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Density distribution of copepods in coastal feeding grounds of herring[1]

by

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Abstract

Examination of seasonal changes in the densities of the dominant copepods in coastal waters of the western Gulf of Maine indicated that the depth of the water column rather than any particular range of temperature or salinity is the most important environmental factor shaping distributions. Thirty-six species were in the collections. Distributions of the seven most numerous are discussed. Two species, Pseudocalanus minutus and Calanus finmarchicus constituted over 70 percent of the biomass of copepods in winter, spring, and summer; three species accounted for 85 percent of the biomass in autumn, P. minutus, Temora longicornis and Centropages typicus. The smaller species were in greatest densities over shoal areas; concentrations of larger species were in the adjacent deeper waters. Densities of copepods were significantly greater in the western area of the coast where conditions for feeding and growth were better in the stratified waters than in the turbulent horizontally mixed waters in the eastern area. Vertical distributions were variable. Except for occasional swarming of copepodites at the surface greatest densities of P. minutus and C. finmarchicus were in the mid to lower levels of the water column sampled. Distributions of herring in zooplankton gradients are discussed with regard to possible concentrating mechanisms.

Introduction

Over the past 10 years, the average annual landings for young herring in the fishery in western Gulf of Maine coastal waters have been about 20,000 metric tons. Availability of herring to the fishery based largely on age-classes 1 and 2 is variable. To investigate the effects of environmental changes on the abundance and availability of the coastal herring a study was undertaken of their zooplankton food base. Among the zooplankters eaten, copepods are the most important constituents (Battle et al., 1936; Legare and Maclellan, 1960; Sherman and Honey, 1968, 1971; Sherman and Perkins, 1971). Earlier reports described the coastal zooplankton assemblage (Sherman, 1968). In this study maximum densities of copepods are located and examined with respect to hydrography and possible relationships to herring distributions.

Methods

Collections of copepods and associated hydrographic observations were made on four seasonal cruises (winter, spring, summer, and autumn) in 1966 between Cape Ann, Massachusetts, and Machias Bay, Maine. Comparisons of copepod distributions were made among three coastal areas described in an earlier report (Sherman, 1968),---western, Cape Ann to Cape Elizabeth; central, Cape Elizabeth to Mt.

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Desert Island; and eastern, Mt. Desert Island to Machias Bay. In each area, collections were made from the seaward ends of two estuaries to the 100 m isobath, a distance of approximately 28 kilometers from the coast. Station locations and periods of sampling are given in Fig. 1. At each station calibrated Clarke-Bumpus samplers were towed simultaneously at the surface, 10, 30, and 60 m depending on bottom topography. Tows were made during daylight. The mouth opening of the sampler measured 12.7 cm, and the net apertures were 0.366 mm nylon mesh, limiting the collection to late copepodites and adults. All tows were made between two and three knots for 15 minutes, and strained approximately 15 m^3 of water per sampler. At each towing location a bathythermograph was lowered and a Nansen cast for salinity samples was made. In the laboratory to obtain subsamples of about 500 organisms, the zooplankton samples were divided into aliquots ranging from a half to a sixty-fourth depending on the mass of the sample, and sorted into major taxonomic groups. Copepods were identified to species, and the numbers of copepods per 10 m^3 of water were calculated. Species distributions of copepods were compared for seasonal changes in abundance among the three coastal areas, and from inshore to offshore along each of the 6 transects. Individual statistics to measure the relative abundance of the species were obtained from the dominance method of Fager and McGowan (1963). The Kruskal-Wallis analysis of variance and Mann-Whitney U tests (Siegel, 1956) were used to test for differences in abundance along the coast. Inshore-offshore comparisons were made on transects with four or more stations by plotting a scatter diagram of copepod abundances at stations arranged sequentially from inshore to offshore, showing their gradients of abundance and testing the relationship with the Spearman rank correlation coefficient (r_s). Species abundances were plotted on distributional charts of temperature, salinity, and bottom topography along each transect to examine the data for possible relationships between copepods and water types. Observed changes in vertical distributions are considered only with respect to large scale seasonal differences as calanoids are known to respond rapidly to changes in illumination (Banse, 1964; Sherman and Honey, 1970) and collections were made at various times of the day under widely differing light conditions. The percentage occurrence of the eight dominant species was plotted by depth to compare seasonal distributions within the water column in each of the areas. Profiles of vertical distributions are based on the mean-number-at-depth for both inshore (0-10 m) and offshore (0, 10, 30 m and 0, 10, 30, and 60 m) plankton tows. In locations where the combined mean of a species within the water column was $\leq$ 50 organisms/10 m^3 of water strained, no vertical profiles were prepared.

Hydrography

Temperature and Salinity

Measurements were made of temperature and salinity to distinguish water types and frontal zones, and to investigate their possible influences on the distribution of copepods.

Bigelow (1927), in his classic study of the physical oceanography of the Gulf of Maine, described the seasonal variations in temperature and salinity of the waters along the Gulf coast. His major conclusions were that: (1) the seasonal variations in temperature and salinity of the inner Gulf are the result of the atmospheric changes characteristic of the North Temperate climate, rather than

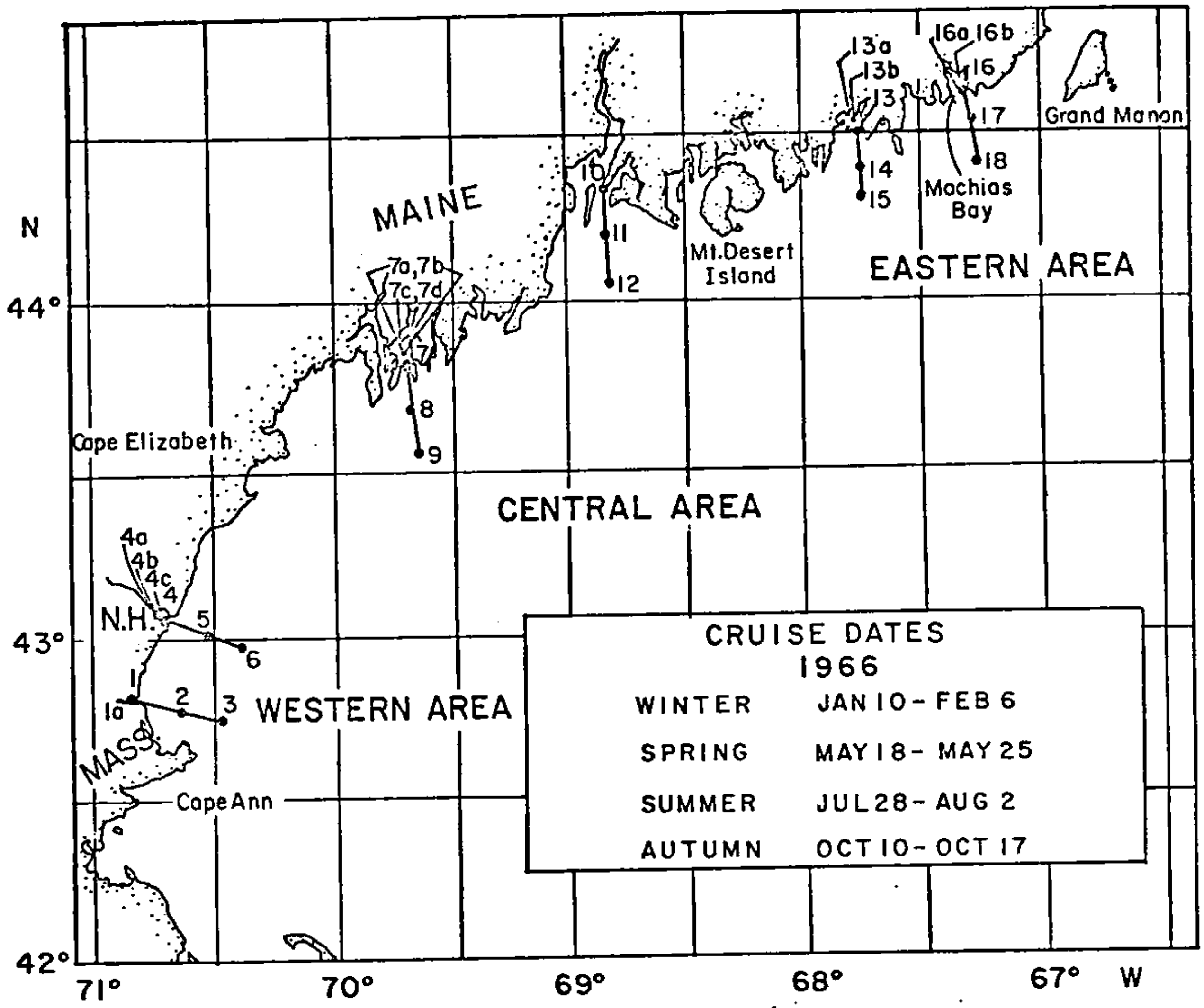


Fig. 1. Cruise dates and station locations for three coastal areas sampled in the western Gulf of Maine.

from any large-scale advection of warm or cold water; (2) water temperatures are largely influenced by changes in air temperature and the velocity and direction of winds; (3) the dominant cyclonic eddy system of the Gulf is generated by the spring runoff from the rivers of the northern New England coast; and (4) the seasonal variations in salinity are caused by river runoff which reduces the coastal salinity to an annual low in spring; salinities subsequently increase to an annual high in winter through wind and tide induced mixing in the water column.

In the present description of the seasonal variations of temperature and salinity, the causative agents of the changes described have been based on the findings of Bigelow (1927) which have been corroborated recently by Hurlburt (1968) and Graham (1970).

In winter, conditions are similar along the coast. The waters are mixed vertically under the influence of the winds. Temperatures throughout the water column are low (< 4.5°C); the difference from surface to bottom is less than 1°C. The lowest temperatures are within the estuaries. Salinities are at the annual high; waters greater than 32.0 o/oo bathe the coastal region to the seaward ends of the estuaries (Fig. 2).

Temperatures in spring decrease from west to east along the coast. The base of the developing thermocline is between 20 and 30 m in the western and central areas. In the east the considerable range of tides (4 to 6 m) generate vertical mixing through the water column, inhibiting the formation of a thermocline and resulting in lower temperatures. The highest temperatures are in the shallow waters of the estuaries. The range of temperature within the water column decreases from west to east. Salinities are reduced by river runoff, which displaces the 32.0 o/oo isohaline to below 20 m along the coast; the greatest salinity gradients are within the estuaries (Fig. 2).

Coastal water in the western area in summer is highly stratified; the base of the thermocline is diminished eastward where the water column is well mixed through tidal stirring. Surface temperatures are warmer in the western area than in the east. Bottom temperatures, however, are cooler in the western area (< 5.0°C), where the stability of the water column inhibits vertical mixing. The dilution of the salinity in coastal waters is greatly diminished following the spring freshets. Waters greater than 32.0 o/oo salinity move toward the surface and shoreward. The estuarine advance of the outer coastal water is limited, and sharp salinity gradients are formed in the seaward ends of the estuaries (Fig. 3).

