u>	<u>bot</u>	<u>top</u>	LP4 <u>mid</u>	<u>bot</u>	<u>top</u>	LP5 <u>mid</u>	<u>bot</u>	<u>top</u>	LP6 <u>mid</u>	<u>bot</u>	LP7 <u>area</u>
4 cm	5.18 14	0.83 13	0.63 12	1.42 12	0.71 14	0.25 14	0.21 12	0.50 13	1.96 12	1.21 12	0.39 14	1.04 12	8.62 12
6 cm	3.71 14	0.79 12	1.62 13	1.23 13	0.73 11	0.29 12	0.25 12	0.04 13	2.15 13	0.62 12	3.58 12	0.29 12	13.29 12
8 cm	3.07 14	1.86 11	2.54 12	0.25 12	0.71 12	1.00 12	0.09 11	1.29 12	1.77 11	0.62 12	1.67 12	0.33 12	24.42 12
10 cm	3.46 14	0.45 11	2.68 11	0.17 12	0.77 11	0.54 11	0.73 11	0.04 12	3.79 12	0.37 12	1.58 12	1.08 12	15.29 12
12 cm	15.45 11	0.88 12	1.91 11	0.59 11	0.46 12	0.42 12	0.08 12	0.23 11	1.21 12	0.04 11	2.14 11	2.00 11	20.73 11
14 cm	12.64 11	0.70 10	5.77 11	0.27 11	2.73 11	1.04 12	0.45 11	0.77 11	2.00 11	0.32 11	2.25 10	1.45 11	28.32 11
16 cm	7.85 10	0.21 12	0.50 12	0.36 11	0.45 11	0.75 11	0.40 10	2.79 12	1.92 12	0.54 11	3.27 11	0.71 12	13.91 11
18 cm	2.90 10	0.77 11	1.00 10	3.72 11	1.25 10	0.44 10	0.29 12	0.25 10	3.25 10	0.18 11	4.46 12	0.15 10	10.41 11

Table 6b. Values of pooled variance between paired units for the LP series areal projections. Degrees of freedom shown below values.

<u>distance</u>	<u>LP3</u>	<u>LP4</u>	<u>LP5</u>	<u>LP6</u>
4 cm	7.92 12	1.73 13	1.58 12	2.41 11
6 cm	4.38 12	1.12 12	3.75 12	5.96 12
8 cm	12.88 12	2.46 12	1.79 12	7.04 13
10 cm	11.69 13	1.23 11	6.21 12	5.31 13
12 cm	21.68 11	1.50 11	5.13 11	3.41 11
14 cm	8.09 11	1.36 11	5.86 11	3.14 11
16 cm	17.05 11	1.99 12	1.12 12	2.58 12
18 cm	7.35 10	4.68 11	7.59 11	4.10 10

Table 7.. Values of pooled variance between paired units for the LP series- highest variance pair dropped from each spacing. D.F. below.

