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Habitat dimensions of calanoid copepods in the western Gulf of Mexico

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ABSTRACT

The vertical distributions of 49 species (53 taxa) of calanoid copepods were determined in cyclonic and anticyclonic hydrographic features in the western Gulf of Mexico for three seasons of the year. The relative intensities of the features varied among seasons, while within seasons the physical structure between features was different. Since the same copepod species were present in both features for all seasons sampled, the contrasting hydrography provided a natural experiment in which to study the mechanisms, biological or physical, acting to influence species vertical distribution patterns.

Hierarchial classification analysis revealed that groups of samples characterized by relatively homogeneous biotic characteristics were related more to depth of the sample than to the season or location (hydrographic feature) in which the sample was taken. Species groups defined by the classification analysis also tended to occupy different depth zones, but the species groups overlapped strongly in the vertical dimension. Significant species structure was found as well, with stability of the rank order of species abundances. Both species and vertical structure persisted over time and were resistant to nonseasonal hydrographic variability. A weighted version of multiple discriminant analysis was used to relate the species patterns to the environmental patterns. The most important extrinsic variable correlated with where species were likely to occur was depth, although the depth distributions of chlorophyll and nitrate cannot be ignored. In the absence of corresponding abiotic patterns, biotic factors are suggested as the dominant causative agents of copepod vertical distribution patterns. It is proposed that on a broad scale the observed constancy of copepod species and vertical spatial structure is related to the "nutrient-limited" and "light-limited" physiological regimens documented for oceanic phytoplankton species.

1. Introduction

Many aspects of oceanic ecosystems cannot be studied easily by controlled experimental approaches. Instead, the ecosystem must be observed as it naturally occurs, usually with devices or methods that are rarely 100% efficient or unbiased. In the absence of controlled studies, the investigator must work with correlational data which theoretically are insufficient to prove cause and effect. However, if geographic areas can be found where environmental variables are distributed differently between areas

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while the species composition remains similar, then this would be a natural experiment (Cody, 1974) in which correlations between the biotic and abiotic patterns can be studied.

Such a situation occurs in the western Gulf of Mexico. Previous studies of copepod systematics and distribution in the oceanic western Gulf of Mexico (Park, 1970) indicate little in the way of strong zoogeographic barriers, but strong differences exist in the hydrography of the region. An area of relatively high dynamic height regularly occurs between 22 and 25N, and, north of this high, a region of lower dynamic height is usually present (Merrell and Morrison, 1981). Although the mechanisms by which these hydrographic features occur are under debate (Sturges and Blaha, 1976; Hurlburt and Thompson, 1980; Elliot, 1979), in a region of high dynamic height isoclines of physio-chemical variables are displaced downward along isopycnals, with upward displacement occurring in regions of lower dynamic height. Essentially the only environmental variable expected to exhibit the same depth distribution between features is hydrostatic pressure. Habitat selection by a species on the basis of temperature, for example, would mean that the species occurs at shallower depths in a region of low dynamic height (cyclone) than in a region of high dynamic height (anticyclone).

In this study I present vertical distributions of calanoid copepods collected for three seasons of the year in each hydrographic feature. The sampling design provides information on the variability of the copepod community composition among seasons and between hydrographic features within seasons, as well as the vertical dimension. Classification analysis is used to delimit biotically similar sampling sites, and the biological patterns are related to the environmental patterns with a modified form of multiple discriminant analysis. The modifications include sample weightings which allow utilization of the quantitative components of the biological data.

Classification methods are appropriate when the hypothesis is that species are best regarded as comprising an unknown number of partly dissociated subpopulations (Williams, 1971). The resulting groups, or clusters, of samples are by definition characterized by relatively homogeneous species-assemblages. The distribution of the species-assemblages over an environmentally heterogeneous area should then provide insight into the mechanisms (biological or physical) which separate the species into different assemblages or communities; that is, the habitat dimensions (Whittaker *et al.*, 1973). Species which occupy different niches because, for example, they feed on different types of food in the same place will not be separated. The niche dimensions, that is, the mechanisms which separate species within communities (Whittaker *et al.*, 1973), do not necessarily have to be the same as those that separate species between communities and separate analyses should be carried out at each level. There are indications that the study of niche dimensions in marine planktonic copepods will require measurement of different biotic and abiotic variables on finer time and space scales than that of the present study (Steele and Frost, 1977; Frost, 1980).

2. Materials and methods

a. Sample collection. The data presented here were collected in the western Gulf of Mexico on RV *Gyre* cruise 80-G-1 (April 1980), RV *Columbus Iselin* cruise 80-CI-6 (July 1980), and RV *Gyre* cruise 80-G-11 (November 1980). Biggs *et al.* (1980) have archived the cruise tracks, and Brooks and Eble (1982) discuss the hydrographic data. Zooplankton collections were made with a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) (Wiebe *et al.*, 1976). The system has a mouth area of 1 m × 1.4 m (effective area 1 m^2 when towed at a 45° angle) and fishes nine nets of 333 μm mesh. The system collects nine separate samples each tow by sequentially tripping nets on commands transmitted along conducting cable from the surface. Flow through the net, depth of the system, net angle, and temperature are monitored continuously onboard ship.

Station locations, date, and depth of all tows analyzed in this study are given in Table 1. Station locations and sampling depths were selected in as biologically meaningful a way as possible. Figure 1 shows the contours of the 14°C isothermal surfaces observed during each cruise. On the spring and fall cruises, paired cyclonic "low" and anticyclonic "high" circulation fields were observed, whereas on the summer cruise only an anticyclonic hydrographic feature was clearly present. By maximizing horizontal differences in the depth of the 14°C isotherm the biological stations were selected near the apparent centers of each feature. At each biological station, parachute drogues were set at a depth of 50 m except for the fall cyclonic station where the drogue was set at 130 m. Repetitive MOCNESS tows were taken at each station while following surface buoys attached to the drogue for periods of 2 to 4 days. Depth horizons for each net in each tow were determined from vertical profiles of temperature and relative fluorescence taken immediately before the tow. Depth strata above, below, and within the thermocline and fluorescence maximum layers were thus repeatedly sampled.

b. Sample processing. Formalin-preserved samples were identified and counted (1,000 + individuals per sample), with identification usually to species, sex, and developmental stage. For the purposes of this study, however, adults are not separated on the basis of sex. Flow meter readings from the MOCNESS system were used to calculate abundance per m^3 of water filtered, assuming 100% filtration efficiency. Quantitative counts of calanoid copepods were made only from night hauls in order to adequately document the night–time distribution of the migrating species; *a priori* an unknown portion of the copepod community. Taxa were eliminated from further analysis if they occurred in fewer than 10 samples (frequency of occurrence <20%) or in concentrations less than one individual per cubic meter total abundance. This was done because the data for many of the less frequently occurring or rare species are insufficient for finding meaningful environmental correlations. The data matrix that resulted was 48 samples by 53 taxa (49 species).

Table 1. Date, time, location, and depth of all samples analyzed.