The cool air temperatures and increased wind velocities of autumn reduce the thermocline gradient; bottom waters mix with the warm waters of the upper strata bringing bottom temperatures to an annual high. In the western Gulf the temperatures of the upper waters are about 4°C cooler than in summer; bottom temperatures, however, advance in this area about 2°C over summer. In the eastern area tidal stirring maintains similar temperatures through the water column. Salinities are near the winter maximum; the 32.0 o/oo isohaline is close to the surface. Gradients of salinity are sharpest in the estuaries where waters are generally less

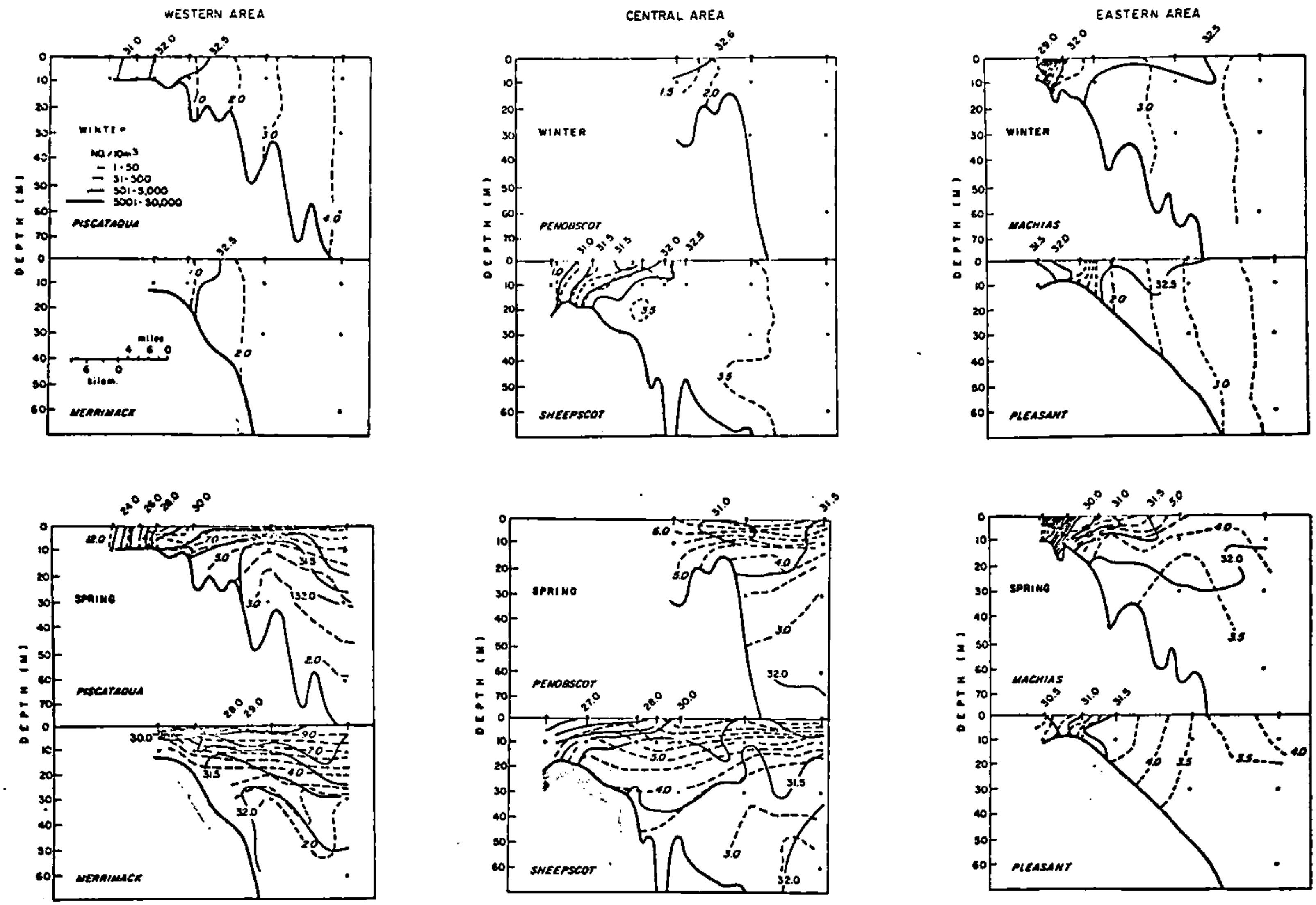


Fig. 2. Vertical profiles of temperature, salinity and station locations in winter and spring along six transects in coastal waters of the western Gulf of Maine.

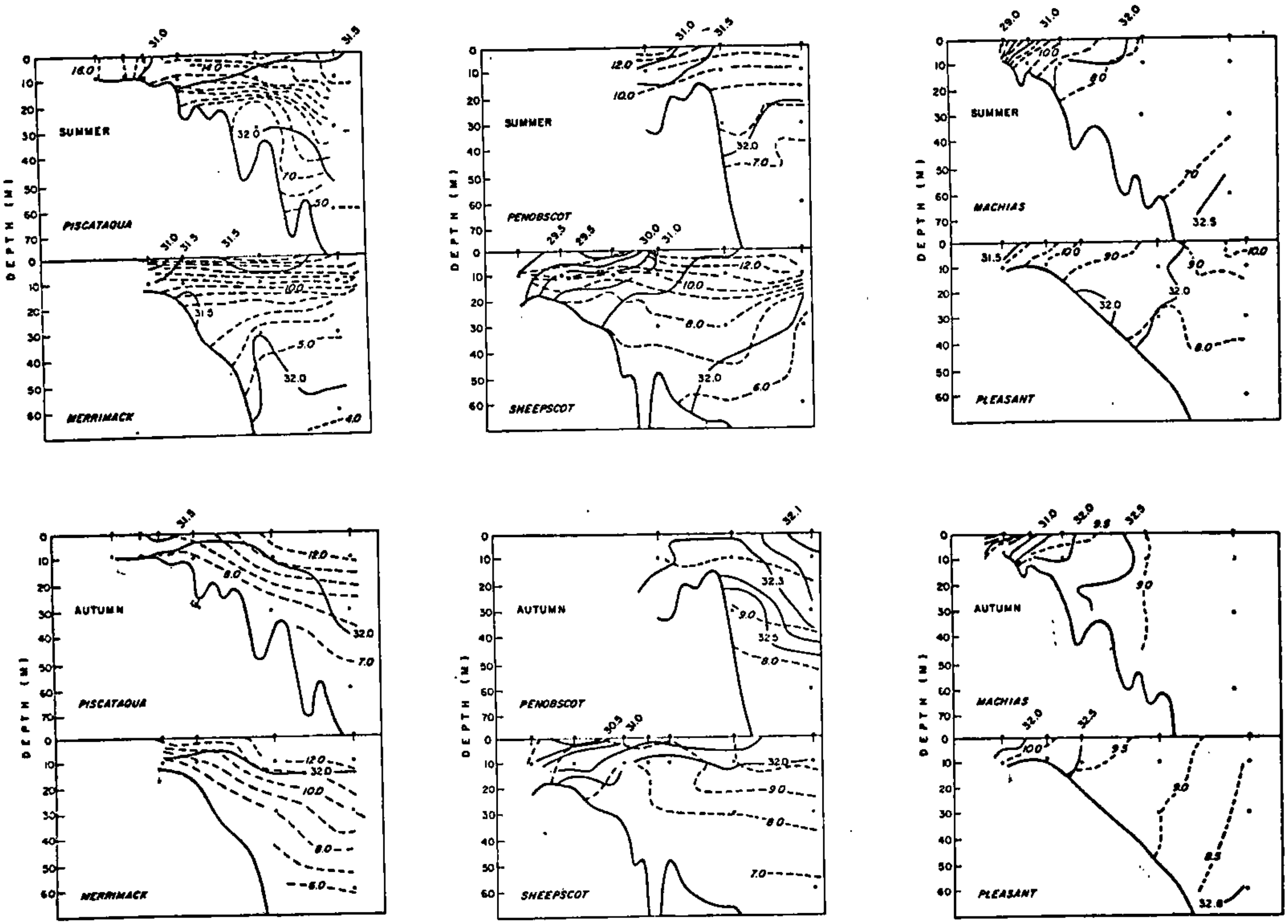


Fig. 3. Vertical profiles of temperature, salinity and station locations in summer and autumn along six transects in coastal waters of the western Gulf of Maine.

than 32.0 o/oo (Fig. 3).

In each of the seasons waters in the central area are intermediate in temperature and salinity to the extremes of the western and eastern areas.

Water Types and Circulation

Water types in the coastal Gulf of Maine region, where seasonal temperatures vary markedly, can best be identified by salinity characteristics. In the coastal region two types of water predominate, the low salinity (< 32.0 o/oo) waters at the seaward ends of the estuaries, and the higher salinity outer coastal water (> 32.0 o/oo) occupying the upper 100 m of the water column from the northern edge of Georges Bank to the headlands as shown in Colton, Marak, Nickerson, and Stoddard (1968). Along the coast hydrographic differences are greatest between the generally stratified water (except for winter) west of Penobscot Bay and the vertically mixed waters of the eastern coast from Penobscot Bay to Machias Bay.

The major non-tidal movement of surface waters is the south-westerly drift from Machias Bay to Cape Ann and beyond: in winter, the non-tidal drift is poorly developed (< 4 km per day); with the addition of the freshets in spring the drift becomes well developed (up to 13 km per day); velocity is reduced in summer, (ca. 9 km/day) and in autumn the drift is further reduced to about 4 km per day, approaching the winter period of minimal alongshore movement (Bigelow, 1927; Bumpus and Lauzier, 1965). Within the immediate vicinity of the coast (10 km) bottom waters move shoreward, particularly in spring, to compensate for the seaward movement of the less saline and surface waters; ephemeral eddies and upwellings are also generated through the interaction of surface drift, wind, and tidal forces (Graham, 1970).

Seasonal Changes in Copepod Densities and Distributions

Among area and inshore-offshore distributions the abundance of copepods varied seasonally. The annual low was in winter. Numbers increased in spring, were highest in summer, and declined in autumn. Seven of the 36 species in the samples were dominant at one or more of the sampling locations in a season--*Acartia clausi*, *A. longiremis*, *Calanus finmarchicus*, *Centropages typicus*, Harpacticoid spp. (mostly *Zaus abbreviatus* and *Harpacticus uniremis*), *Pseudocalanus minutus*, and *Temora longicornis*. The species *Calanus finmarchicus* and *P. minutus* were predominant in winter, spring, and summer, and *P. minutus*, *C. typicus*, and *T. longicornis* in autumn. Distributions of the dominant species also varied seasonally from inshore to offshore and among the three coastal areas.

In winter, four species and one group predominated in the coastal waters, *A. clausi*, *A. longiremis*, *C. finmarchicus*, *P. minutus* and harpacticoids (Table 1). Although they were widely distributed along the coast, differences in their abundances among the three areas were not significant ($P > 0.05$) (Fig. 4a, b). The greatest distributional changes were along the inshore-offshore transects; *A. clausi*, *A. longiremis*, and harpacticoids were concentrated in the vicinity of the embayments, and *C. finmarchicus* was abundant in the outer coastal waters.

Table 1. Relative abundance of copepods in Gulf of Maine Coastal waters, Winter, 1966.

	Mean[1/] Rank	Dominance[2/]	Abundance[3/] Range	Median	Mean	Standard Deviation	Dispersion[4/]	Frequency of Occurrence	% Occurrence
Pseudocalanus minutus	23.72	20/29	11-547	127	148.4	10.71	1.295	29/29	100
Acartia longiremis	21.10	1/29	1-194	3	22.7	7.02	.460	28/29	96.55
Calanus finmarchicus	20.98	2/29	1-173	33	37.3	6.35	.925	26/29	89.66
Metridia lucens	16.21	0	1-7	1	1.3	1.34	.745	19/29	65.52
Temora longicornis	15.22	0	1-244	3	1.4	6.86	.290	16/29	55.17
Harpacticoid sp.	14.97	2/29	1-468	2	3.6	10.73	.311	15/29	51.72
Acartia clausi	13.72	1/29	1-301	1	12.2	7.40	.222	12/29	41.38
Oithona spinirostris	12.90	0	1-3	1	0.5	.82	.665	11/29	37.93
Centropagus typicus	12.40	0	1-7	1	0.7	1.28	.420	9/29	31.03
Calanus hyperboreus	11.97	0	1-2	1	0.3	0.78	.572	8/29	27.59
Cyclopoid sp.	11.91	0	1-3	1	0.4	0.82	.570	9/29	31.03
Eurytemora herdmani	11.17	0	2-9	3	0.8	1.40	.428	6/29	20.69
Tortanus discaudatus	10.45	0	1-1	1	0.2	0.62	.456	5/29	17.24
Oithona similis	9.97	0	1-1	1	0.1	0.55	.340	3/29	10.34
Eurytemora hirundoides	9.72	0	5-6	5	0.4	1.18	.271	2/29	6.90
Centropages typicus imm.	9.60	0	1-1	1	0.07	0.51	.272	2/29	6.90
Xanthocalanus sp.	9.29	0	2-2	2	0.07	0.60	.189	1/29	3.45
Eurytemora affinis	9.29	0	2-2	2	0.07	0.60	.189	1/29	3.45
Calanoid sp. imm.	9.29	0	2-2	2	0.07	0.60	.189	1/29	3.45
Metridia longa	9.28	0	1-1	1	0.03	0.43	.189	1/29	3.45
Euchaeta norvegica	9.24	0	1-1	1	0.03	0.43	.189	1/29	3.45
Euchaeta sp.	9.22	0	1-1	1	0.03	0.43	.189	1/29	3.45
Eurytemora lacustris	9.21	0	1-1	1	0.03	0.43	.189	1/29	3.45
Diaptomus sp.	9.16	0	1-1	1	0.03	0.43	.189	1/29	3.45

1/ Species were ranked within each sample on the basis of numbers of individuals. Ranks for each species were averaged over the 29 stations samples.