<u>distance</u>	<u>top</u>	LP3 <u>mid</u>	<u>bot</u>	<u>top</u>	LP4 <u>mid</u>	<u>bot</u>	<u>top</u>	LP5 <u>mid</u>	<u>bot</u>	<u>top</u>	LP6 <u>mid</u>	<u>bot</u>	LP7 <u>area</u>
4 cm	1.71 13	0.28 11		0.82 11		0.23 13	0.45 11	0.17 12	0.50 11	0.59 11	0.27 13	0.73 11	5.73 11
6 cm	2.11 13	0.71 12		0.96 12		0.14 11	0.09 11	0.00 12	0.83 12	0.27 11	2.27 11	0.13 11	5.59 11
8 cm	0.84 13	1.63 11		0.23 11		0.91 11	0.05 10	0.27 11	0.15 10	0.27 11	1.09 11	0.18 11	18.95 11
10 cm	1.26 13	1.70 10		0.14 11		0.15 10	0.35 10	0.00 11	2.49 11	0.23 11	0.99 11	0.77 11	5.04 11
12 cm	2.55 10	0.85 10		0.45 10		0.27 11	0.04 11	0.20 10	0.91 11	0.00 10	1.10 10	1.40 10	6.60 10
14 cm	9.85 10	3.15 10		0.10 10		0.73 11	0.30 10	0.65 10	0.95 10	0.15 10	1.11 9	0.79 10	18.35 10
16 cm	4.22 9	0.36 11		0.20 10		0.37 10	0.22 9	1.41 11	0.96 11	0.39 10	2.35 10	0.36 11	14.75 10
18 cm	1.83 9	0.61 9		2.30 10		0.27 9	0.14 11	0.22 9	0.89 9	0.15 10	3.23 11	0.11 9	4.25 10
		<u>by area</u>			<u>by area</u>			<u>by area</u>			<u>by area</u>		
4 cm		4.96 (11)			0.83 (12)			0.99 (11)			1.85 (10)		
6 cm		3.14 (11)			0.81 (11)			1.86 (11)			1.95 (11)		
8 cm		3.83 (11)			1.55 (11)			1.54 (11)			2.58 (12)		
10 cm		8.50 (12)			0.90 (10)			5.14 (11)			4.25 (12)		
12 cm		17.80 (10)			0.40 (10)			3.82 (10)			1.30 (10)		
14 cm		4.85 (10)			1.05 (10)			1.45 (10)			2.20 (10)		
16 cm		12.71 (10)			1.03 (11)			0.82 (11)			1.68 (11)		
18 cm		4.61 (9)			3.35 (10)			1.15 (10)			1.83 (9)		

Table 8. Bartlett's test statistic M for homogeneity of paired-unit variances. Significance level shown.

	<u>Including all pairs</u>		<u>Excluding highest-variance pair</u>	
<u>LP level</u>	<u>M</u>	<u>α</u>	<u>M</u>	<u>α</u>
3- top	18.98	.01	25.76	.001
middle	14.17	.05	24.47	.001
bottom	25.43	.001	--- not available---	
4- top	47.48	.001	42.41	.001
middle	15.93	.025	--- not available---	
bottom	12.06	.10 ns	18.47	.01
5- top	20.55	.005	25.34	.001
middle	79.88	.001	134.19	.001
bottom	5.25	.60 ns	19.81	.01
6- top	29.15	.001	54.34	.001
middle	19.87	.01	20.29	.005
bottom	26.13	.001	28.01	.001
<u>by area</u>				
3	10.18	.20	14.63	.05
4	9.72	.25 ns	14.93	.05
5	19.02	.01	23.70	.005
6	6.54	.50	5.30	.70
7	6.64	.50	14.57	.05

Table 9. Values of intra-patch dispersion
chi-squared statistic for LP
series data.

<u>LP level</u>	<u>χ_p^2</u>	<u>d.f.</u>	<u>$1 - \alpha$</u>
3- top	5.89	9	.5-.7
middle	1.63	5	.8-.9
bottom	4.07	11	.9-.95
4- top	1.81	5	.8-.9
middle	3.96	14	.99-.995
bottom	0.50	6	.99-.995
5- top	0.00	4	.995
middle	0.53	3	.75-.8
bottom	6.52	10	.5-.7
6- top	0.24	2	.5-.7
middle	3.01	9	.9-.95
bottom	1.06	6	.95-.995
all patches	29.22	84	.995
3- area	6.97	11	.7-.75
4- area	2.38	11	.95-.975
5- area	1.75	7	.9-.95
6- area	2.83	7	.8-.9

Table 10. Summary of patch composition variables
for LP6.