Tow	Date	Time	Location	Environment	Net #	Depth Range (m)
MOC-2	8 April 80	0209	26°7.6'N 94°10.1'W	Cyclone	2	150–200
					3	125–150
					4	105–125
					5	85–105
					6	65–85
					7	45–65
					8	25–45
					9	0–25
MOC-12	12 April 80	2054	23°51.1′ 95°3.3′	Anticyclone	2	160–200
					3	140–160
					4	120–140
					5	100–120
					6	80–100
					7	60–80
					8	30–60
					9	0–30
MOC-14	19 July 80	2140	24°28.6′ 95°1.3′	Anticyclone	2	160–180
					3	140–160
					4	120–140
					5	100–120
					6	80–100
					7	50–80
					8	30–50
					9	0–30
MOC-24	25 July 80	0143	26°23.7′ 95°4.6′	Cyclone	2	150–200
					3	130–150
					4	110–130
					5	90–110
					6	70–90
					7	50–70
					8	30–50
					9	0–30
MOC-52	1 Nov 80	2124	23°47.8′ 95°10.1′	Anticyclone	2	150–200
					3	120–150
					4	100–120
					5	80–100
					6	60–80
					7	40–60
					8	20–40
					9	0–20
MOC-60	8 Nov 80	0109	26°6.8′ 94°6.8′	Cyclone	2	150–200
					3	130–150
					4	110–130
					5	90–110
					6	70–90
					7	50–70
					8	25–50
					9	0–25

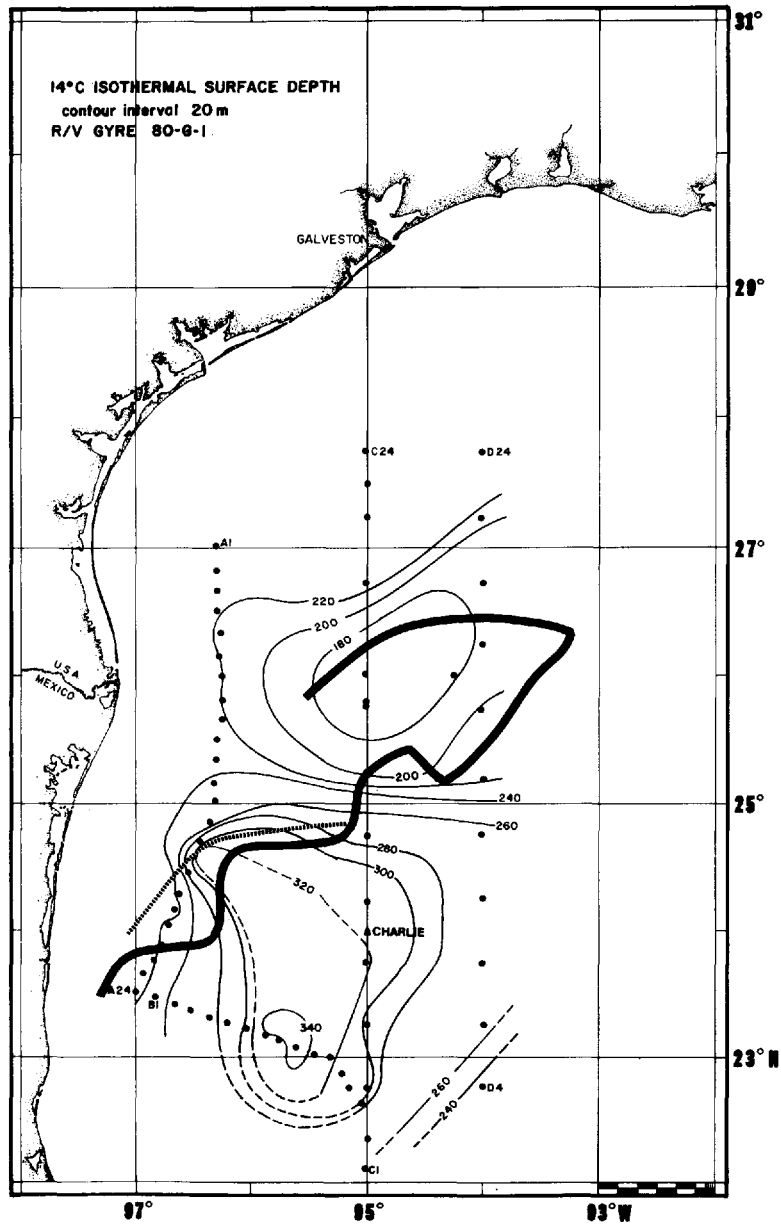

Figure 1. Contoured depth (m) of the 14°C isothermal surface. Uncertain contour lines are dashed. (a) Spring, R/V *Gyre* cruise 80-G-1. The heavy solid line shows the position of a meandering surface thermal front seen in satellite infrared images of the western Gulf taken on April 14–15. The heavy dashed line shows the position of a warm filament associated with the front. (b) Summer, R/V *Iselin* cruise 80-I-6. (c) Fall, R/V *Gyre* cruise 80-G-11 (from Brooks and Eble, 1982).

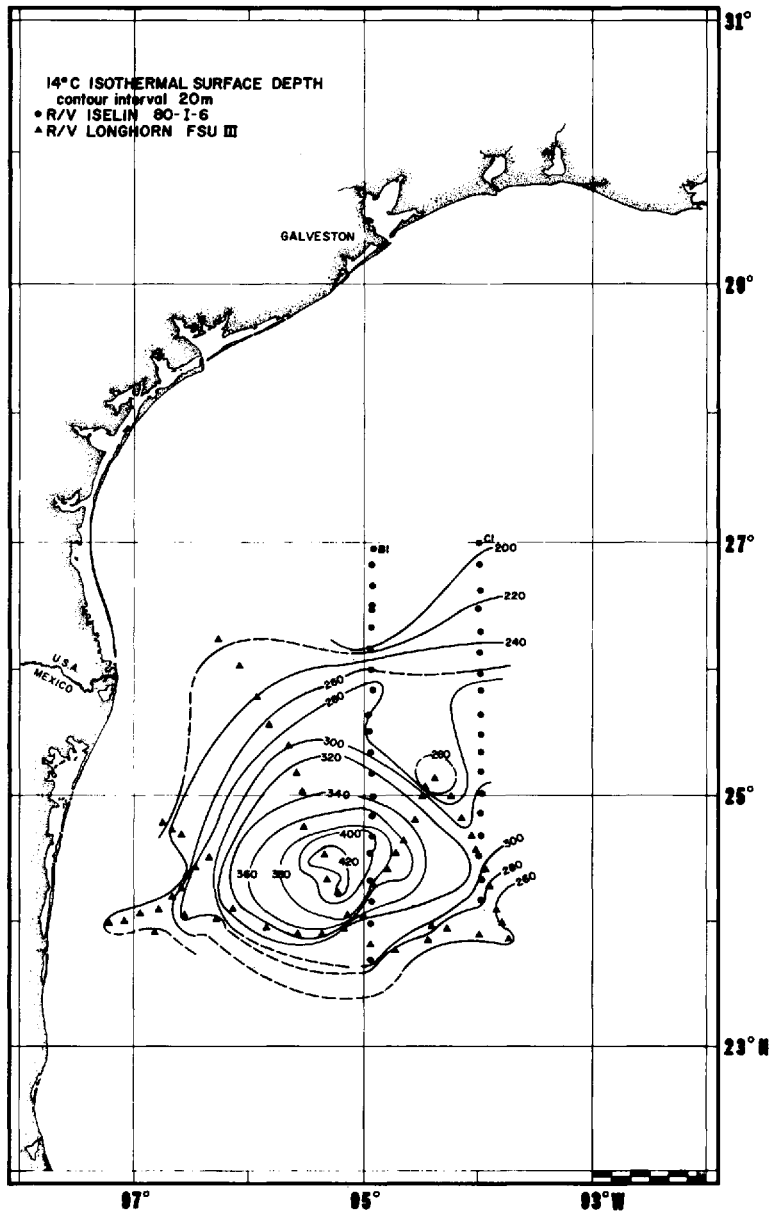

Figure 1. (Continued).