2/ Proportión of samples in which the species was among those making up 50 percent of the individuals.

3/ Range, median, and mean of mean numbers of individuals per $10m^3$ of water in samples in which the species was found.

4/ The ratio of the standard deviation to the mean; the expected value for a random (Poisson) distribution is 1.0.

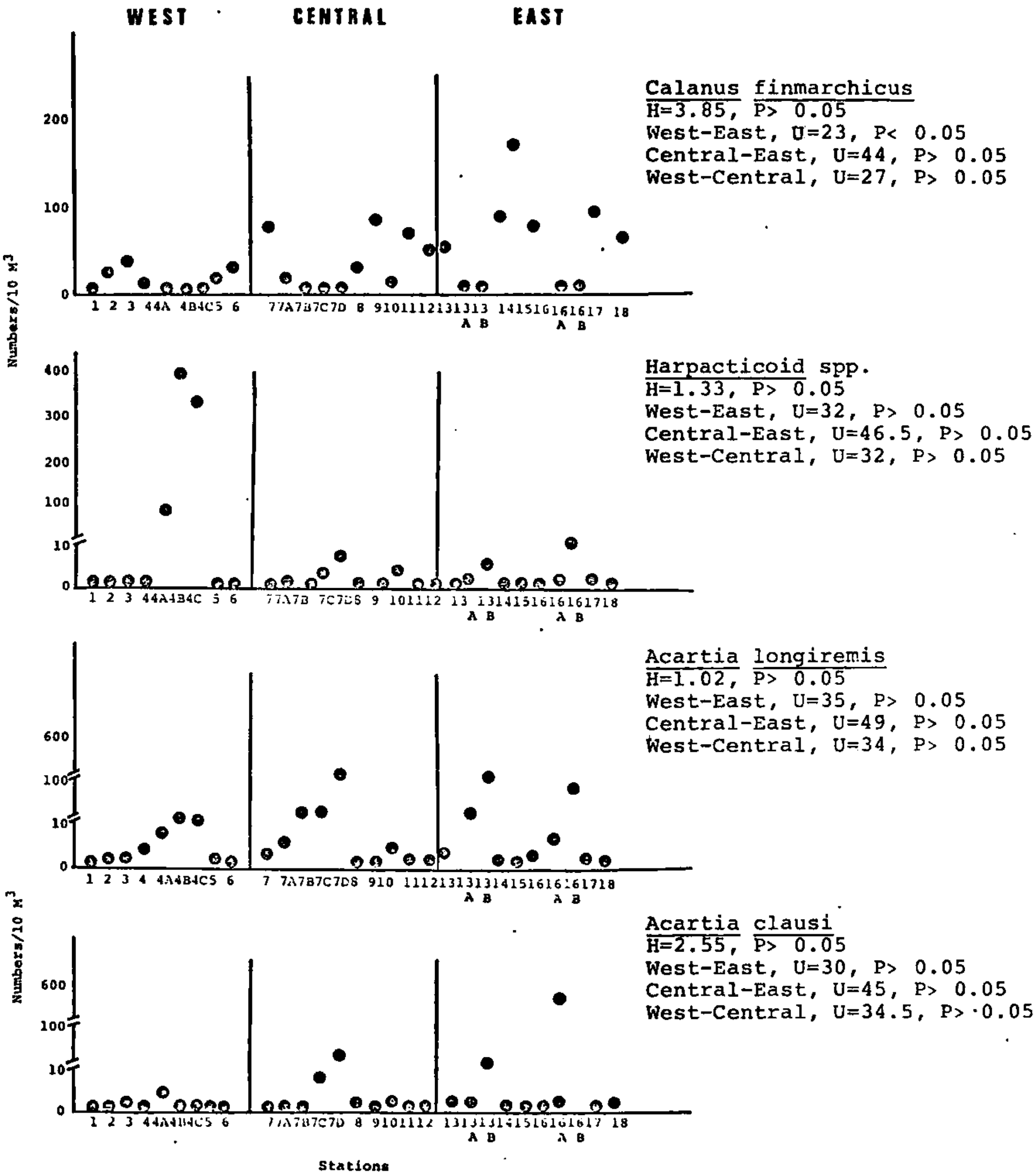


Fig. 4a. Comparisons of densities (N/10M^3) of *A. longiremis*, *A. clausi*, *C. finmarchicus*, and harpacticoids in winter among three coastal areas of the western Gulf of Maine. Kruskal-wallis one-way analysis of variance H and P values are given for each of the species comparisons among areas. Mann-Whitney U and P values are given for between area comparisons.

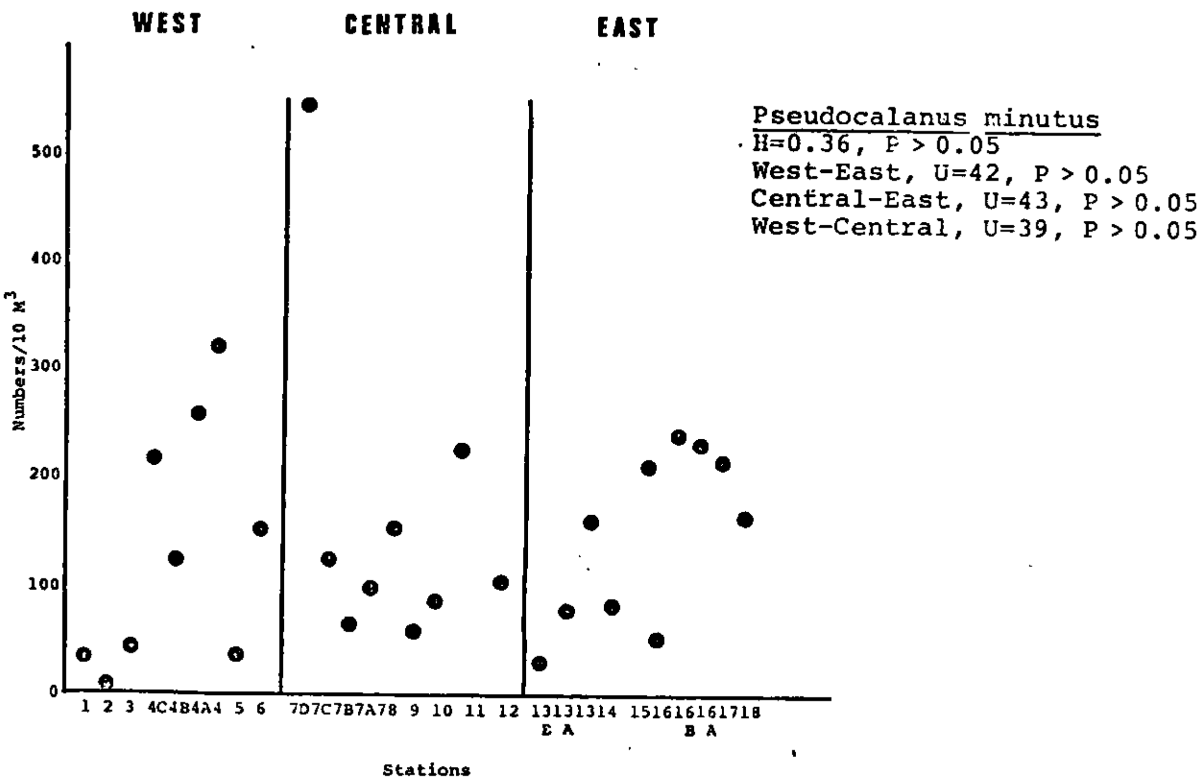


Fig. 4b. Comparisons of densities (N/10M^3) of *P. minutus* in winter among three coastal areas of the western Gulf of Maine. Kruskal-wallis one-way analysis of variance H and P values are given for the comparisons among areas. Mann-Whitney U and P values are given for between area comparisons.

The most numerous species, P. minutus, was widely distributed; concentrations were inshore in the Sheepscot estuary and lower end of Penobscot Bay, offshore on the Pleasant transect, and widely scattered on the Merrimack, Piscataqua, and Machias transects (Fig's. 5a, b, c).

In this season the inshore species A. clausi and harpacticoids were mixed in the water column between 0 and 10 m; some swarming of these species at the surface was observed (e.g., A. clausi in the eastern area and harpacticoids in the central area). The greatest densities of A. longiremis were within the 0 to 10 m level in the inshore segments of the transects, whereas offshore, this species was concentrated in the upper 10 m in all areas. The most numerous species, C. finmarchicus and P. minutus (constituting approximately 70 percent of the biomass) were concentrated at different depths: C. finmarchicus was numerous in depths ≥ 10 m both inshore and offshore; but, P. minutus was mixed inshore through the 0 to 10 m levels and widely distributed through the 0 and 60 m levels offshore, with an occasional swarm at the surface as observed in the western area (Fig. 6).

Three species and one group were dominant in spring (Table 3). Three of them, A. longiremis, C. finmarchicus, and P. minutus, declined in abundance from west to east ($P < 0.05$); harpacticoids were widely distributed along the coast ($P > 0.05$) (Fig's. 7a, b). The more numerous species, C. finmarchicus and P. minutus, generally diminished in numbers from the seaward ends of the transects into the embayments; both species decreased in abundance at the seaward end of the Penobscot transect. Distributions of the other dominants were variable; they decreased in abundance from inshore to offshore, except for an apparent anomalous increase of A. longiremis seaward off the Merrimack, and the abrupt decrease of this species at the shoreward end of the transects within Pleasant and Machias Bays (Fig's. 8a, b).

Vertical distributions of two species constituting 80 percent of the copepod biomass, C. finmarchicus and P. minutus, were similar in all inshore segments; greatest densities were at the lower levels sampled. Offshore copepodites of C. finmarchicus were swarming at the surface in the western area. It is in this area that Bigelow (1926) reported the onset of the spring phytoplankton bloom and subsequent swarming of C. finmarchicus copepodites at the surface. In the central and eastern areas the larger over-wintering adults remain in the lower part of the water column in depth ≥ 30 m. Greatest densities of P. minutus were in the lower depths sampled ≥ 30 m. The other species were less numerous. Inshore they were generally near the bottom. The exception was A. longiremis in the western area. Offshore T. longicornis densities were greatest between 10 and 30 m in all areas. Distributions of A. longiremis were variable. They were concentrated between the 10 to 30 m layer in the central and eastern areas and were most numerous in the upper 10 m in the west (Fig. 9).

Twenty-four species were in the samples in summer, but only three were dominant, P. minutus, C. finmarchicus and T. longicornis (Table 4). All three species decreased from west to east ($P < 0.01$) (Fig's. 10a, b). P. minutus and C. finmarchicus decreased in abundance from offshore to inshore. The single exception was the concentration of P. minutus at the mouth of the Merrimack River.

