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ECOLOGICAL ANALYSIS OF SPATIAL AND TEMPORAL
PATTERNS OF PELAGIC ECOSYSTEM COMPONENTS POTENTIALLY
INTERACTING WITH AN OTEC PLANT NEAR PUNTA TUNA, PUERTO RICO

ZOOPLANKTON CHARACTERISTICS

FINAL REPORT

Submitted to:

DOE/OHER

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CENTER FOR ENERGY AND ENVIRONMENT RESEARCH

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FOREWORD

This document is part of the final report for the Department of Bneray Project under Contract No. DE~ACOS-760R01833, which includes five main sections: Physical Characterization, Plankton, Primary Productivity, Chemical Characterization, and Summary and Synthesis. The dccument is primarily organized as a

collection of preprints of articles being submitted for journal

publication, Once all sections are completed, the entire series will be combined as a five chapter volume dealing with the

environmental aspects of

We siting, construction and operation
of an Ocean Thermal Energy Conversion Plant based off the south
coast of Puerto Rico. Of prime concern in these studies, as
suggested by the title, is the relationship among the scale of
distribution of natural phenomena, the scientific detectability
of pattern, and the allocations of pattern Likely to be caused by
the hypothetical 100 MWe power plant adopted as the design unit.

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SPATIAL AND ?TEMPORAL VARIATIONS OF OCEANIC
ZOOPLANKTON NEAR PUERTO RICO

Pinal Report

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ansTRACT

Diel and bimonthly variations in horizontal distributions of selected zooplankton higher taxa and species were followed within the upper 100 meters off the south coast of Puerto Rico during 1980. Spatial pattern examined encompassed scales of kilometers to hundreds of kilometers. A series of oblique tows with 0.75 m diameter, 202 μ mesh nets were taken to estimate zooplankton abundances and hyérocasts made for measures of a number of habitat variables.

analysis of sampling variability relative to scale revealed

2 general lack of pattern associated with spatial scales larger than several kilometers. A statistically significant seasonal variability component was detected in most zooplankton categories. Maximum abundances occurred in July. The observed seasonal pattern is compatible with the hypothesis that the forcing mechanism driving seasonality is input of nutrients into euphotic zone by upwelling along the periphery of large, low salinity lenses of surface water passing through the region.

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INTRODUCTION

Ecological processes organizing zooplankton communities

affect and are affected by the spatial and temporal patterns

shown by individuals and species. For this reason, the quantitative description of pattern is of fundamental importance in marine ecology. This pattern can arise from a variety of causal mechanisms (Stava, 1971) and is expressed over wide spatial and temporal scales (Cassie, 1963; Star and Mullin, 1981; Fasham et al., 1974; Wiebe et al., 1976; Bernal, 1961 and Johnson

and Britton, 1963). The association of pattern over a range of spatial and temporal scales with characteristic environmental

Processes are reviewed by Haurey et

(1978). They define six

classes within a spatial continuum from 1 cm to 104 km, mega-scale (>3000km) macro-scale (1000 to 3000km), meso-scale (100 to 1000 km) coarse scale (1 to 100 km), fine (1 to 1000m) micro-scale (<1m)

?The purpose of this paper

to describe horizontal patterns

of abundance within the intermediate spatial scales (fine, coarse 2nd meso-scale) for some zooplankton components in the surface waters south of Puerto Rico and to discuss temporal variation in this pattern relative to several parameterizations of the environment, viz salinity, temperature, oxygen and chlorophyll.

The major physical features of the eastern Caribbean are well-known and have recently been reviewed by Nowlin and Morcison (1982). The survey area lies in the northeast corner of the

Venezuela Basin. Surface flow in this region is complex, but the mean flow is to the west (Metcalf, 1976; and Fornshell, 1961).

The upper 30 to 90 m of water with salinities generally below

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36.58, Caribbean Surface Water, has its origin in the North

Equatorial and Guiana Current systems. It is formed from a mixture of these waters and large inputs of Amazon and Orinoco River water, carried into this region by prevailing winds and currents (Nowlin and Morcison, 1982; Froelich et al., 1977).