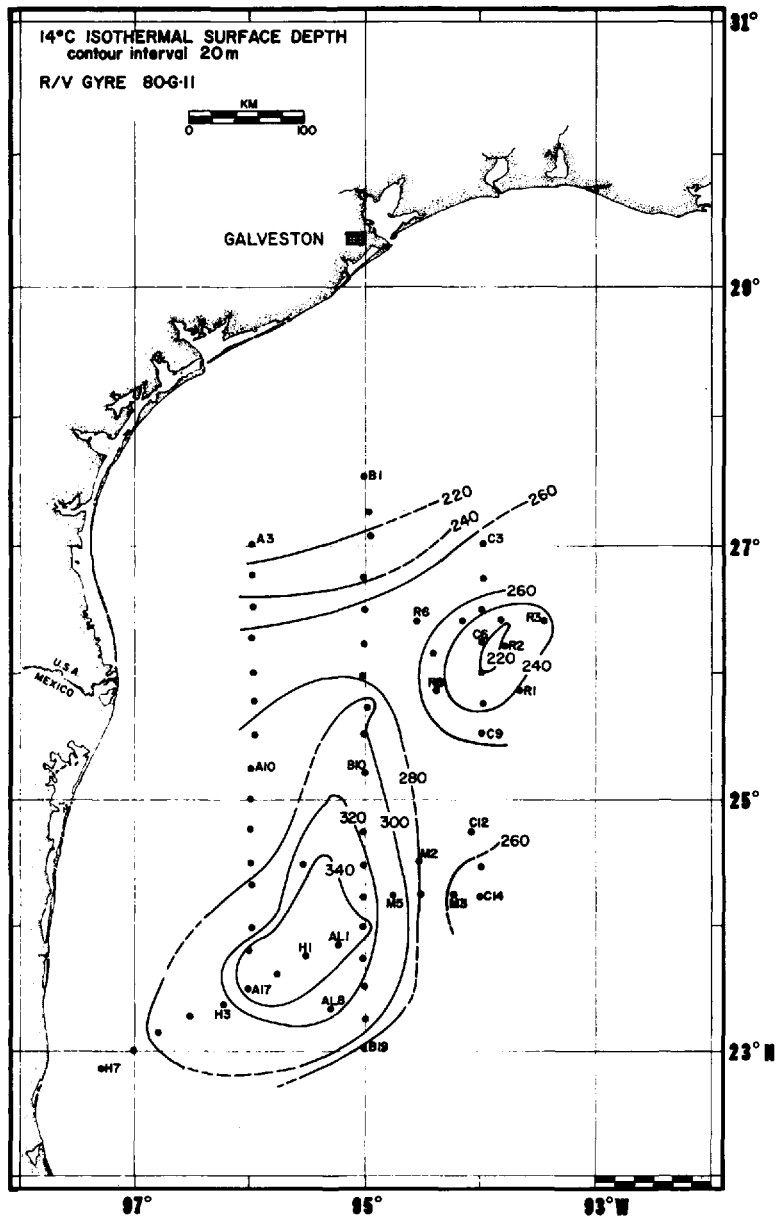

Figure 1. (Continued).

c. Classification analysis. An agglomerative hierarchial classification method was used to define groups of samples which show similar biotic characteristics. The Bray–Curtis index (Bray and Curtis, 1957) was used as the distance measure,

$$D_{ij} = \frac{\sum_{k=1}^{n} |X_{ki} - X_{kj}|}{\sum_{k=1}^{n} (X_{ki} + X_{kj})} \tag{1}$$

$D(ij)$ is the distance between entities i and j, $X(ki)$ and $X(kj)$ are the values of attribute k in entities i and j, respectively, and n is the number of entities. An entity is the unit to be classified (species or samples). Entities with similar attribute measurements will be separated by only a small distance, and those with more dissimilar measurements will be relatively more apart. When biotic data are used, the distances are referred to as "ecological" distances (Whittaker, 1967).

When using the Bray–Curtis measure, the distance contributed by each species to the final ecological distance between two sampling sites is not additive. This is due to the fact that the measure is a single quotient and the contribution of a species in a comparison is partially dependent on the values for the other species at the sites being compared. For this reason, a species standardization is necessary to give each species relatively large standardized values in place of its maximum abundance. Without the standardization, absolute abundance, which will vary from species to species, will be emphasized rather than an estimate of peak occurrence for each species. Following Smith (1976), a square–root transformation was applied to the raw data to remove overdominance of species with highly skewed distributions, followed by a species mean standardization for classification of the sampling sites and a species maximum standardization for classification of the species. The end result of each standardization is the convergence of the scales of the data values for each species. The species mean standardization provides a measure of the abundance level of a species when it does occur and is defined as

$$X_{ij} = X_{ij} / \left(\sum_{j=1}^{n} X_{ij}/n \right) X_{ij} > 0 \tag{2}$$

where X_{ij} is the count of species i in sample j and n is the number of samples. The species maximum standardization rescales each species counts to vary between 0 and 1;

$$X_{ij} = X_{ij}/X_i \,(\max) \tag{3}$$

where X_{ij} is as before and X_i (max) represents the maximum count of species i.

Flexible clustering strategy (Clifford and Stephenson, 1975) with a variable β coefficient of -0.25 was used to construct dendrograms displaying relationships between samples (or species) and groups of samples (or species). The algorithm which

creates the dendrogram was enhanced to give a more meaningful order of entities (Smith, 1976). The distances are used to calculate polar ordination scores (axis 1 only) for each entity (Bray and Curtis, 1957). As the dendrogram is constructed the entity with the lowest average ordination score is placed first on the dendrogram and the entity with the higher average score is placed second. When this is done the order of the entities will tend to follow the main trend in the input data. It also avoids the problem of ties between distance values which can occur in agglomerative classification schemes. When ties occur the distance representing the entities with the lowest average score is chosen first. This should make the results independent of the order of entry of the entities into the program.

In the species analysis the Bray–Curtis index forms groups of species largely dependent on species frequency; species occurring in a similar number of samples are classified together. The problem is most evident in the rare species groups where often the only thing in common is their rarity. To alleviate this, an asymmetric, two step comparison was used (Belbin, 1980). Asymmetry is achieved because comparisons are made only when species are present; species sharing an absence in a sample do not appear more similar. The analysis is run in two steps; the similarity of species i with j will not be the same as the similarity of species j with i, if the species do not always occur together. After the TWOSTEP procedure the distances are rescaled to a maximum value of one. The distances calculated by this procedure are thus related more to relative habitat preference than to a simple measure of species overlap.

d. Discriminant analysis. Multiple discriminant analysis is more commonly used to assign observations to predefined groups, but it can also be used to describe and test between-group differences in ecological studies (Green, 1971, 1974). In such an analysis, each sample is a point in a multidimensional space defined by biotic or abiotic aspects of the environment. The samples are projected onto axes that minimize the within-group variation while maximizing the between-group variation. These axes are independent and are correlated with variables potentially important in group separation. Classification techniques have been used to generate the groups necessary for the analysis (Bernstein *et al.*, 1978), but by weighting the calculations groups can be formed directly from the species-site data matrix (Smith, 1976). This is a way to directly analyze the biological patterns, avoiding any errors of group membership that other techniques (e.g., clustering) may introduce.

In weighted discriminant analysis, each species is a group, and each environmental variable is given a weight proportional to the relationship between the environmental variable and the corresponding group (species). In this study, species abundances are used as weights. These are appropriate weights, since the environmental information at a sampling site in which a species is relatively more abundant is considered more typical of that species than is the environmental information at a site in which the species is less abundant. Completely overlapping species can be distinguished in this way, as long as their relative abundances are not identical in all samples.

Following Smith (1976) the total cross products matrix (T) for the weighted multiple discriminant analysis method was calculated as

$$T_{jm} = \sum_{k=1}^{g} \sum_{i=1}^{N_k} [(X_{ijk} - \bar{X}_j)(X_{imk} - \bar{X}_m) W_{ik}] \tag{4}$$

where T_{jm} is the weighted sum of the cross products of enviromental variables j and m, g is the number of groups (species), N_k is the number of sites in group k, X_{ijk} is the value of variable $j(m)$ in the ith site in group k, and $\bar{X}_j$ and $\bar{X}_m$ are the grand means of variables j and m, respectively, over all sites in all groups, which for variable j is

$$\bar{X}_j = \sum_{k=1}^{g} \sum_{i=1}^{N_k} X_{ijk} W_{ik} / \sum_{k=1}^{g} \sum_{i=1}^{N_k} W_{ik}. \tag{5}$$

The weights (W_{ik}) are a measure of the relative abundance of species k at the ith site. In this study, species maximum standardized values with a prior square root transformation were used as weights. This was done so that each species will have the same weight at its maximum value, since there was no *a priori* reason to assume that a more abundant species is more representative of a sampling site than a less abundant species. Species occurring at more sites will also have more overall weight in the analysis, which is similar to unweighted multiple discriminant analysis where the larger groups also contribute more weight.