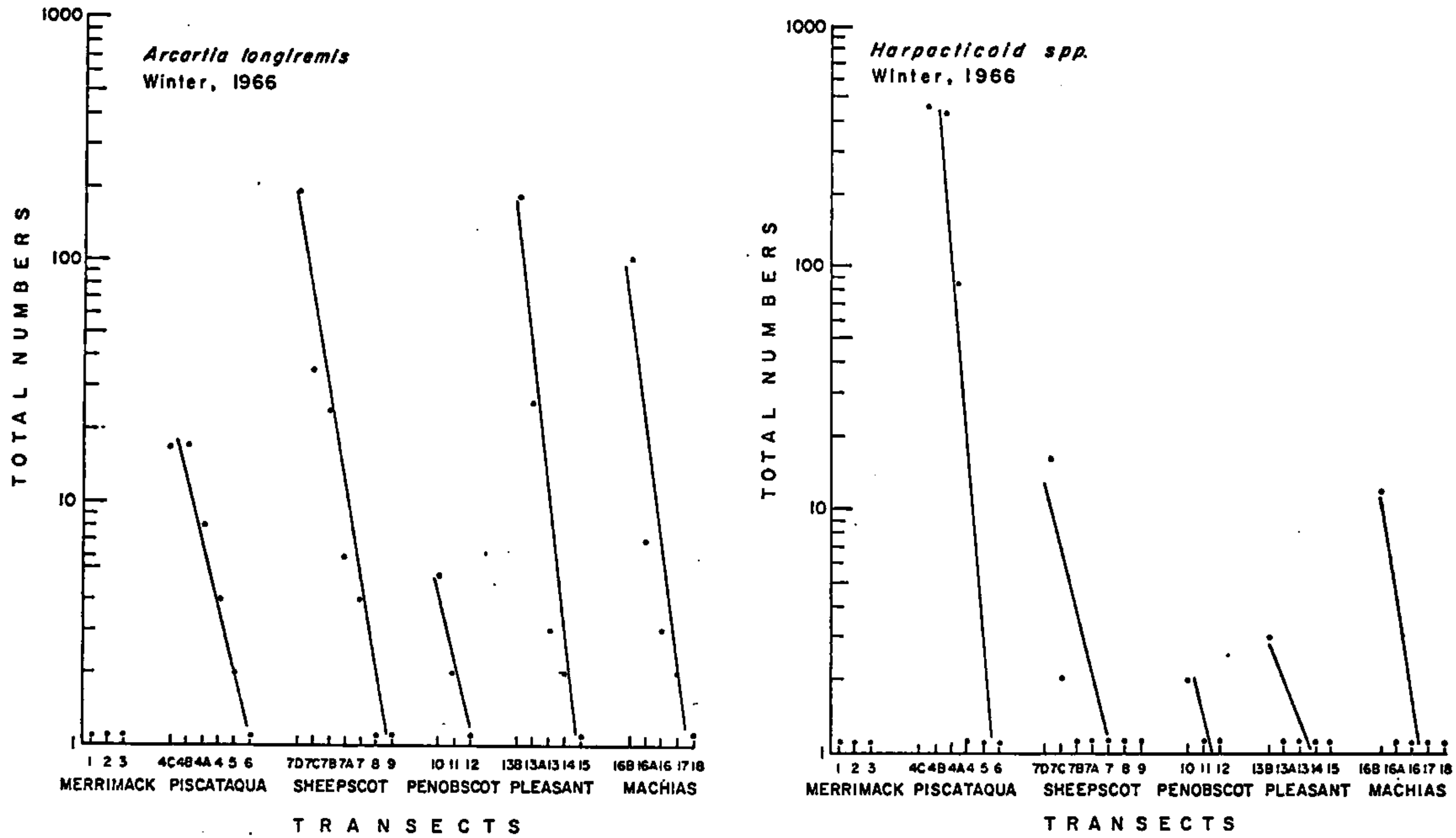


Fig. 5a. Changes in the inshore-offshore densities of A. longiremis and harpacticoids ($N/10M^3$) along six transects in coastal waters of the western Gulf of Maine. Spearman rank correlation coefficients for each species are given in Table 2.

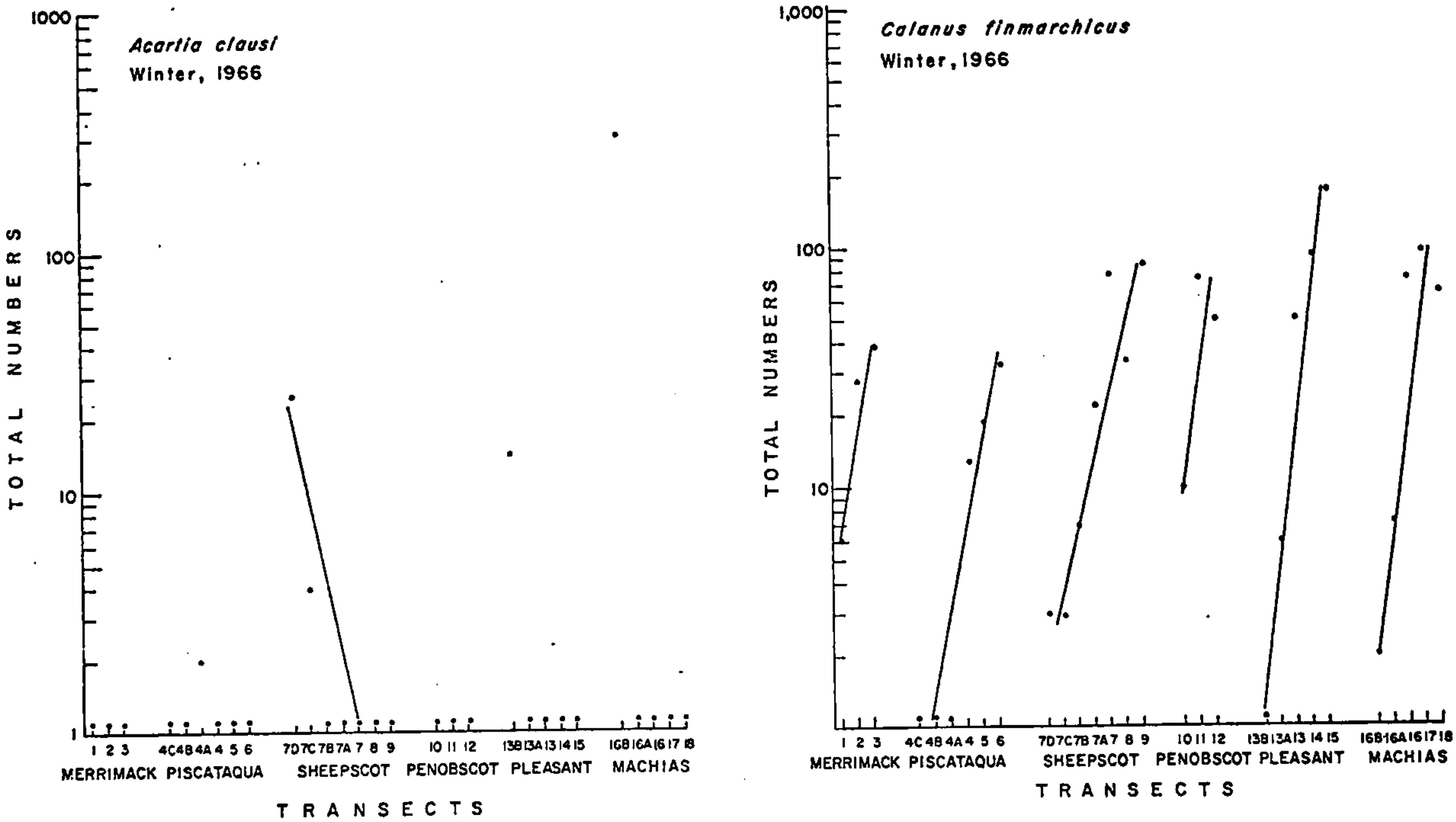


Fig. 5b. Changes in the inshore-offshore densities of Acartia clausi and Calanus finmarchicus ($N/10M^3$) along six transects in coastal waters of the western Gulf of Maine. Spearman rank correlation coefficients for each species are given in Table 2.

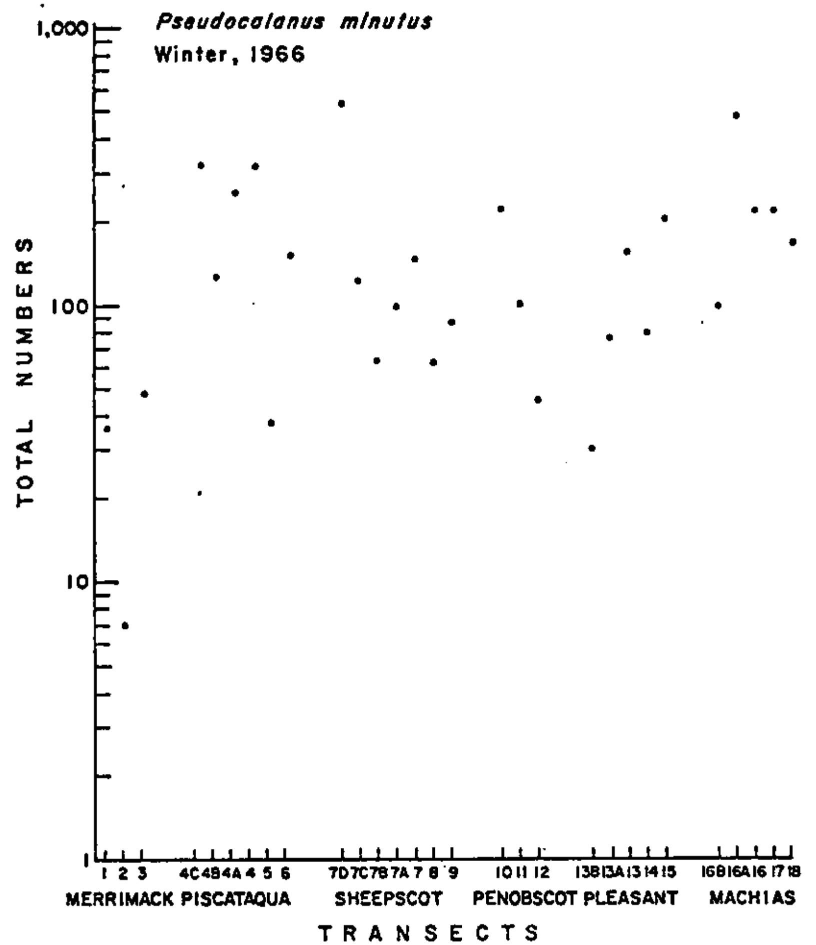


Fig. 5c. Changes in the inshore-offshore densities of Pseudocalanus minutus ($N/10M^3$) along six transects in coastal waters of the western Gulf of Maine. Spearman rank correlation coefficients are given in Table 2.

Table 2. Summary of Spearman Rank Correlation Coefficient (r_s) and P values. Results are for inshore-offshore comparisons in density changes of dominant copepods in western Gulf of Maine coastal waters for four seasons in 1966.

Species and Season	Transects: Merrimack (4) r_s	P	Piscataqua (6) r_s	P	Sheepscot (7) r_s	P	Pleasant (5) r_s	P	Machias (5) r_s	P
Acartia clausi										
Winter			0.20	>0.05	·0.46	>0.05	·0.85	>0.05	·0.45	>0.05
Acartia longiremis										
Winter			0.96	<0.01	0.97*	<0.01	1.00*	<0.01	1.00*	<0.01
Spring	1.00*	<0.05	0.60	>0.05	0.75*	<0.05	0.40	>0.05	0.23	>0.05
Calanus finmarchicus										
Winter			0.94*	<0.01	0.96*	<0.01	1.00*	<0.01	0.70	>0.05
Spring	0.60	>0.05	0.77	>0.05	0.93*	<0.01	0.90*	<0.05	1.00*	<0.01
Summer	1.00*	<0.05	1.00	<0.01	1.00*	<0.01	0.90*	<0.05	0.98*	<0.05
Centropages typicus										
Autumn	0.20	>0.05	0.60	>0.05	0.52	>0.05				
Harpacticoid spp.										
Winter			0.83*	<0.05	0.64	>0.05	0.70	>0.05	0.65	>0.05
Spring	0.50	>0.05	0.20	>0.05	0.71*	<0.05	0.50	>0.05	0.25	>0.05
Pseudocalanus minutus										
Winter			0.31	>0.05	0.57	>0.05	0.90*	<0.05	0.08	>0.05
Spring	0.40	>0.05	0.71	>0.05	0.36	>0.05	0.90*	<0.05	0.90*	<0.05
Summer	0.40	>0.05	0.77	>0.05	0.54	>0.05	0.90*	<0.05	0.90*	<0.05
Autumn	0.80	>0.05	0.59	>0.05	0.93*	<0.01	0.70	>0.05	0.88	>0.05
Temora longicornis										
Autumn	1.00	<0.05	0.14	>0.05	0.11	>0.05	0.60	>0.05	0.30	>0.05
Summer	0.60	>0.05	0.49	>0.05	0.32	>0.05	0.40	>0.05	0.70	>0.05
Tortanus discaudatus										
Spring	0.50	>0.05	0.70	>0.05	0.55	>0.05	0.70	>0.05	0.38	>0.05

* significant differences; P <0.05

Note: Since fewer than four stations were sampled for the Penobscot Bay transect, it is not included in Table 2.