Seasonal variation in the depth of the mixed layer ranged from 90 meters in January to 30 m in September. Internal waves, oscillating with a period approximating a semi-diurnal tide, can cause diel variations of 20 to 30 m in the depth of the upper layer (Fornshell and Capella, 1982).

Below the Caribbean Surface Waters lies the Subtropical Underwater. Extending down to approximately 200 m, it is characterized by a salinity maximum $>37\text{‰}$, located at around 125

m This water has its origin in the surface waters of the North Atlantic central gyre, and moves into the survey region through the Jungfern-Anegada Passage (Nowlin and Morrison, 1982).

Seasonal variations in nutrients, salinity, temperature and oxygen are confined to these two upper layers. Values of phosphate-P, nitrate/nitrite-N and ammonium-N are near the minimum levels of detection throughout the year in the upper 100 meters. The nutricline starts at depths between 120 and 150 meters near the base of the Subtropical Underwater.

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Sampling: Bimonthly collections of zooplankton and auxiliary environmental data were carried out between January and November, 1980 within a 7.5×10^3 km² area south of Puerto

Rico. The zooplankton were sampled with 0.75 m diameter, opening

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and closing nets of 202 μ mesh. Oblique tows were taken through the upper 100 m of the water column, a zone which encompasses the total vertical extent of the Caribbean Surface Water and varying

portions of the Subtropical Underwater. An average tow trailed a

linear distance of approximately 1 km and filtered 377 m³ of water. Details of methods, times, and locations of sampling are available elsewhere (CEER, 1980 a-f). A brief description of the sampling design is presented here.

Zooplankton distribution patterns were investigated on three different horizontal spatial scales (Fig. 1). Within station variability was assessed from a three tow day/night replicate series taken within a 24 hr period at a site (Benchmark) 5 km SE of Puerto Rico (17°56.3'N, 65°51.5'W). Collections were made within a 15 km radius of this position, a spatial scale roughly corresponding to the "fine" pattern of Haurey et al. (1978). A series of day/night samples was also taken within a three by two station grid (coarse scale grid) with inter-station distances of 6.4 km. The six stations of the coarse grid bracketed the Benchmark site. Mesoscale pattern was examined within a grid consisting of four north-south station transects spaced 50 km apart (65° 30' W to 66°48" W). Each transect contained four stations located from 5 km to 50 km offshore.

Hydrocasts with 52 or 121 Niskin bottles were made to a depth of 1000 m at most stations for calculation of the

baroclinic flow

jattern within the survey region.

Water samples

from these casts were used for measurements of salinity, oxygen,

?and chlorophyll a. Continuous temperature profiles were made

through the upper 100 meters, These were supplemented by

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temperature measurements with paired reversing thermometers from the hydrocasts.

Data Analysis. The 196 samples taken during the survey have been analyzed for total zooplankton biomass, total copepods, total larvaceans, total chaetognaths, and the copepod species

Clausocalanus fure:

Bavo, and *Oithona plunitera*.

?The species selected for analysis are frequent and abundant

within the study area. Literature review indicates that their vertical populations distribution centers are, generally, located within the upper 100 m (e.g., Moore and O'Berry, 1957; Michael and Foyo, 1976

MeGowan and Walker, 1979; Roe, 1972; and zoppi, 1961).

Zooplankton biomass was measured using a volume displacement method (Ahlstrom and Thraillkill, 1963). Subsamples for zooplankton were taken with a Stempel pipette after the contents of a sample had been randomly distributed by a series of stirrings and back stirrings. Replicate determinations of biomass measurements and zooplankton counts were not more variable than expected from a random (Poisson) distribution. Relevant information on subsample size and error estimates is summarized in Table 1, Examination of within station variability indicates that the counting error is small relative to the field sampling error.

Within each sampling scale analysis of variance procedures (ANOVA) were used to determine variance components associated with seasonal and, when appropriate, station position, day/night,

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and interaction effects. Preliminary analysis of the data revealed that sample variances were positively correlated with the mean. A $\log(X+1)$ transformation was performed to equalize the variances and normalize distributions. A procedure outlined by Steel and Torrie (1960) was used to correct for missing data points.