The elements of the within-group cross products matrix (D) are calculated as

$$D_{jm} = \sum_{k=1}^{g} \sum_{i=1}^{N_k} [(X_{ijk} - \bar{X}_{jk})(X_{imk} - \bar{X}_{mk}) W_{ik}] \tag{6}$$

where $\bar{X}_{jk}$ and $\bar{X}_{mk}$ are the means of variables j and m, respectively, in group k which for variable j is defined as

$$\bar{X}_{jk} = \sum_{i=1}^{N_k} X_{ijk} W_{ik} / \sum_{i=1}^{N_k} W_{ik}. \tag{7}$$

The among-groups cross products matrix (A) is calculated from the relationship $A = T - D$. The discriminant function vectors and roots are associated with the determinantal equation $|W^{-1}A - \partial I| = 0$. The vectors associated with each root provide the discriminant function coefficients (one coefficient for each variable). Coefficients of separate determination (Hope, 1969), expressed as percentages, were used to interpret the results. In addition, mean values of each important variable in groups defined by the classification analysis of the sampling sites were calculated and related to the positions of the groups in discriminant space. In this way, trends of mean values for a variable at an angle between two axes can easily be observed.

In the weighted version of multiple discriminant analysis, as used here, species are groups separated in ecological space by linear additive functions of ecological parameters. This assumption is usually met with most biotic–environmental data sets

(Green and Vascotto, 1978). In other methods, such as multiple regression analysis with species as dependent variables or canonical correlation analysis, species are supposedly related to the ecological parameters in a linear additive manner. This ignores the fact that the curve of a species abundance along any environmental gradient is usually unimodal, with the maximum at some ecological optimum. In such a case, strict assumptions of linearity are not met and methods requiring linear additive relationships between the species and the ecological parameters are not appropriate (see Pielou, 1977 for a complete discussion). Green (1971) contains a good summary of the statistical assumptions involved in the multiple-discriminant method. Many of the assumptions become less critical when no formal statistical tests in relation to group separation are applied. In this study, evaluation of "success" of group separation was done by plotting the discriminant score of each MOCNESS net in the reduced discriminant space and visually judging group separation on ecologically interpretable discriminant functions. Often, this can be a more conservative approach than the use of powerful multivariate tests of significance.

3. Results

a. Classification analysis. Classification of the samples yielded nine distinct sample groups (Fig. 2). Similarity among samples on the basis of relative abundance of species is related more to sample depth (net number) than season or hydrographic feature in which the tow was taken (MOC number) (compare Fig. 2 and Table 1). From the dendrogram, it can be seen that sample groups G, H, and I are related more to each other than to the other sample groups, which corresponds generally to samples taken less than or greater than 100 m depth. The cohesiveness of the groups (i.e., the internal biological similarity) are about equal, with the exception of groups A and B which are connected highest on the dendrogram. These groups include the shallowest depths sampled, and show the greatest biological heterogeneity. The other groups include progressively deeper samples, and are relatively more homogeneous groups.

Results of the species classification are presented in Figure 3. Six faunal groups are indicated. Table 2 presents summary statistics and Figure 4 shows the depth distributions of the species in their respective groups. By examining individual species depth distributions, it is evident that the species groups tend to occupy different depth zones. Some groups of species tend to show relatively restricted depth ranges (i.e., groups 1, 3 and 6), and the species in these groups are consistent in a statistical sense on where they are most abundant in the water column. In other groups (i.e., groups 2, 4, and 5), the species have broader depth ranges, with some species more abundant at some depths, some at others. Species groups 1, 2, and 3 are related more to each other than with groups 4, 5, and 6, and Figure 4 shows this is due to species in these latter groups being less abundant below 100 m. Hence, both the species and sample groups can be divided into shallow and deep groups, separated by a transition region between

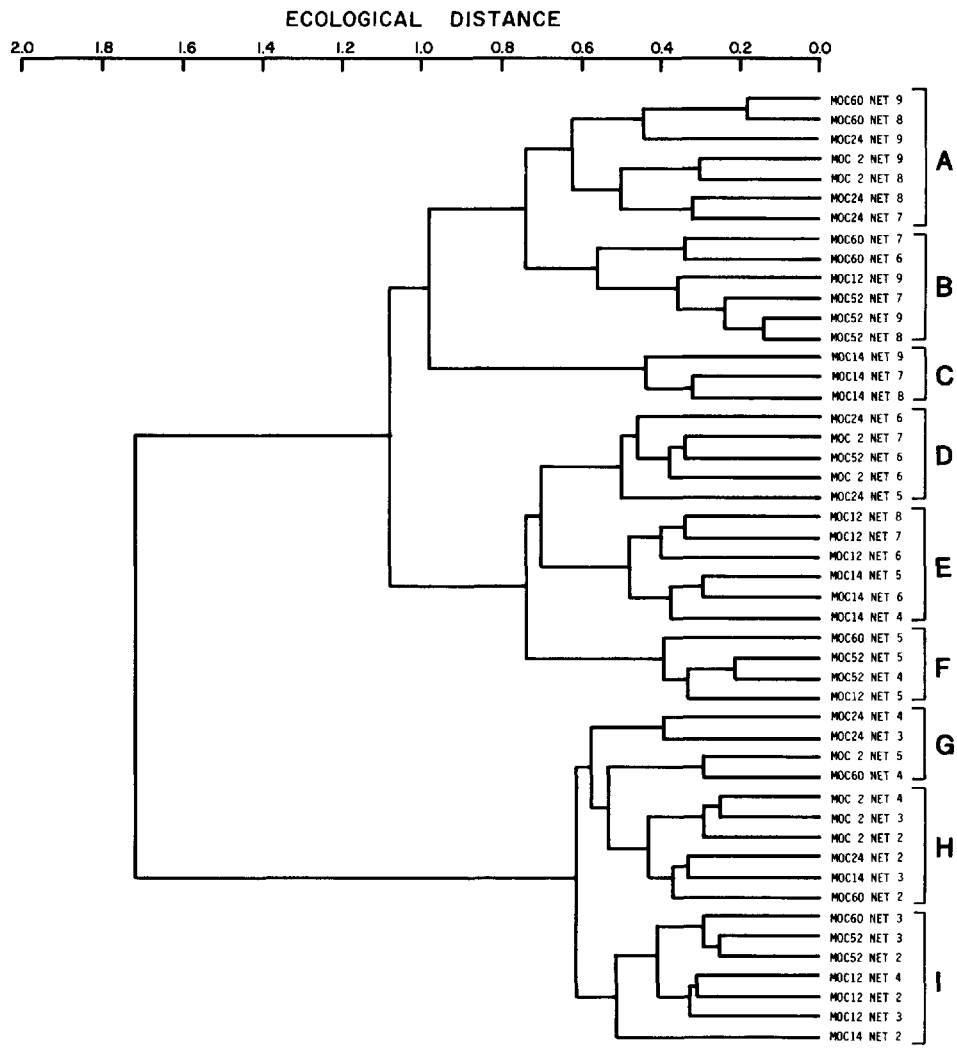

Figure 2. Classification of the sites (MOCNESS samples).

80 and 100 m. As will be shown, this depth range corresponds to that of the chlorophyll maximum layer and nitracline.