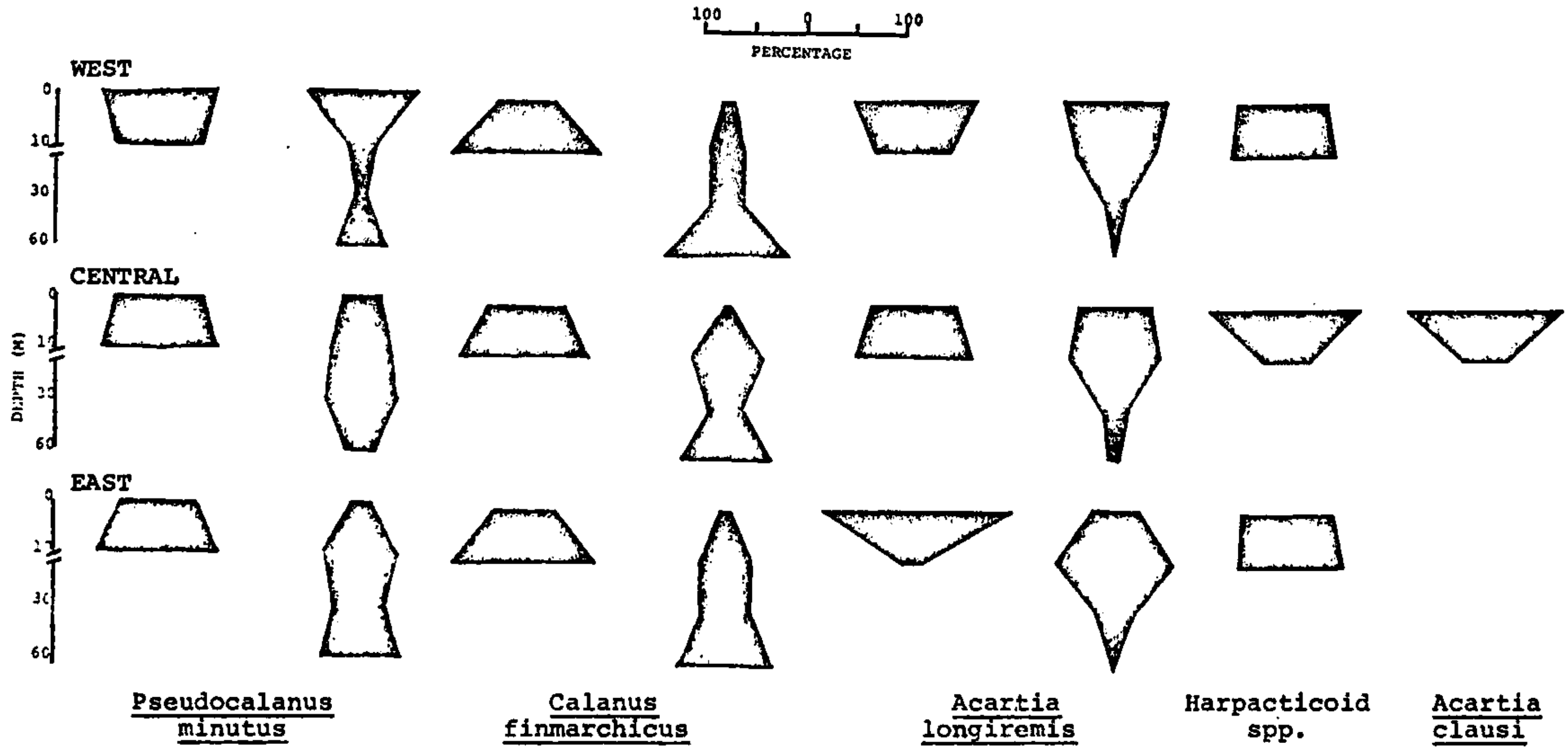


Fig. 6. Comparisons of the percentage occurrence of P. minutus, C. finmarchicus, A. longiremis, Harpacticoid spp., and A. clausi in winter at two depths inshore (0,10m) and four depths offshore (0,10,30,60 m) in three coastal areas of the Gulf of Maine (West, Central, East).

Table 3. Relative abundance of copepods in Gulf of Maine coastal waters, Spring, 1966.

	Mean Rank	Dominance	Abundance Range	Abundance Median	Abundance Mean	Standard Deviation	Dispersion	Frequency of Occurrence	% Occurrence
Pseudocalanus minutus	20.55	7/30	1-3483	533	874.9	31.48	.883	29/30	96.67
Acartia longiremis	20.08	4/30	1-1368	51	181.1	17.17	.614	29/30	96.67
Calanus finmarchicus	19.87	10/30	1-9247	469	131.5	47.25	.589	28/30	93.33
Temora longicornis	16.52	0	1-319	7	32.0	8.68	.424	24/30	80.00
Acartia clausi	14.15	0	1-115	4	8.9	4.61	.418	19/30	63.33
Tortanus discaudatus	13.58	0	1-91	7	9.5	4.57	.453	17/30	56.67
Centropages hamatus	11.75	0	2-51	14	7.2	3.68	.528	11/30	36.67
Harpacticoid sp.	11.43	1/30	1-20	3	2.0	2.04	.470	12/30	40.00
Metridia lucens	10.95	0	2-28	5	2.6	2.35	.464	10/30	33.33
Eurytemora herdmani	10.37	0	1-138	21	7.7	5.07	.300	7/30	23.33
Acartia spp. imm.	10.17	0	1-30	4	1.6	2.33	.300	7/30	23.33
Oithona spinirostris	9.82	0	2-19	9	1.7	2.07	.406	6/30	20.00
Cyclopoid sp.	9.30	0	1-19	16	1.9	2.28	.365	5/30	16.67
Oithona similis	8.95	0	1-6	2	0.4	1.10	.306	4/30	13.33
Calanoid sp. unknown	8.60	0	1-1	1	0.1	0.55	.333	3/30	10.00
Calanoid sp. imm.	8.28	0	1-1	1	0.06	0.50	.267	2/30	6.67
Calanus hyperboreus	8.15	0	9-9	9	0.03	1.27	.186	1/30	3.33
Eurytemora lacustris	8.13	0	1-1	1	0.03	0.42	.186	1/30	3.33
Centropages typicus	8.10	0	1-1	1	0.03	0.42	.186	1/30	3.33
Eurytemora affinis	8.08	0	4-4	4	0.01	0.85	.186	1/30	3.33
Centropages sp. imm.	8.08	0	2-2	2	0.07	0.60	.186	1/30	3.33
Diaptomus sp.	8.08	0	8-8	8	0.03	1.20	.186	1/30	3.33

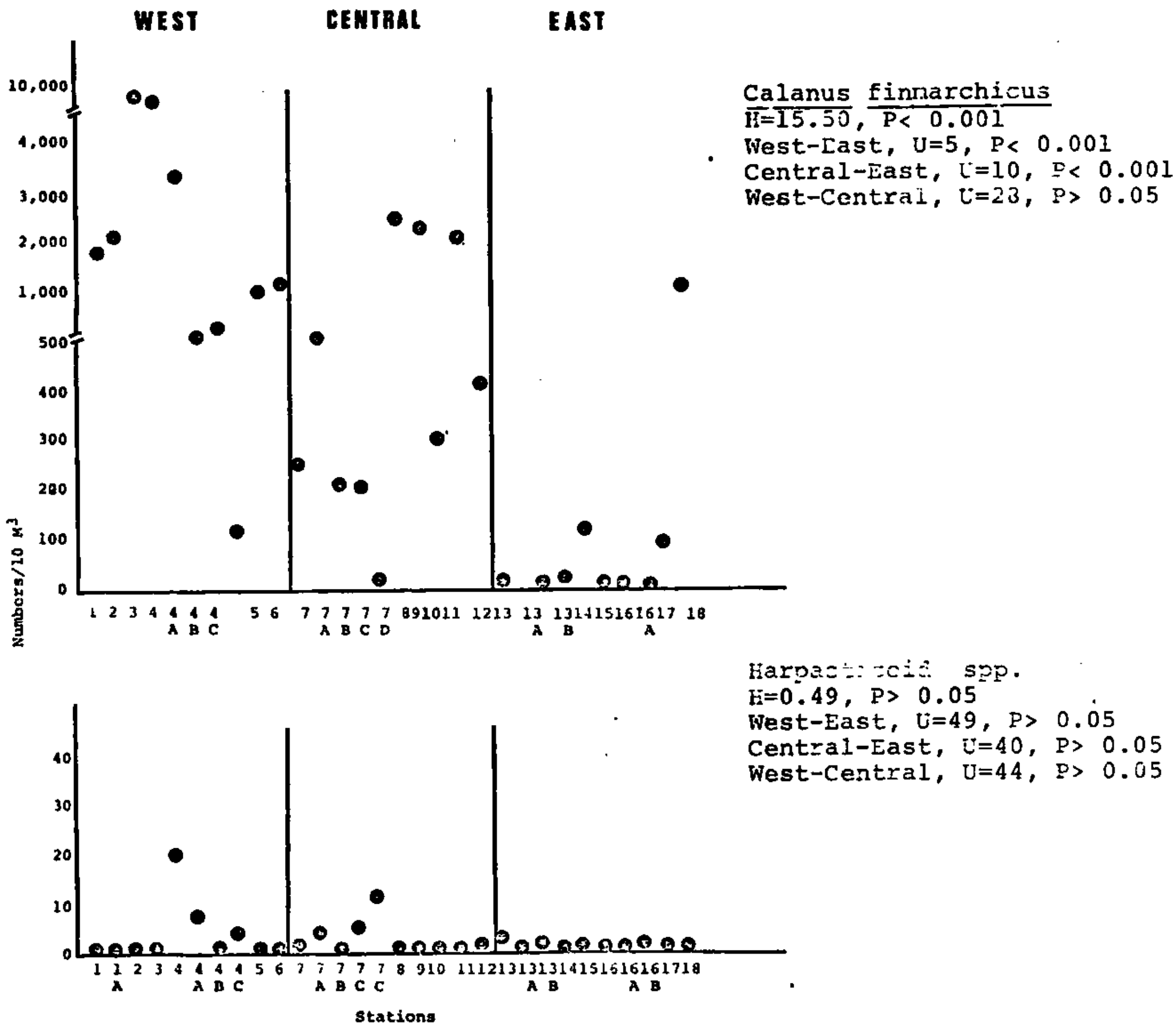


Fig. 7a. Comparisons of densities (N/10M^3) of C. finmarchicus and harpacticoids in spring among three coastal areas of the western Gulf of Maine. Kruskal-wallis one-way analysis of variance H and P values are given for each of the species comparisons among areas. Mann-Whitney U and P values are given for between area comparisons.

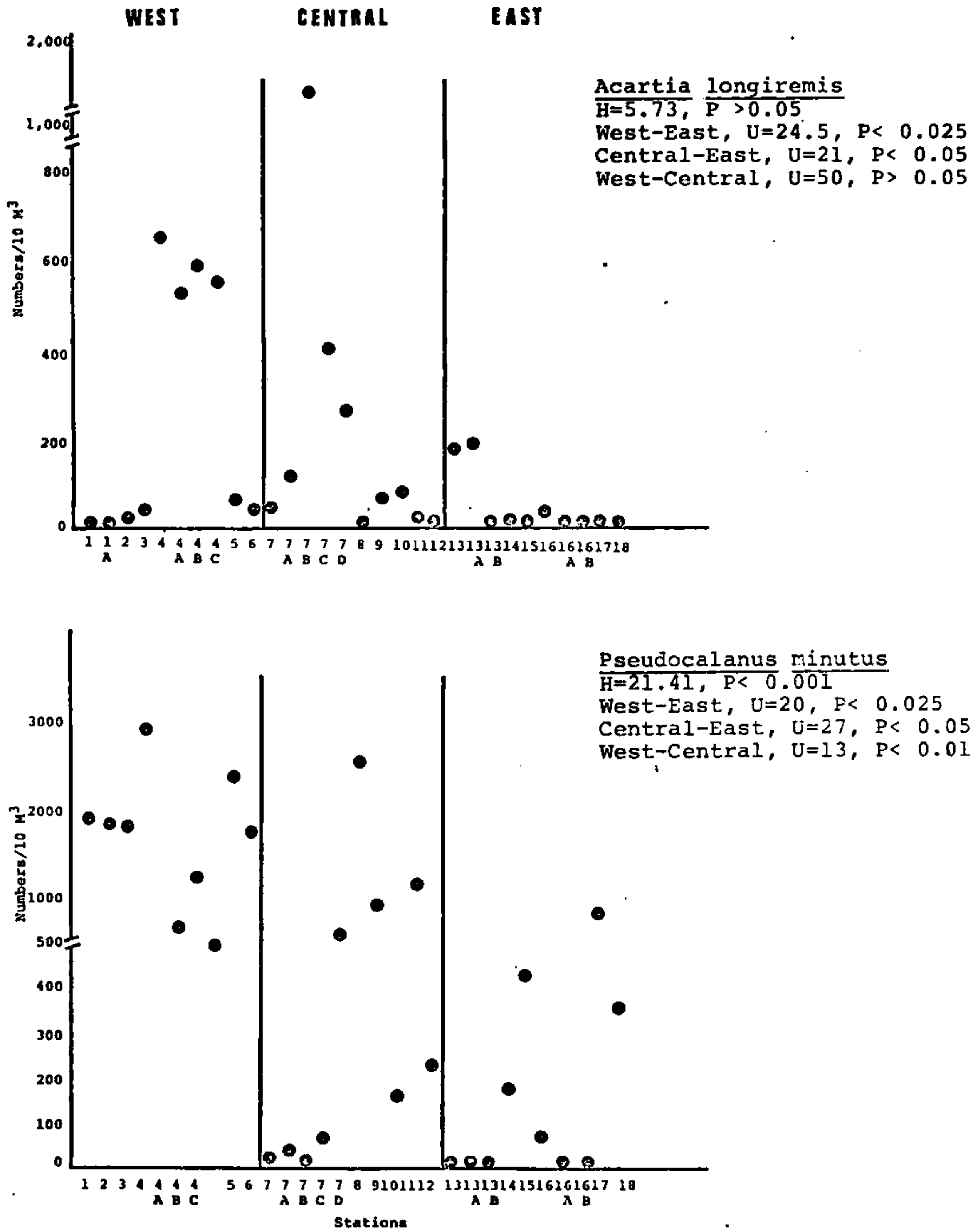


Fig. 7b. Comparisons of densities (N/$10M^3$) of A. longiremis and P. minutus in spring among three coastal areas of the western Gulf of Maine. Kruskal-wallis one-way analysis of variance H and P values are given for each of the species comparisons among areas. Mann-Whitney U and P values are given for between area comparisons.