The variance components generated by the ANOVA testing were used in a hierarchical analysis of variance relative to spatial scale to determine intensity of pattern associated with different spatial scales (e.g., Grieg-Smith, 1964). In this analysis it is

assumed that the sample variance attributable to a given spatial scale is superimposed on the variability observed within the smaller scales. Due to these added variance components overall variability should increase with increases in scale if characteristic patterns exist on those scale.

Correlations between the environmental parameters and zooplankton spatial patterns were determined using the variance components associated with the within cruise spatial and the bimonthly temporal scales. Relationship between pairs of variables were expressed as covariances and correlation coefficients (2) calculated from the following formulae:

$$\text{var}(x+y) = \text{var}(x) + \text{var}(y) + 2 \text{Cov}(xy)$$

$$= \text{COV}(xy) / \sqrt{\text{var}(x) \times \text{var}(y)}$$

where x and y represent zooplankton data and environmental variables, respectively, (Kershaw, 1960). Data used in this analysis were largely derived from the coarse and mesoscale grids since hydrocast for estimation of habitat variables and net tows

at Benchmark were not taken concurrently. The additional

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parametric and non-parametric procedures used are described in standard statistics texts (e.g., Tate and Clelland, 1954; Sokal and Rohlf, 1968).

RESULTS

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Mean abundances per sampling event for the seven zooplankton categories are shown in Figs. 263. The results of the anova testing for this set of data are found in Table 2, Although some caution should be exercised in interpreting these results, due to the potential for multiple testing effects, several trends are apparent. (If an individual ANOVA probability for an "alpha" error $p < 0.001$ is accepted, the "survey wide" significance level is $p < 0.02$).

ALL categories showed either non-significant ($P < 0.05$) of inconsistent day/night variations in abundance. There is no large variability component which can be associated with mace

vertical migration. Excluding 0: plumifera significant

seasonal differences ($p < 0.001$) were observed over all spatial scales in most zooplankton categories (Table 2).

It is possible that the significant "temporal" variability is an artifact produced by interactions of spatial pattern and

temporal effects within a given sampling scale (i

+ the

Presence or absence of fine scale patchiness at benchmark

uring a particular sampling episode) rather than "true"

bimonthly temporal variations, To assess the possibility of this

effect havi

g occurred, the agreement in bimonthly abundances

among the three sampling scales was examined for each zooplankton

category using Kendall's concordance test. Significant positive

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concordance was observed ($p < 0.01$) within the six zooplankton categories having significance between cruise variation. *Oithona plumifera* was inconsistent in regard to spatial scale in its within cruise response. Since concordance is most easily explained by assuming similar changes in background this result constitutes circumstantial evidence for true temporal changes in abundance between cruise periods.

Kendall's concordance method was also used to examine Similarity in seasonal abundance trends within the groups showing within cruise concordance between the spatial scales. The sums of the ranks over the three spatial scales for each cruise from the preceding concordance test were used to rank each cruise and the Kendall's concordance test reapplied. Zooplankton biomass and total copepods were omitted from this analysis since these groups have as components all or some of the remaining entities. There was significant agreement ($p < 0.05$) among the remaining categories suggesting that zooplankton responds similarly to bimonthly changes within the study area. Student-Newmann-Keuls multiple range tests showed that densities tended to be higher for most categories in the sampling period after the surface salinity drop, July to November, with significantly higher abundances occurring in July. The size of the annual Fluctuations were low. Ranges in the mean bimonthly abundances

varied from 3x for most higher taxa categories to 10x for ©

avo, an amplitude roughly equivalent to the range in sampling variability within a cruise.

Spatial Effects: Significant station effects within a

spatial scale were interpreted as an indication of stable pattern

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at that level (Lewis, 1978). Within the mesoscale grid significant station effects were observed for total larvaceans and total chaetognaths (Table 2). A posteriori examination of these results using the Student-Neuman-Keuls procedure showed that the significance originated from higher abundances at the inshore stations on the two westernmost transects. In a companion study run concurrently with this survey a series of samples were taken from the insular shelf out to 2.5 km. These nearshore samples showed consistently higher biomass and abundance levels (CEER, 1980 af). At the inshore terminus of

the western transects this zone of higher abundances appears to have been shifted offshore due to a broadening of the shelf and possible outwelling effects from two nearby bays. The higher abundances of Larvaceans and chaetognaths in this region is a reflection of an abundance gradient associated with an "island mass effect" rather than a stable mosaic within the survey area

(Jones, 1962; Sanders and Stevens, 1973; Gilmarin, 1974).