All of the species groups tend to overlap in the vertical dimension, in particular groups 4 and 5. Group 4 and 5 species all had high frequencies of occurrence over the entire set of samples, but the classification analysis indicated differences in abundance trends between the two groups. For these species, frequency of occurrence is only weakly dependent upon abundance ($r = .331$); species occurring in the same number of samples differed in total abundance by almost two orders of magnitude. This suggests

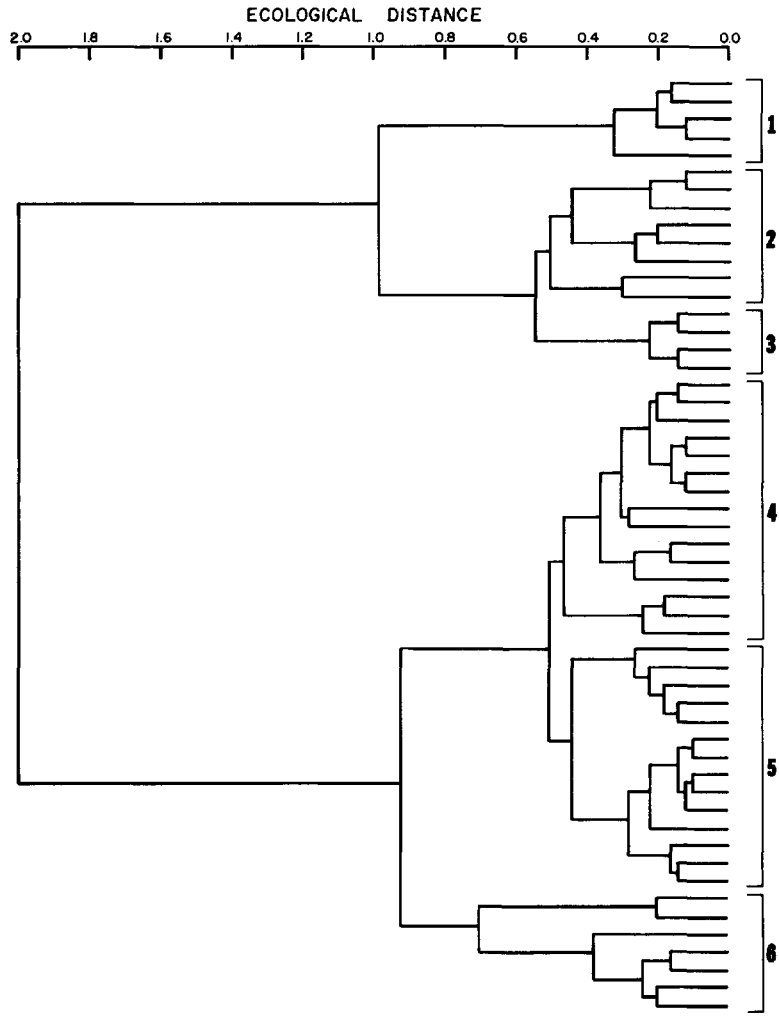

Figure 3. Classification of the species.

differences in patch intensities among species, with group 5 species patches more dense than group 4 species. However, much of this patch structure must coincide in a regular way, since the groups overlap strongly in the vertical dimension.

Constancy of numerical dominance is an important attribute of species structure. The classification analyses revealed that there is a constancy of species vertical distributions between hydrographic features and among sampling times, but the question may be asked, do the same species tend to be dominant in tows taken at different seasons of the year or in contrasting hydrographic regimes? If the rank order of species abundances is not altered by seasonal changes or by hydrographic variabili-

Table 2. Summary statistics of species in their respective species groups. The order of the species is identical to that of the dendrogram in Figure 3. All counts are standardized to #/100 m^3. #OCC—number of occurrences >0.

	#OCC	Total	#/OCC	Mean	Maximum
GROUP 1					
Lucicutia clausi	17	136.0	8.0	2.8	25.1
Chiridius poppei	15	117.8	7.9	2.5	21.4
Scottocalanus securifrons	18	75.3	4.2	1.6	9.3
Haloptilus ornatus	21	119.8	5.7	2.5	17.7
Scottocalanus helenae	10	19.9	2.0	0.4	3.8
GROUP 2					
Chirundina streetsi	21	154.1	7.3	3.2	44.3
Gaetanus minor	23	216.3	9.4	4.5	88.6
Heterorhabdus spinifrons	17	105.4	6.2	2.2	48.0
Euaugaptilus hecticus	15	62.2	4.1	1.3	20.1
Gaidius tenuispinus	12	74.2	6.2	1.5	40.2
Aetideopsis multiserrata	7	104.0	14.9	2.2	48.7
Lucicutia spp.	8	109.4	13.7	2.3	44.3
Aetideus geisbrechti	15	296.6	19.8	6.2	53.0
GROUP 3					
Aetideus acutus	29	1999.0	68.9	41.6	255.9
Haloptilus longicornis	44	9413.0	214.0	196.1	1464.3
Euchaeta media	28	510.4	18.2	10.6	120.5
Haloptilus oxycephalus	19	104.0	5.5	2.2	20.7
GROUP 4					
Heterorhabdus papilliger	46	1320.7	28.7	27.5	101.5
Phaenna spinifera	30	146.1	4.9	3.0	26.6
Euchirella spp. (immatures)	18	108.7	6.0	2.3	26.0
Undeuchaeta plumosa	47	1940.2	41.3	40.4	254.2
Pleuromamma xiphias	39	936.5	24.0	19.5	200.8
Calanus tenuicornis	45	6027.9	134.0	125.6	735.0
Scolecithrix bradyi	30	700.1	23.3	14.6	157.1
Haloptilus acutifrons	17	132.8	7.8	2.8	22.1
Euchirella amoena	14	75.2	5.4	1.6	26.7
Rhincalanus cornutus	33	482.1	14.6	10.0	78.2
Eucalanus monachus	19	470.2	24.7	9.8	156.4
Candacia varicans	18	397.5	22.1	8.3	182.5
Lucicutia gausse	28	978.9	35.0	20.4	140.5
Paracandacia bispinosa	27	713.7	26.4	14.9	91.2
Pontellina plumata	9	101.3	11.3	2.1	39.3
GROUP 5					
Eucalanus hyalinus	14	1450.0	103.6	30.2	782.8
Acartia danae	29	1525.0	52.6	31.8	421.6
Candacia longimana	23	509.1	22.1	10.6	240.3
Eucalanus sewelli	31	1951.4	62.9	40.7	638.7

Table 2 (continued).

	#OCC	Total	#/OCC	Mean	Maximum
GROUP 5 (continued)					
Calocalanus pavo	35	2457.1	70.2	51.2	573.5
Lucicutia flavicornis	48	9662.3	201.3	201.3	964.2
Pleuromamma gracilis	48	7709.7	160.6	160.6	983.8
Neocalanus gracilis	44	2172.1	49.4	45.3	508.3
Pleuromamma abdomalis	42	3155.1	75.1	65.7	843.2
Candacia spp (immatures)	32	895.7	28.0	18.7	128.2
Euaugaptilus longiantennalis	25	983.2	39.3	20.5	144.2
Euchaeta spp (immatures)	45	3731.9	82.9	77.7	613.5
Scolecithrix danae	30	2329.3	77.6	48.5	432.5
Euchaeta marina	24	2749.6	114.6	57.3	528.5
GROUP 6					
Lucicutia gemina	6	161.9	27.0	3.4	87.2
Paracandacia simplex	8	111.3	13.9	2.3	54.5
Temora stylifera	12	777.4	64.8	16.2	545.8
Centropages caribbeaninsis	8	136.2	17.0	2.8	35.1
Undinula vulgaris	18	1620.2	90.0	33.8	472.2
Nannocalanus minor	22	4476.8	203.5	93.3	971.0
Candacia pachydactyla	9	207.7	23.0	4.3	65.4

ty, then this would be evidence for strong species structure as well. Table 3 shows that there are significant rank correlations among integrated water column abundances of the species for all possible tow pairings.