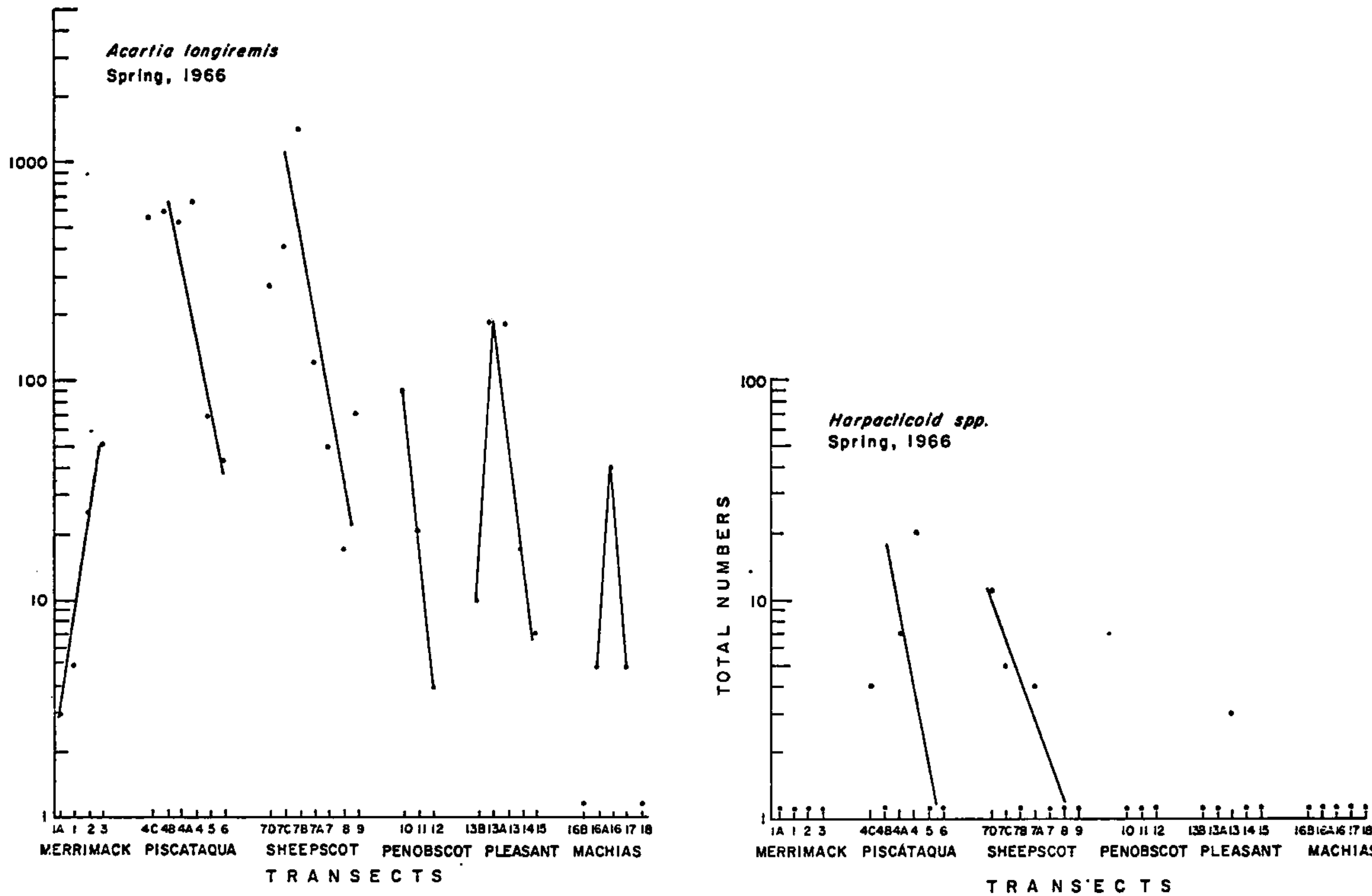


Fig. 8a. Changes in the inshore-offshore densities of A. longiremis and Harpacticoid spp. ($N/10M^3$) in spring along six transects in coastal waters of the western Gulf of Maine. Spearman rank correlation coefficients for each species are given in Table 2.

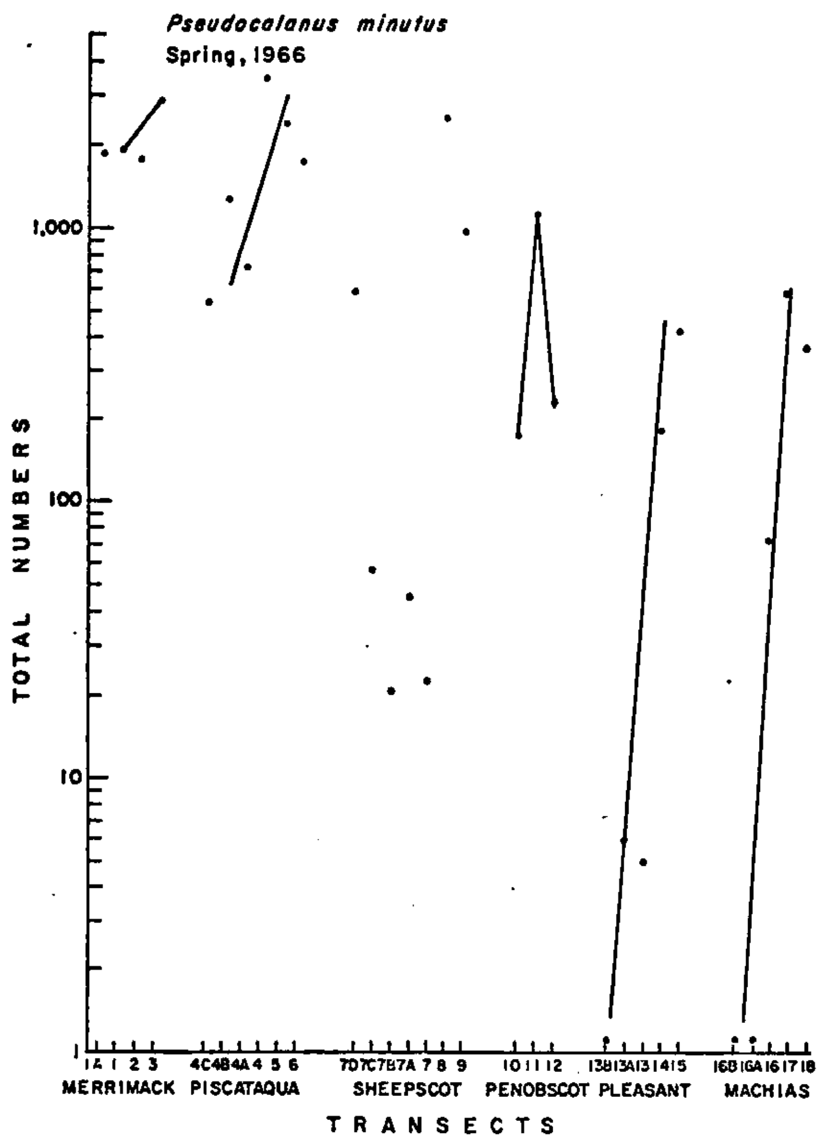


Fig. 8b. Changes in the inshore-offshore densities of P. minutus ($N/10M^3$) in spring along six transects in coastal waters of the western Gulf of Maine. Spearman rank correlation coefficients are given in Table 2.

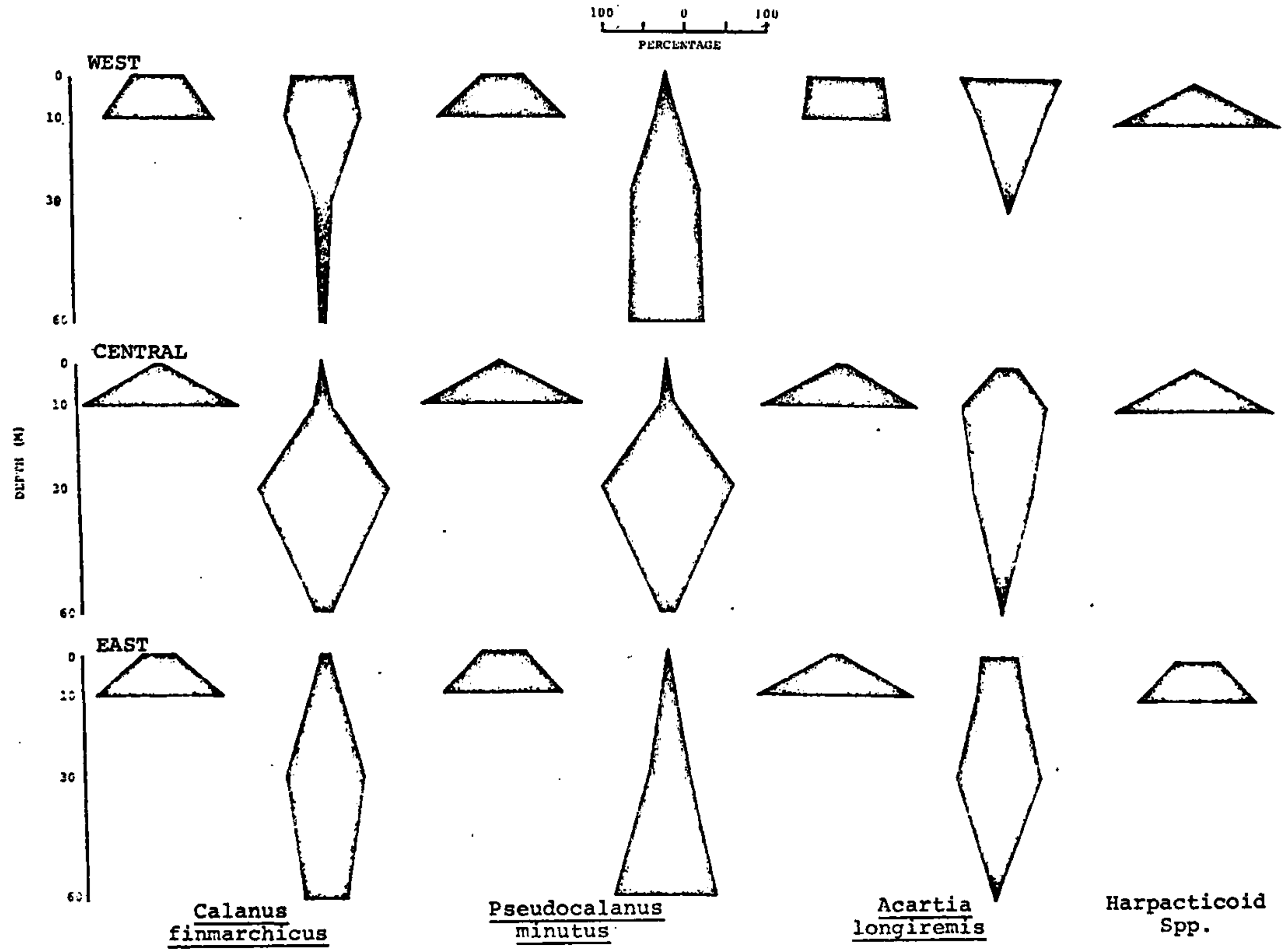


Fig. 9. Comparisons of the percentage occurrence of C. finmarchicus, P. minutus, A. longiremis, and Harpacticoid spp. in spring at two depths inshore (0,10m) and four depths offshore (0,10,30,60m) in three coastal areas of the Gulf of Maine (West, Central, East).