Lack of significant station effects for a zooplankton category within @ spatial scale does not, in itself, imply a lack of characteristic spatial pattern only the lack of stable structure. Temporary pattern (ephemeral pattern due to spatial-temporal interactions) could still be present (Lewis, 1978). To test for the existence of ephemeral pattern the sums of the squares and degrees of freedom for the day/night effects and eviuse-day/night interaction effects for the Benchmark site and the coarse scale grid were added to their respective error sum of squares, The same procedure was carried out for the station

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effect sum of squares and degrees of freedom within the mesoscale grid. In most instances this involved a pooling of non-significant mean squares

Error mean squares were then recalculated (Table 3). Assuming that the error mean square at the Benchmark site is an unbiased estimate of fine scale variability, increases in error mean square within coarse and mesoscale grids would be attributable to the added effects of their stable and ephemeral pattern. No general trend in variability is evident. Increasing distances between samples are not accompanied by the introduction of any statistically detectable variance components that would be associated with larger scale pattern.

Excessively large fine scale sampling variability can produce a result that would be wrongly interpreted as a lack of larger scale pattern by overwhelming the larger pattern variance components in a hierarchical analysis of variance. Antilogs of the square root of the mean squares at the Benchmark site (Table 2) can be used as an estimate of sampling variability at a given site and time. Expressed on a proportional basis to their respective means, these values ranged from 1.18 x (total

copepods) to 2.00% (*Paracalanus cf parvus*). This range is within the sampling variability in the literature values reported for net caught zooplankton observed in similar studies (Wiebe, 1971). The lack of larger spatial pattern doesn't appear to be a statistical artifact.

It seems that the oceanic environment off Puerto Rico is relatively uniform over the coarse and mesoscales examined in the

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sense that little characteristic pattern, stable or ephemeral, is associated with these spatial scales.

Environa. 1

1 S\$: Cruise averages for the

environmental parameters m

sured (temperature, salinity, oxygen, and chlorophyll a) are plotted in Fig. 4, Maximum surface salinities were observed during March and May. Surface salinities dropped in July reaching a minimum in September. The observed seasonal variation follows the reported pattern for this region and is related to precipitation and Amazon-Or inco River @ischarge within the Caribbean Surface Waters source regions rather than local runoff and precipitation (Froelich 1978).

face temperatures seasonal trenés oppose surface salinities with minimum values recorded in February and maximum temperatures in September. Dissolved oxygen values are highest in the January and March cruises, a reflection of the lower Surface temperatures during this period. A sub-surface oxygen

maximum around 75 meters was present during the May, July, and September cruises. This maximum was associated with a chlorophyll maximum and generally below the thermocline. The chlorophyll a seasonal maximum occurred in July. Relatively high values were also seen during the January and September cruises. In general, little correlation was found between the abundances of the eight zooplankton categories and habitat variables. Among and within cruise correlations are listed in Table 4. Working at an overtly significant level of $p < 0.06$, two zooplankton categories showed significant correlations, zooplankton biomass with chlorophyll a on 2 seasonal basis and

zooplankton biomass with salinity and temperature on a within cruise basis. The

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tendencies toward negative correlations with salinity and oxygen and positive correlations with temperature among cruises reflects the dichotomy in abundances between high and low surface salinity periods. A more interesting relationship in terms of a possible direct cause-effect interaction is the positive correlation

between most zooplankton categories and chlorophyll a both on a

among and within cruise basis. The relationship is most consistent and shows greatest significance between chlorophyll a and biomass. Individual cruise linear regressions of chlorophyll a on biomass showed that the relationship between the two varied with respect to both slope and explained variability, r^2 (Fig.