Thus it appears that there are strong trends in both species and vertical spatial structure in the copepod fauna of the western Gulf of Mexico. Since the species tend to occupy different depth zones, they are exposed to different physical and biotic aspects of the environment. It is of interest therefore to determine what environmental factors, if any, are related to differences among samples in terms of their biological properties (i.e., species composition). A modified form of multiple discriminant analysis was used to investigate these relationships.

b. Multiple discriminant analysis. Parameters chosen to make up the original discriminant space are as follows:

1. Temperature—This effects all biological rate processes, and energetic or demographic advantages have been postulated for copepods exposed to variations in temperature (McLaren, 1974). In this study, temperature exhibited the greatest variation of the environmental parameters; primarily because horizontal differences in temperature were maximized in locating each station. Figure 5 shows the vertical temperature structure observed on the MOCNESS hauls. The upper 75 m of the western Gulf of Mexico shows strong seasonal effects, while below 75 m differences between the cyclonic and anticyclonic features dominate the temperature profiles.

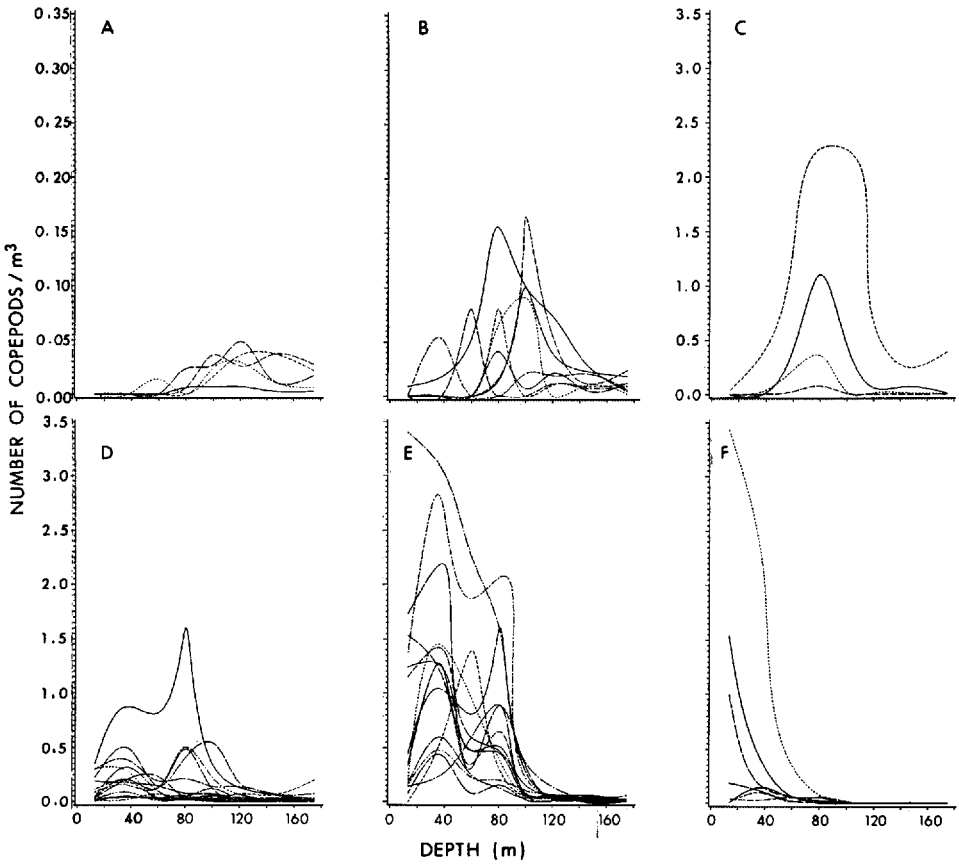

Figure 4. Depth distributions of species groups defined by classification analysis. Individual curves were obtained by plotting the mean abundance values for each depth stratum sampled, at the midpoints of the strata. Curves were fit by smoothing straight line connections between the points. (a) Species group 1, 5 species; (b) Species group 2, 8 species; (c) Species group, 3, 4 species; (d) Species group 4, 15 species; (e) Species group 5, 14 species; (f) Species group 6, 7 species.

Table 3. Spearman ρ rank-order correlation coefficients. (*$p < .01$). See Table 1 for information on MOCNESS tow numbers.

	MOC12	MOC14	MOC24	MOC52	MOC60
MOC2	.710*	.625*	.644*	.525*	.554*
MOC12		.620*	.663*	.785*	.790*
MOC14			.546*	.560*	.519*
MOC24				.590*	.783*
MOC52					.775*

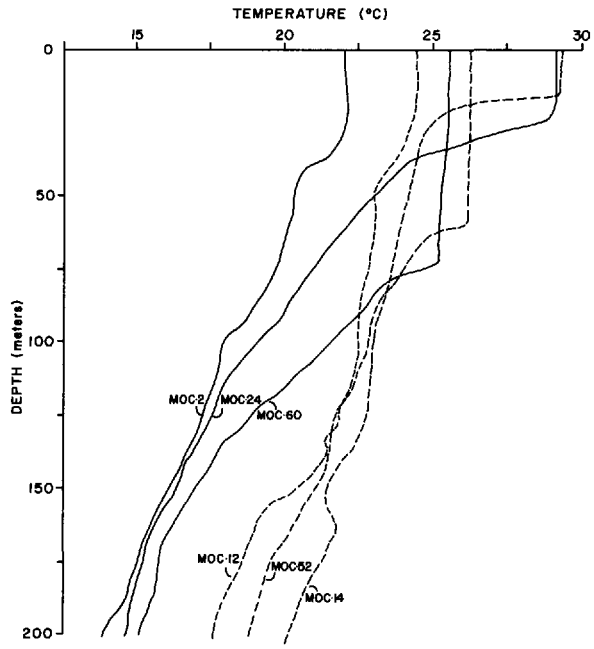

Figure 5. Temperature profiles from MOCNESS casts used in the seasonal data study. Solid line—tows taken in the cyclonic feature; Dashed line—tows taken in the anticyclonic feature. See Table 1 for further information on MOCNESS numbers.

2. Chlorophyll *a*—As an estimate of phytoplankton abundance, the concentration of chlorophyll *a* is clearly important to herbivores and to first-order carnivores that prey upon them. Chlorophyll *a* exhibited subsurface maxima in both features for all seasons sampled, but differences exist in the location and strength of the maximum among seasons and between features (Fig. 6). No chlorophyll extractions were performed on the summer cruise, so relative fluorescence had to be used as an indicator of phytoplankton abundance in the discriminant analysis. Fluorescence maxima are chlorophyll maxima, but because of variation in the amount of chlorophyll *a* per cell and the fact that fluorescence is subject to variations in the nutritional history of the cells (see Cullen, 1982), fluorescence profiles for each MOCNESS cast were standardized to fluorescence maximum values.

3. Salinity—Anticyclonic rings which separate from the Loop Current and migrate westward are at first distinguishable by a core of high salinity subtropical underwater at approximately 130–150 m. Waters within this core have salinities greater than 36.60‰ while Gulf Common Water at similar depths typically has salinities of about 36.45‰ (Merrell and Morrison, 1981). In the western Gulf of Mexico, copepod species composition may vary with salinity because species otherwise not typical of the western Gulf may be advected within the high-salinity core of subtropical underwater.