Table 4. Relative abundance of copepods in Gulf of Maine coastal waters. Summer, 1966.

	Mean Rank	Dominance	Abundance			Std. Dev.	Dispersion	Frequency of Occurrence	% Occurrence
			Range	Median	Mean				
Pseudocalanus minutus	23.20	9/30	2-7983	766	1348	40.80	.810	30/30	100.00
Temora longicornis	21.10	1/30	3-4443	188	517.2	29.62	.589	28/30	93.33
Calanus finmarchicus	20.93	4/30	1-7322	259	808.3	28.18	.555	30/30	100.00
Acartia longiremis	20.72	0	2-529	47	106.8	11.14	.860	30/30	100.00
Centropages hamatus	19.28	0	1-2558	90	238.3	22.10	.488	27/30	90.00
Eurytemora herdmani	17.53	0	1-449	22	7.0	10.39	.651	25/30	83.33
Acartia clausi	16.78	0	1-310	11	38.6	8.43	.544	26/30	86.67
Tortanus discaudatus	14.37	0	1-39	17	10.2	3.46	.850	20/30	66.67
Metridia lucens	13.43	0	1-91	15	1.2	4.61	.564	17/30	56.67
Oithona spinirostris	13.00	0	1-37	14	7.8	3.34	.697	17/30	56.67
Harpacticoid sp.	11.98	0	1-60	1	4.3	3.38	.376	16/30	53.33
Acartia spp. imm.	9.68	0	1-19	5	1.8	2.17	.382	7/30	23.33
Eurytemora lacustris	9.42	0	1-28	3	1.4	2.25	.283	7/30	23.33
Oithona similis	9.22	0	2-24	3	1.7	2.28	.333	6/30	20.00
Centropages typicus	8.42	0	1-19	14	1.1	2.04	.272	3/30	10.00
Monstrilloida	8.35	0	2-17	13	1.1	1.94	.282	3/30	10.00
Anomalocera pattersoni	7.93	0	1-1	1	0.07	0.50	.267	2/30	6.67
Cyclopoid sp.	7.93	0	1-7	4	0.3	1.12	.211	2/30	6.67
Eurytemora sp.	7.92	0	1-3	2	0.1	0.75	.237	2/30	6.67
Eurytemora affinis	7.82	0	1-1	1	0.03	0.42	.186	1/30	3.33
Euchaeta norvegica	7.77	0	2-2	2	0.07	0.60	.186	1/30	3.33
Calanus hyperboreus	7.77	0	2-2	2	0.07	0.60	.186	1/30	3.33
Metridia longa	7.73	0	2-2	2	0.07	0.60	.186	1/30	3.33
Oithona sp.	7.72	0	11-11	11	0.04	1.41	.186	1/30	3.33

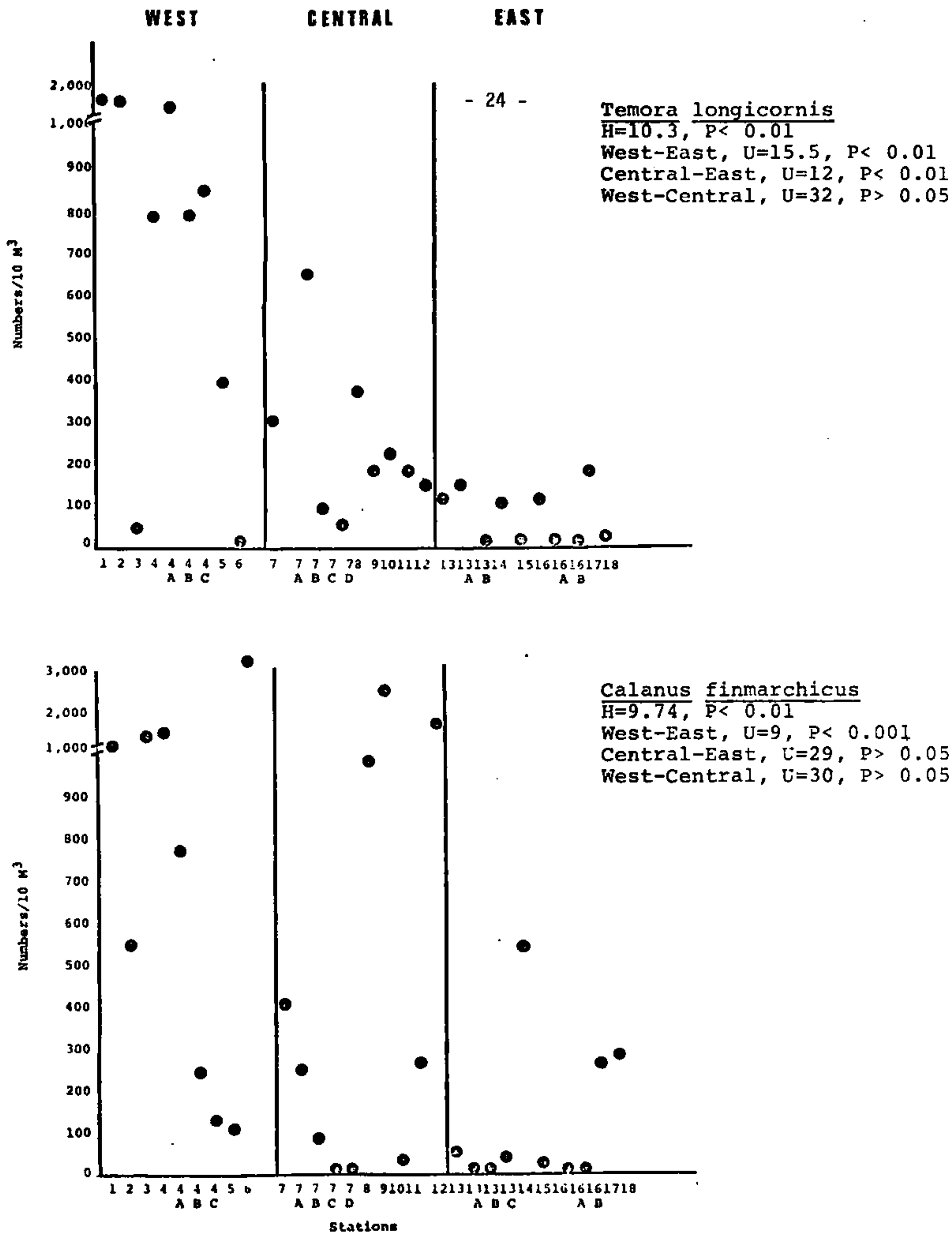


Fig. 10a. Comparisons of densities (N/10M^3) of T. longicornis and C. finmarchicus in summer among three coastal areas of the western Gulf of Maine. Kruskal-wallis one-way analysis of variance H and P values are given for each of the species comparisons among areas. Mann-Whitney U and P values are given for between area comparisons.

Within the area sampled T. longicornis concentrations were variable. Swarms were found along the length of the Merrimack transect, inshore in the Piscataqua transsect and along the lengths of the Sheepscot and Penobscot transects. On the eastern transects numbers were greatly reduced over the deeper water (Fig's. 11a, b).

In this season about 70 percent of the copepod biomass is represented by C. finmarchicus and P. minutus. Greatest densities of both species are near the bottom in the inshore waters with the exception of some swarming (probably copepodites) at the surface in the west. Concentrations of C. finmarchicus decreased with depth from west to east moving from the surface in the west to 10 m in the central area and down to 60 m in the eastern area. A similar pattern is found for P. minutus offshore with densities increasing from 10 m in the west to 30 m in the central area and between 30 and 60 m in the eastern area. In all areas T. longicornis was generally concentrated between the surface and 10 m. The one exception was at the offing of Penobscot Bay at 30 m (Fig. 12).

Centropages typicus, P. minutus, and T. longicornis were dominant in autumn (Table 5). As in summer, concentrations of the dominants were greatest in the western Gulf ($P < 0.01$) (Fig. 13). P. minutus decreased in abundance from offshore to nearshore in all areas. C. typicus was swarming at the mouth of the Merrimack and declined in abundance in the estuary and on the seaward end of the transect. Concentrations increased from inshore to offshore on the Piscataqua, Sheepscot, and Penobscot transects; low numbers precluded assessment of the inshore-offshore distribution of this species in the east. T. longicornis swarmed along the length of the Merrimack transect, but numbers were reduced off the Penobscot estuary; on the other transects concentrations decreased in two directions, from the lower ends of the embayments to offshore, and within the Piscataqua, Sheepscot, Pleasant, and Machias estuaries (Fig's. 14a, b).

Three species constituted 85 percent of the copepod biomass in autumn, P. minutus, C. typicus and T. longicornis. Inshore greatest densities of all species were near the bottom of the water column. A notable exception was the swarming of P. minutus at the surface in the eastern area. Although C. typicus was the only species between the surface and 10 m offshore, this occurrence should be treated with caution as the numbers in the samples were extremely low. In the west where the abundance of this species was centered, maximal numbers were in the upper 30 m of the water column. T. longicornis was concentrated between 10 and 30 m; P. minutus was abundant at 30 m in the western and central areas and between 10 and 60 m in the eastern area. Both species avoided the surface layers offshore (Fig. 15).

Copepod Distributions and Hydrography

The dominant copepods in the samples are all endemic to the Gulf of Maine (Bigelow, 1926), but their centers of abundance in the Gulf differ temporally and spatially. The seasonal changes in abundance result from local fluctuations in water temperature and stability, rather than from large-scale advection of waters. Evidence supporting this relationship is available from several sources. The annual warming and increased stability of the water column begins in the

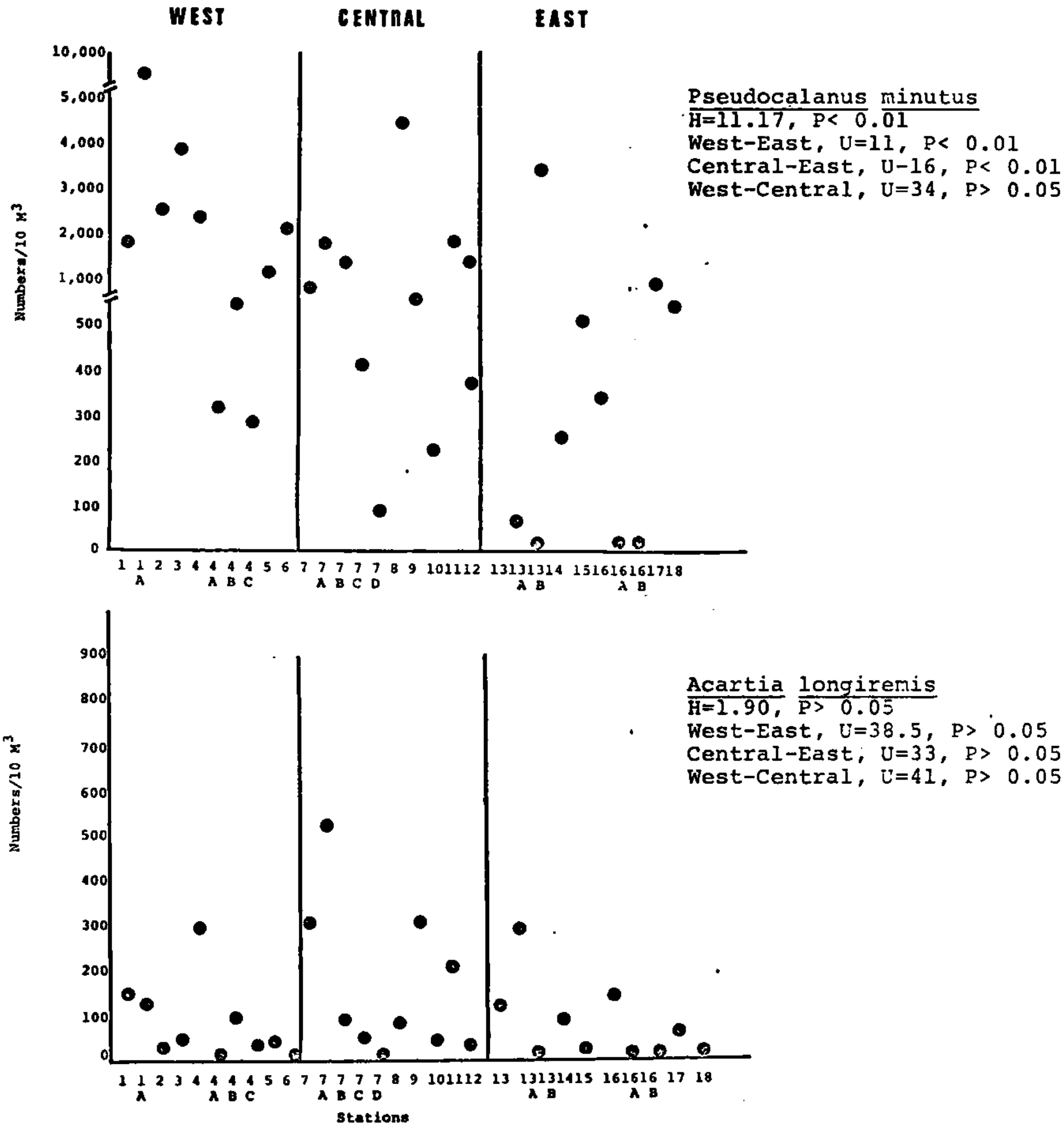


Fig. 10b. Comparisons of densities (N/10M^3) of Pseudocalanus minutus and Acartia longiremis in summer among three coastal areas of the western Gulf of Maine. Kruskal-wallis one-way analysis of variance H and P values are given for each of the species comparisons among areas. Mann-Whitney U and P values are given for between area comparisons.