5). Higher slope values and less scatter are associated with cruises showing low mean chlorophyll a concentrations. The Product-moment correlation coefficient between mean chlorophyll a concentrations and the slope of the regression lines was Significant at the $p < 0.05$ level, and at the 0.10 level with r^2 .

In both respects, a closer coupling between phytoplankton and zooplankton is evident as the former decreases in abundance. Such an affect could develop if there existed a quasi-equilibrium between phytoplankton growth, zooplankton grazing and nutrient recycling that is periodically destroyed by the advective input of nutrients into the euphotic zone (Sharp et al., 1980).

DISCUSSION

Whether temporal variations such as those described in this study represent a "true" seasonality or short term haphazard variations caused by local biological or hydrographic

conditions, has not been well-established for the eastern

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Caribbean (e.g., Calef and Grice, 1967; Beers et

+ 1968;

Lewis and Fish, 1969; Stevens, 1971; and Moore and Sanders, 1977), The uncertainty reflects both the lack of offshore studies with long term time series sampling (>2 yr.), and the size of sampling effort needed to detect the relatively small temporal variability observed. The duration of the present study is too short to address the problem of seasonality directly, but Several characteristics of the temporal distribution of biomass and abundances suggest the zooplankton are responding to a strict Seasonal cycle. Most zooplankton categories showed concordance in their seasonal pattern with highest abundances occurring in the summer. The nature of the coupling observed between Phytoplankton (chlorophyll a) and zooplankton biomass fluctuations suggest that hydrographic conditions leading to nutrient enrichment within the euphotic zone underlie the observed variation in both groups. Within any cruise, a general

agreement exists over all spatial scales sampled on environmental suitability as expressed in size of the plankton standing stocks.

The forcing agent that produces between cruises variability appears to operate over large spatial scales affecting overall Production rather than a few isolated components. This is consistent with the character of a true seasonal response.

Further evidence for regularly reoccurring variations of a Seasonal nature of a more direct nature comes from other studies in the eastern Caribbean, and western tropical Atlantic. Nutt and Yeaman (1975) reported similar seasonal trends in total zooplankton biomass and abundance levels at their offshore station during a year's study of the north coast of Puerto Rico.

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In Barbados, Lewis (1962) and Kidd and Sanders (1979) also

found higher summer zooplankton standing crops. Lewis and Fish (1969) reported higher summer densities in many zooplankton groups, but concluded that the temporal changes in abundance resulted from local hydrographic factors. In contrast, Moore and Sanders (1977) observed no strong evidence for strict

seasonality. However, there is a noticeable trend in their data for large zooplankton fluctuations with higher peaks in late winter and summer. Elsewhere in the Caribbean, Calef and Grice (1967) found a threefold increase in zooplankton from winter to summer season off the northeast coast of South America.

Seasonality in the oligotrophic subtropical waters of the North Atlantic central gyre has been linked to the yearly migration of the thermocline with maximum phytoplankton followed by increases in zooplankton abundances occurring in the spring after nutrient enrichment by winter mixing of the surface waters to the depth of the permanent thermocline (Menzel and Ryther, 1960 and 1961; Deevey, 1971). This mechanism of nutrient

enrichment may account for the relatively high chlorophyll

concentrations during the January cruise, but would not explain the high phytoplankton and zooplankton levels during the summer when the mixed layer is shoaling and vertical stability is at a maximum. Seasonal changes in the strength of the Caribbean current also occur which can generate hydrographic conditions leading to increased productivity. Geostrophic data from the six cruises show a definite bi-seasonality in the current field

with flow from May through September characterized by the

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Presence of eddies and strong meanders (Fornshell, 1981). Mean dynamic heights increased steadily during this period. Eddies of this type have been associated with regions of higher production elsewhere in the Caribbean (Ingham and Mahnken, 1967; Powles, 1976). The mesoscale variability observed is comparable to or incorporated within the mesoscale sampling grid. Increases in Production due to mesoscale turbulence should ultimately be reflected in higher mesoscale zooplankton spatial variability. No evidence of this phenomenon was observed within our study

tower salinities, indicating an increased presence of Amazon and Orinoco source water, have been associated with higher zooplankton abundances (Lewis et al., 1962; Kidd and Sanders, 1979 and Calef and Grice, 1967). In this study no consistent correlation was observed between standing stocks within the various zooplankton categories and surface salinities. Peak abundances occurred at the initiation of the surface salinity shift, but declined thereafter while salinities continue to drop until September. This lack of correlation may reflect a nonlinear relationship between these factors. Ryther et al.