<u>level</u>	<u>#males</u>	<u>#females</u>	<u>mean size</u> <u>of males</u>	<u>s²</u>	<u>mean size</u> <u>of females</u>	<u>s²</u>	<u>overall</u> <u>mean size</u>	<u>s²</u>	<u>area in</u> <u>units</u>	<u>total</u> <u>in patch</u>
top	2	0	5.50	0.00	--	--	5.50	0.00	1	2
	1	2	5.25	--	5.75	4.50	5.58	2.33	1	3
	0	2	--	--	7.00	--	7.00	--	1	2
	2	0	4.75	0.12	--	--	4.75	0.12	1	2
	13	5	5.09	1.20	5.00	2.22	5.07	1.37	7	18
	3	1	5.08	0.77	4.25	--	4.87	0.69	2	4
middle	4	1	5.38	1.32	4.75	--	5.20	1.04	2	5
	15	9	5.50	1.98	5.39	2.72	5.46	2.16	6	24
	4	1	5.80	1.29	6.00	--	5.83	1.04	2	5
	1	1	3.75	--	4.00	--	3.87	0.03	1	2
	7	3	5.96	1.69	5.58	0.77	5.85	1.33	4	10
	5	1	5.90	1.83	7.00	--	6.08	1.66	3	6
	1	1	4.00	--	7.50	--	5.75	6.12	1	2
	2	0	4.25	0.12	--	--	4.25	0.12	1	2
	24	25	5.61	1.50	6.19	1.64	5.91	1.62	16	50
	1	1	5.00	--	7.00	--	6.00	0.50	1	2
	3	4	5.00	1.19	5.00	1.00	5.00	0.89	3	7
	2	0	5.50	2.00	--	--	5.50	2.00	1	2
	10	4	5.60	1.66	5.00	0.46	5.43	1.33	5	14
	0	2	--	--	6.87	0.03	6.87	0.03	1	2
	17	20	5.79	2.11	5.97	1.46	5.89	1.72	9	37
bottom	3	1	7.00	0.25	6.00	--	6.75	0.42	2	4
	2	4	6.37	0.78	6.75	1.04	6.62	0.82	3	6
	6	6	7.12	0.77	6.33	2.36	6.73	1.59	5	12
	2	2	7.12	0.03	5.62	0.28	6.37	0.85	1	4
	2	0	7.37	0.03	--	--	7.37	0.03	1	2
	6	9	6.54	1.38	6.64	1.91	6.60	1.59	7	15
	4	3	5.81	0.68	6.00	1.31	5.89	0.79	2	7
	12	10	5.87	2.09	6.75	1.47	6.24	1.89	10	22
	1	1	7.75	--	6.75	--	7.25	0.50	1	2
	2	0	5.87	0.03	--	--	5.87	0.03	1	2

Table 11. Matrix of correlations between LP6 patch composition variables.

MSM -mean size of males
 MSF -mean size of females
 MSALL -mean size of all individuals
 VMSALL -variance of MSALL

MALES -number of males per patch
 FEMALES -number of females per patch
 AREA -area of patch in units
 PSIZE -sum of MALES + FEMALES
 DENSITY -ratio PSIZE/AREA = per-unit density

MSF	-	.557							
MSALL	-	.866	.828						
VMSALL	-	.030	.121	-.023					
MALES	-	.058	-.044	-.080	.668				
FEMALES	-	.100	.091	.094	.657	.747			
AREA	-	.088	.094	.033	.653	.921	.860		
PSIZE	-	.075	.019	-.023	.690	.948	.899	.963	
DENSITY	-	-.043	-.305	-.223	.537	.530	.533	.324	.540
		MSM	MSF	MSALL	VMSALL	MALES	FEMALES	AREA	DENSITY

Table 12. Correlations between principal components and LP6 patch composition variables (factor structure matrix). See Table 11 for abbreviations.

	<u>PC1</u>	<u>PC2</u>	<u>PC3</u>	<u>PC4</u>	<u>PC5</u>	<u>PC6</u>	<u>PC7</u>	<u>PC8</u>	<u>PC9</u>
MSM -	.037	.901	.202	.244	-.28	.011	.002	-.04	-.29
MSF -	.202	.861	-.18	-.22	.361	-.06	.009	-.03	.355
MSALL -	.115	.986	.028	.075	-.02	.004	-.01	.071	-.03
VMSALL -	.678	.072	.289	-.64	-.16	.045	-.01	.000	-.15
MALES -	.955	-.16	-.08	.073	-.08	-.20	-.05	.000	-.05
FEMALES-	.951	-.02	-.13	.161	.103	.199	-.03	.000	.123
AREA -	.940	-.02	-.30	.029	-.09	-.01	.121	.008	-.07
PSIZE -	.980	-.09	-.11	.121	.014	.001	-.04	.000	.036
DENSITY-	.533	-.14	.789	.183	.193	-.02	.035	.004	.200
% total variation	49.6	28.8	10.1	6.9	3.4	1.0	0.2	0.1	0.0

Table 13. Area of patches, number per patch,
and number of patches per layer
versus layer density for LP series.