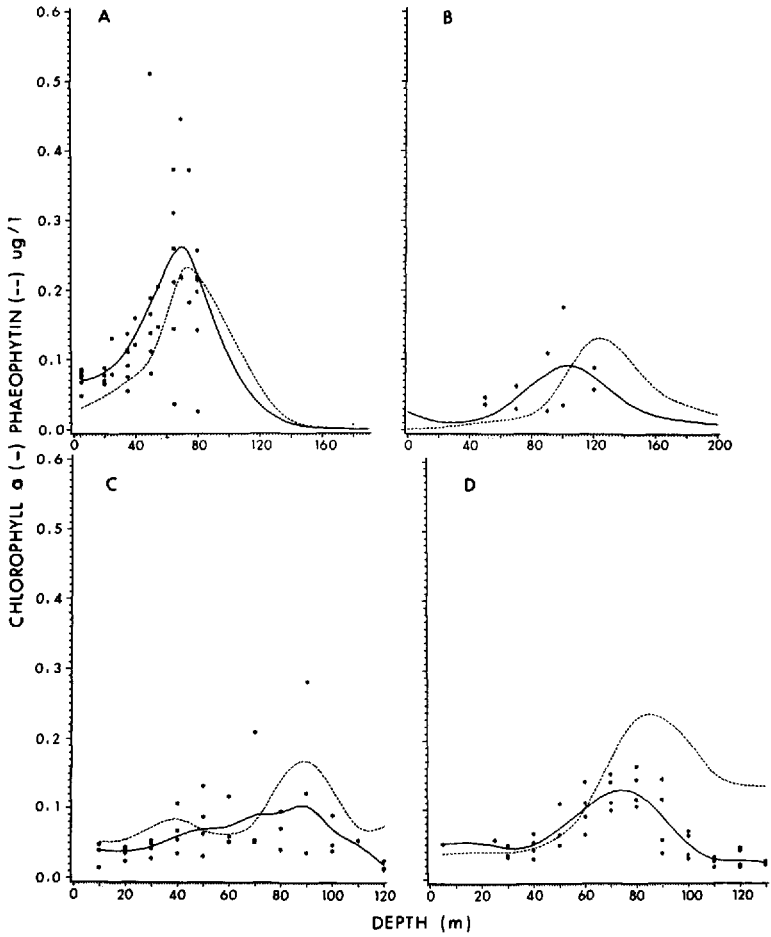

Figure 6. Vertical distributions of chlorophyll *a* (solid lines) and phaeophytin (dashed lines). The lines are smoothed averages of extracted values. For depths where no extractions were made, chlorophyll and phaeophytin were estimated from regression relationships with relative fluorescence. Individual extracted chlorophyll values (*) are shown to illustrate horizontal variability of chlorophyll along each drogue path. Individual phaeophytin values are not shown to increase clarity. No chlorophyll extractions were made on the summer cruise. (a) Spring cruise, cyclonic feature; (b) Spring cruise, anticyclonic feature; (c) Fall cruise, cyclonic feature; (d) Fall cruise, anticyclonic feature.

4. Oxygen—Avoidance of low oxygen environments by copepods has been observed off Peru (Judkins, 1980), but in areas where an oxygen minimum is a permanent feature in the water column, day depths of vertically migrating species have been found to be within the low oxygen layer, presumably advantageous for metabolic reasons (Childress, 1975). Longhurst (1967) found that oxygen levels below 0.2 ml/l may constrain the vertical distribution of zooplankton. Although not falling below 2.5 ml/l

Table 4. Weighted discriminant analysis of Gulf of Mexico copepods.* A. Discriminant functions (axes). B. Coefficients of separate determination (%).

A.

Axis	Root	%	Cum. %
1	11.93	66.3	66.3
2	1.64	9.1	75.3
3	1.44	8.0	83.3
4	1.17	6.5	89.9
5	0.82	4.6	94.5
6	0.67	3.7	98.2
7	0.32	1.8	100.0

B.

Variable	Discriminant Axes						
	Axis1	Axis2	Axis3	Axis4	Axis5	Axis6	Axis7
Z	61.8	3.2	6.7	3.3	0.4	1.1	4.0
T	4.4	0.4	23.1	8.3	26.3	31.1	0.1
S	0.6	0.8	1.6	4.2	21.7	10.6	60.1
NO_3	11.5	0.6	23.7	59.7	10.3	6.0	11.3
O	21.6	7.8	25.4	13.4	1.8	49.9	1.5
C	0.0	85.5	11.3	0.3	0.9	0.1	1.0
dT/dz	0.1	1.7	8.2	10.9	38.4	1.3	22.0

*Definitions: *Z*-depth (m); *T*-temperature (°C); *S*-salinity (‰); NO_3-nitrate (μg-at/l); O-oxygen (ml/l); *C*-relative fluorescence (an index of chlorophyll *a*); *dT/dz*-change in temperature with change in depth.

in the present study, oxygen is included in the analysis since the discriminant method is used here as an exploratory tool. It was considered more meaningful to follow the suggestion of Pielou (1977) and include in the analysis all measured variables even though they may or may not affect copepod distributions directly.

5. Nitrate—Large gradients in nitrate exist in the upper 130 m of the western Gulf of Mexico. The gradient is most likely due to a curtailment in the flux of the nutrient salt into the upper layers by consumption at a sufficiently high rate by phytoplankton in the chlorophyll maximum. Nitrate was undetectable at the surface, and exceeded 1 μM immediately below the fluorescence maximum. The depth distribution of nitrate is thus a consequence of the interaction between phytoplankton growth and light, and represents distinct ecological depth zones (Eppley *et al.*, 1973; Venrick, 1982).

6. *dT/dz*—The density gradient of the water column in the western Gulf is due mostly to temperature variations with depth (Merrell and Morrison, 1981). *dT/dz* therefore is an indicator of strong density gradients, independent of the magnitude of temperature. Harder (1968) and Boyd (1973) have shown that zooplankton tend to

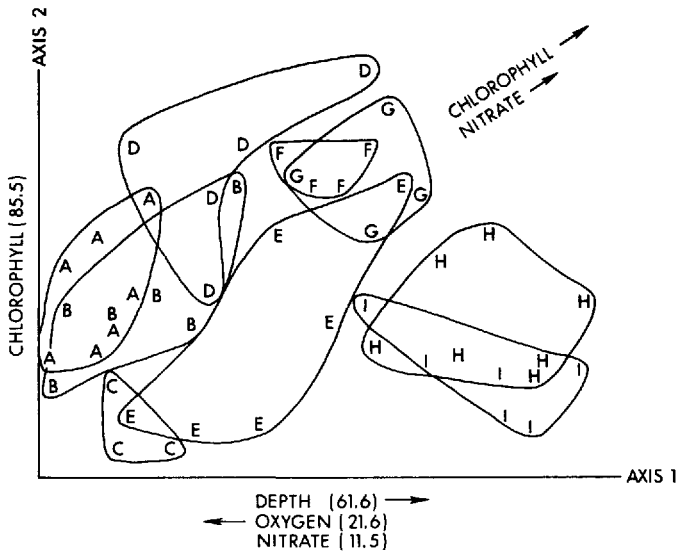

Figure 7. Placement of the MOCNESS samples in the plane created by the first two discriminant axes. External variables important in constructing axes are shown along each axis, and arrows indicate direction in which external variables increase along axes. Coefficients of separate determination (%) for each external variable are given in parentheses. The site groups defined by the classification analysis are enclosed within envelopes and appropriately labeled (See Fig. 2).

accumulate at density discontinuities, and Backus *et al.* (1969) note that midwater fishes often aggregate at the bottom of the thermocline.

7. Depth—Depth (hydrostatic pressure) was entered directly into the discriminant analysis since it could represent environmental parameters not measured in this study, but varying with depth in similar ways (i.e., linearly).

Table 4 presents the eigenvalues and coefficients of separate determination for the discriminant axes. Figure 7 is a plot of the discriminant scores of the samples in discriminant space. The sample groups defined in the classification analysis are enclosed within envelopes, but it should be remembered that the classification analysis was not used to generate the groups used in the discriminant analysis; the two analyses are independent. Discriminant axis 1 explains 66.3% of the total variance, and is related primarily to depth and secondarily to oxygen and nitrate. The second axis explains an additional 9.1% of the variance, with chlorophyll contributing heavily to axis 2. From Figure 7 and Table 5, it can be seen that depth increases and oxygen decreases along axis 1, while chlorophyll and nitrate both increase toward the upper ends of axes 1 and 2. This oblique relationship of chlorophyll and nitrate shows that the effects of depth and oxygen cannot be considered without reference to these variables. Sample groups ABD, CEFG, and HI were completely separated by the first two

Table 5. Mean values, in samples that make up the site groups, of discriminant axis 1 and 2 variables. [Depth (m); oxygen (ml/l); nitrate (μg at/l)]. Chlorophyll was measured as relative fluorescence and has been rescaled to vary between 0 and 1 within each profile. Higher values indicate more samples in or near the chlorophyll maximum layer.