(1967) found that the low salinity waters originating from the Amazon runoff generally contained low nutrient levels (silicate remained at relatively high levels) negating the possibility of direct nutrient enrichment from this source. They suggested that upwelling of nutrient-rich water at the periphery of large anticyclonic eddies (33°S core diameters of 400 to 600 km) of low salinity water originating from Amazon runoff contributed to or cause the increase in plankton levels they observed. Kidd and

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Sanders (1979) associated higher summer plankton standing stocks within the study area off Barbados with the nutrient enrichment that occurs as these low salinity "bubbles" move through the region, Maximum Amazon runoff occurs from May to June (Gibbs, 1970). Much of this

outflow is diverted into the open ocean.

Since surface waters from this

region enter the eastern Caribbean

it is likely that large lenses of Amazon water are transported into the Caribbean and contribute to the low salinity surface water which passes through this region during the summer (Gordon, 1967; Forbes-ortega and Heccere, 1976; and Mazeiba et al., 1980). Froelich et al, (1979) reported that the first appearance of this low salinity water south of Puerto Rico occurs in the June-July Period with minimum surface salinities occurring during the fall, which agrees with our observations. Upwelling associated with larvae, low salinity lenses as the forcing mechanism underlying the summer increases in plankton would be consistent with the Peaks of chlorophyll a and zooplankton occurring in July. If the lenses maintained their initial spatial integrity any upwelling which accompanied them would occur on scales beyond those which could be distinguished as distinct pattern by this study.

From the results of this study and others in the region, it

Seems clear that a true seasonal response occurs within the

zooplankton assemblages in the eastern Caribbean. This

variability doesn't appear to be the res

of any instability

within local hydrographic systems, but rather is forced by large

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scale physical changes affecting the whole of the eastern

Caribbean. The question of the exact process or processes:

involved is yet to be resolved.

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THE MEASUREMENT OF ZOOPLANKTON PATCHINESS

Final Report

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Average abundance as well as the intensity of patchiness (degree of aggregation) influence the frequency of encounters among individuals in the plankton and, consequently, both factors play important roles in the dynamics of planktonic communities

Alternatively, differences between communities may be reflected by differences in abundances or patchiness of their component populations. For example, Star and Mullin (1961) inferred differences in habitat features of the nearshore and offshore plankton communities of the California Current from differences in the intensity of patchiness based on variance to mean ratios.

In this note we discuss some difficulties involved in the

measurement of the inten:

y of patchiness (see Pielou, 1977 for
2 more general review). One of the more common and easily
applied methods used in the analysis of spatial pattern is to
measure the deviation of variability observed in a sample set
from a random (Poisson) expectation by the use of various indices
of aggregation. Although these indices have come under criticism
from numerous authors (e.g., Fasham, 1978) they will probably see
continued use given the sampling and analytical difficulties
associated with the use of more sophisticated analytical
techniques, i.e., spectral analysis or the empirical description
of pattern, The variance to mean ratio, s^2/\bar{x} ,
where: S^2 = sample variance, $\sum (Q_i - \bar{x})^2/n$
aston

\bar{x} = the sample mean, $\sum X_i / n$

X_i » the number of individuals per sample

n = the number of samples

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is one of the more frequently employed indices used to statistically describe pattern. because of scaling effects, to be @ valid measure of patchiness the S^2/X ratio must be calculated on individuals per sample basis rather than using values adjusted to some standard unit, i.e., ϕ/m^3 , Index values less than, equal to, and greater than unity indicate even, random and patchy distributions, respectively.

Unfortunately, as previously noted, variance to mean ratios, and other related indices are subject to scaling effects which impair their usefulness as a comparative measure of the intensity of patchiness between sets of samples showing large differences in mean density (Morisita, 1959), Fer instance, given a set of values, x , and $>$ constant multiplicative scaling effect, c , we find that:

variance (cx) = 2

variance (x)

Thus, variance to mean ratios will vary directly with mean density, a feature commonly observed in plankton studies (e.g.