<u>layer</u>	<u>\bar{x} area</u>	<u>s^2</u>	<u>\bar{x} # indiv.</u>	<u>s^2</u>	<u>layer density</u>	<u># patches</u>
LP3 top	3.25	4.01	17.88	25.97	386	16
middle	2.22	2.05	7.00	7.66	172	18
bottom	1.70	0.95	4.40	2.46	63	10
LP4 top	2.70	2.45	8.50	9.54	121	10
middle	2.00	0.97	5.20	2.42	161	20
bottom	1.73	0.79	4.00	1.73	89	11
LP5 top	1.40	0.52	3.10	0.99	56	10
middle	2.60	2.51	7.80	6.69	67	5
bottom	2.32	1.83	7.53	6.42	195	19
LP6 top	2.00	2.24	4.71	5.91	75	7
middle	3.80	4.16	12.00	15.86	238	15
bottom	2.92	2.94	7.08	7.15	136	12

Table 14. Area of patches, number per patch,
and number of patches in areal maps
versus box density for LP series.

LP3	2.48	2.80	10.46	17.33	621	44
LP4	2.10	1.45	5.68	5.18	371	41
LP5	2.09	1.69	6.26	5.70	318	34
LP6	3.12	3.41	8.76	11.81	449	34

Table 15. Recovery of individuals through tidal cycle in PD trial, 4/19-20/78.

position=	top	2	3	4	5	6	bottom	
core 1	0	1	1	0	0	0	*	
core 2	+	0	1	0	0	0	*	
core 3	0	0	1	0	0	0	*	1015 hrs
core 4	0	0	1	4	0	1	*	high tide
average	0.0	.25	1.0	1.0	0.0	.25		
core 1	0	1	0	0	0	0	0	
core 2	0	0	0	0	0	0	0	
core 3	2	0	0	0	0	0	0	0115 hrs
core 4	0	1	0	0	0	0	0	falling tide
average	0.5	0.5	0.0	0.0	0.0	0.0	0.0	
core 1	0	0	1	0	0	0	0	
core 2	0	0	0	0	0	0	0	
core 3	0	0	0	0	0	0	0	0400 hrs
core 4	0	0	0	0	0	0	0	low tide
average	0.0	0.0	.25	0.0	0.0	0.0	0.0	
core 1	0	0	0	0	0	0	0	
core 2	0	0	2	1	0	0	0	
core 3	3	4	2	1	0	0	0	0745 hrs
core 4	0	0	0	0	0	0	0	rising tide
average	.75	1.0	1.0	0.5	0.0	0.0	0.0	
core 1	1	3	2	2	0	0	0	
core 2	1	0	1	0	0	0	0	
core 3	0	0	0	0	0	0	0	1030 hrs
core 4	0	2	1	1	3	0	1	high tide
average	0.5	1.25	1.0	.75	.75	0.0	.25	

*prior to use of corking to reduce washout of bottom section.

+top section lost in transfer.

Table 16. Number of expected and observed joins between dense units in LP series.

<u>level</u>	<u>number of dense units</u>	<u>critical density</u>	<u>expected joins</u>		<u>observed joins</u>
			<u>mean</u>	<u>variance</u>	
LP3 top	52	3	49.52	85.26	85 ***
middle	40	2	29.18	34.80	43 *
bottom	18	2	5.72	5.50	11 *
LP4 top	26	2	12.16	11.78	40 ***
middle	39	2			34
bottom	19	2	6.39	6.18	12 *
LP5 top	14	2	3.40	3.03	6 near 95%
middle	13	2	2.92	2.68	13 ***
bottom	21	2	7.85	7.85	12 ns
LP6 top	14	2	3.40	3.13	12 ***
middle	57	2	59.71	99.35	90 ***
bottom	15	2	3.93	3.69	51 ***
LP3 area	69	4	87.77	153.83	113 *
LP4 area	59	3	64.01	105.72	94 **
LP5 area	25	4	11.22	11.24	19 *
LP6 area	46	4	38.72	51.19	77 ***

* significantly aggregated, 95% level

** significantly aggregated, 99% level

*** significantly aggregated, 99.9% level

ns not significantly different from
random expectation