Site group	Depth	Oxygen	Nitrate	Chlorophyll
A	30.4	4.94	0.14	0.45
B	40.8	4.93	0.13	0.41
C	40.0	4.97	0.0	0.06
D	76.0	4.45	2.30	0.84
E	89.2	4.88	0.26	0.49
F	102.5	4.54	1.30	0.73
G	118.7	3.26	10.43	0.59
H	154.3	3.75	6.61	0.42

discriminant axes (Fig. 7). Neither axis 3 nor any subsequent axes separated the groups further.

Temperature did not have a high coefficient of separate determination until axis 3, which was constructed chiefly by variables important to the first two axes. Depth, temperature, nitrate, and oxygen were all correlated with each other ($|r| > 0.6$, Table 6), suggesting some redundancy among these variables in the discriminant analysis. This is particularly true for depth and oxygen, since they vary along axis 1 in similar ways. Temperature, however, does not correspond with species separation in either space or time, and thus is not emphasized in the discriminant analysis. This result was unexpected, since copepods have been used previously as indicators of various water masses (e.g., Grice and Hart, 1962), suggesting that their life cycles are, in certain cases, intimately tied to the prevailing physical conditions (i.e., temperature and salinity). The result is also in contrast with that of Wiebe and Boyd (1978), who found that the euphausiid, *Nematoscelis megalops,* remains in its preferred temperature range even though this range sinks continuously as the cold-core ring of the Gulf Stream ages. The lack of an effect of salinity in this study may be due to the fact that the high subtropical underwater salinities in a newly separated Loop Current eddy can be eroded by wind mixing as the eddy drifts across the Gulf (Elliot, 1979). This

Table 6. Between-sample simple correlation matrix for environmental variables in the weighted discriminant analysis. dT/dz—change in temperature with change in depth.

	T	S	N	O	C	dT/dz
Depth	−0.67	0.13	0.65	−0.67	−0.05	0.08
Temperature (T)		0.13	−0.71	0.76	0.06	−0.19
Salinity (S)			−0.38	0.14	0.21	0.04
Nitrate (N)				−0.84	−0.35	0.04
Oxygen (O)					0.26	−0.10
Chlorophyll (C)						0.27

essentially limits the utility of the subtropical underwater salinity maximum as an effective tracer, and it may also indicate that the eddy does not remain ecologically distinct from surrounding water masses. Physical mixing processes as well as copepod migrations into and out of the eddy would tend to dilute any original differences in species assemblages.

Removal of depth from the analysis does not alter the relative importance of the remaining variables. Since oxygen is linearly correlated with depth, it replaces depth as the most important factor. From this it can be concluded that the large contribution of depth to the first discriminant axis does not mask the importance of any of the other included variables in explaining variations in vertical distributions of copepods in the western Gulf of Mexico. Species vertical distribution patterns apparently can be described by any monotonic function increasing (or decreasing) along the depth gradient.

4. Discussion

At the onset of this study a natural experiment was proposed. The vertical distributions of calanoid copepods in contrasting hydrographic features were sampled at different seasons of the year in hopes of discerning the mechanisms acting to influence species distribution patterns in the upper 200 m of the water column. Classification analysis revealed species and sample groups arrayed primarily as functions of depth. Strong species structure was found as well, with stability of the rank order of species abundances. Both species and vertical structure were stable despite differences in sampling times (seasons) and locations (hydrographic features). Thus, the structural trends observed persist over many copepod generations and are resistant to strong hydrographic variability by the mesoscale circulation features. The application of multiple discriminant analysis showed that clusters of samples characterized by relatively homogeneous species assemblages tended to occupy different positions in environmental space, although there was some degree of overlap. The primary habitat dimension was found to be depth, although the depth distributions of chlorophyll and nitrate cannot be ignored. Hence, it appears that only one dimension (the vertical) need be considered to describe calanoid copepod distribution patterns in the western Gulf of Mexico. The observed structure is due primarily to groups of species having separate centers of abundance along vertical environmental gradients. This result is similar to that of Angel and Fasham (1974) in the Canary Current, Marlowe and Miller (1975) in the subartic gyre of the North Pacific, and McGowan and Walker (1979) in the North Pacific central gyre, for copepods as well as other zooplanktonic species groups. In each of the above studies, species groups, defined by either factor analysis or recurrent group analysis, were found to occupy different vertical strata.

The mesoscale ring structures in the western Gulf of Mexico appear to provide relatively stable physical environments for their respective copepod species assemblages. The anticyclone is a persistent flow feature in the western Gulf, evident in

multiyear north-south dynamic topography sections (Nowlin, 1972). Ichiye (1962) has proposed that detached Loop Current eddies could drift across the Gulf and maintain the western anticyclonic circulation. The numerical studies of Hurlburt and Thompson (1980) support this conclusion, suggesting that the eddy shedding is a continuous process. On the other hand, the cyclone located north of the anticyclone is a less persistent feature (Fig. 1), and mechanisms of its creation and maintenance are not well understood (Elliot, 1979; Merrell and Morrison, 1981). Nevertheless, despite temporal variability in the hydrographic structure of the western Gulf, the analyses presented here tend to suggest that the anticyclone is not distinct biologically from the cyclone either when it is clearly present or when it is not. The calanoid copepod species in the western Gulf have apparently evolved toward close association with other species, producing groups of species with similar distribution patterns. These patterns exhibit stable structure along vertical environmental gradients with boundaries sharper than can be explained by physical–chemical factors alone. This suggests strong biological regulating mechanisms underlying the observed vertical stratification in the western Gulf of Mexico.

The mechanisms creating and maintaining the contrasts in the copepod communities among depth zones cannot be determined directly with the available data. Although depth was found to be the most important extrinsic factor correlated with where species are likely to occur, the depth gradient is of doubtful direct biological significance. Copepods and other planktonic crustacea can be behaviorally affected by small changes in hydrostatic pressure (Knight-Jones and Morgan, 1966), but it is more likely that the species are responding to biological cues not measured in this study which vary with depth in similar ways.

In the discriminant analysis, measured variables important in group separation were those controlled in large part by biotic interactions (i.e., chlorophyll and nitrate). The controlling processes are primarily functions of light, and thus there is a strong depth component. The importance of depth and the oblique relationship of chlorophyll and nitrate in discriminant space may be interpreted as evidence for different mechanisms operating within different contiguous depth zones. The classification analyses revealed that the simplest structure for both species and sample groups is a two-layer system, separated by a transition region in the vicinity of the nitracline and chlorophyll maximum layer. In the North Pacific central gyre, Venrick (1982) found two distinct assemblages of phytoplankton species also separated at the depth of the chlorophyll maximum layer and nitracline. While copepods do not subsist on chlorophyll and it is unreasonable to assume that zooplankton respond to depth variations in nitrate directly, these findings are suggestive considering the similarities of the physical environment and copepod species composition between the North Pacific central gyre and western Gulf of Mexico. The recurring associations of oceanic phytoplankton species were related to "nutrient-limited" and "light-limited" physiological regimes (Eppley *et al.*, 1973), which represent ecologically distinct depth zones (Venrick,

1982). Since copepods tend to select food particles on the basis of size and shape (Harbison and McAllister, 1980), the phytoplankton species assemblages may represent qualitatively different food resources if particle size or shape varies between physiological regimes. Hence, it is tempting to speculate that, at least for herbivorous and possibly omnivorous copepod species in oligotrophic oceanic waters, vertical species structure is related to the physiological regimes of the phytoplankton, perhaps along habitat dimensions of prey (particle) availability.

Within the shallow and deep groups in the classification analyses there are smaller species and sample groups which tend to divide the water column further. This may reflect additional partitioning of the resources arrayed along the water column, or it may represent habitat selection on the basis of other factors, such as predator intensity or the presence of competitors. One cannot at this time evaluate the biological meaning of these smaller groups.

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