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© 1970). Also, factors underlying differences in mean abundance and patchiness can operate independently in nature and it would be desirable to obtain independent measures of both.

The index used to measure the intensity of patchiness should ideally be insensitive to changes in the average number of individuals per sample. Lloyd's (1967) index of patchiness and

the nearly equivalent Morisita's (1959) Index of Dispersion

generally satisfy these criteria, Lloyd's index of patchiness is

defined as the ratio of mean crowding to mean density, m^*/m ,

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\bar{x} (mean crowding) = mean density of individuals per sample per individual,

$\sum x_i^2 / Dm$

ist

$B = \text{mean density per sample} = \bar{x} / n$

$N = \text{total number of individuals} = \sum x_i$

$n = \text{number of replicate samples} *$

$X_i = \text{number of individuals per sample.}$

In a random distribution, m^* equals m and Lloyd's index is equal to one, Values greater or smaller than unity indicate the Presence of an aggregated or even distribution, respectively.

We present variance to mean ratios and Lloyd's indices to

iness generated by a series of oceanic zooplankton sample sets to illustrate properties of these indices. Samples were taken on alternate days from 30 January to 5 February 1981 at a depth of 20 m from a platform anchored in 1000 m of water off the

southeast coast of Puerto Rico (179 56.3 N, 65° 51.5 W) using an on-deck pumping system. Each sample set consisted of 4 replicates taken approximately at hourly intervals around local noon and midnight, respectively. Samples were filtered through a 202 μ m mesh net for 8 minutes corresponding to a volume of 5.3 m³ and preserved in 4% buffered formalin. A total of 3 major groups (total calanoids, cyclopoids and harpacticoids) and 22 copepod species were used in the calculations. Only replicate samples representing whole counts were used in the calculations to eliminate possible complications arising from subsampling error

(Venrick 1978). Variance to

ratios and Lloyd's index of

Patchiness are based on either 3 or 4 replicates.

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Results plotted against mean densities are shown in Figures 1 and 2. For comparative purposes the 95% C.I. distinguishing the type of pattern represented is shown in the figures.

. 2

Fisher's Index of Dispersion ($\frac{\sum x_i^2}{n} - \frac{(\sum x_i)^2}{n^2}$) and a formula

modified from Morisita (1959) ($\frac{m^2}{m} \frac{N-n}{N}$) were used in

on one

the calculations of the confidence intervals. Results were

similar

about 40% of the sample sets were judged aggregated and

the remainder not significantly different from random. No

examples of even dispersion were noted. With both Lloyd's index

and the variance to mean ratio, apparent randomness may result

from the inability to statistically differentiate a patchy or

even distribution from a random one at low species abundance, a

feature previously noted in both in

studies (Lloyd, 1966 and Wiebe,

1970). This effect is manifested in greater variability in

Lloyd's index and lower variance to mean ratios at low densities.

As expected, testing showed the variance to mean ratios to be

positively correlated with density. The slope of the geometric mean regression (Sokal and Rohlf, 1981) based on log transformed values was not significantly different from 1.0 (95% cuts, 0.78 ~ 1.14), This suggests that the differences observed in variance to mean ratios among zooplankton samples as a whole can be most simply interpreted as constant multiplicative effects of density changes rather than variation in intensity of pattern.

Comparisons of variance to mean ratios among species may require yet undeveloped Model 11 analysis of covariance techniques (Sokal and Rohlf 1981). More importantly, dependence with mean

Densities implies that it is inappropriate to compare variance to

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mean ratio when the mean densities differ greatly among sample sets.

Because of the unequal variability in the Lloyd's index with respect to mean density, the non-parametric Kendall-tau rank correlation was used to test for relationship between the index and mean abundance per sample. No significant correlation was

index and m

detected between Lloyd's index and mean density. It appears then that Lloyd's index does provide a measure of the intensity pattern seen in various copepod species that is independent of their mean density, at least within observed range of densities. The individual indices values for patchiness can therefore be compared directly, although some caution may be advisable in

cases of low density sets.

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