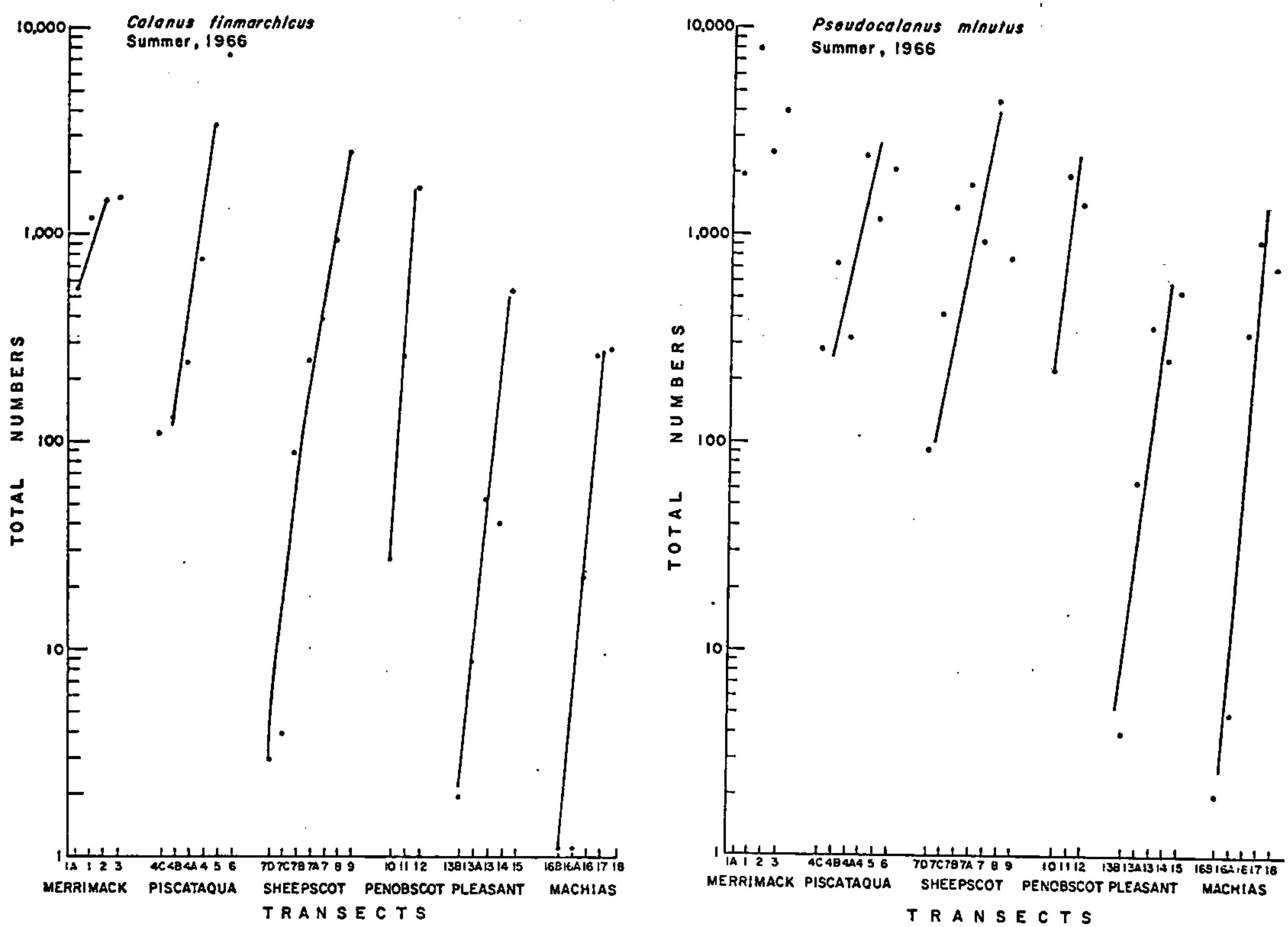


Fig. 11a. Changes in the inshore-offshore densities of C. finmarchicus and P. minutus ($N/10M^3$) in summer along six transects in coastal waters of the western Gulf of Maine. Spearman rank correlation coefficients for each species are given in Table 2.

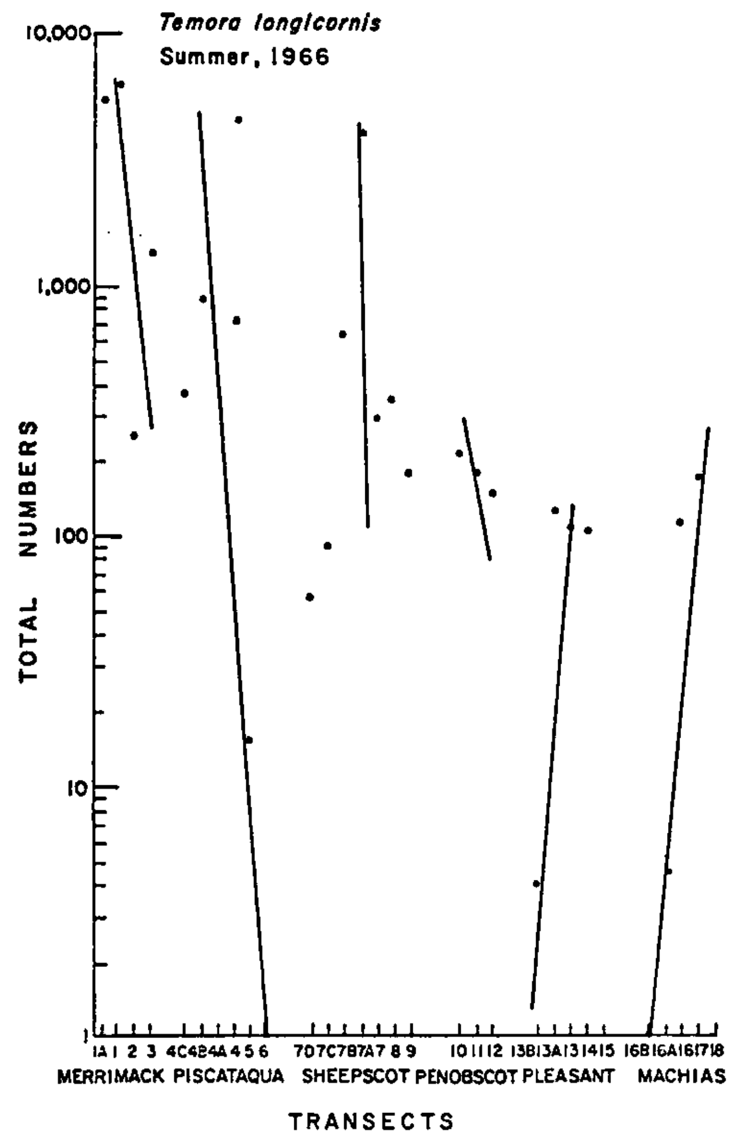


Fig. 11b. Changes in the inshore-offshore densities of T. longicornis ($N/10M^3$) in summer along six transects in coastal waters of the western Gulf of Maine. Spearman rank correlation coefficients are given in Table 2.

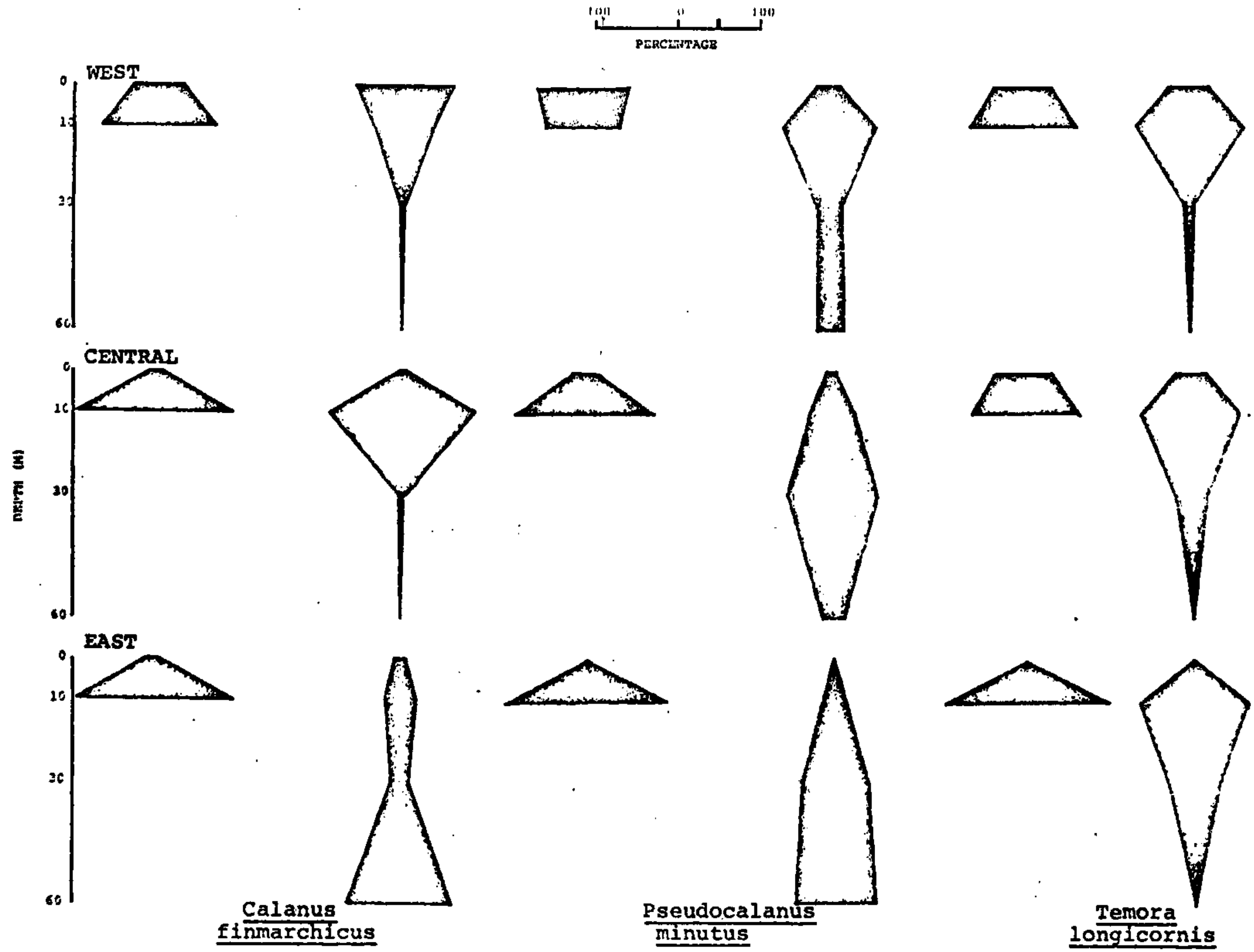
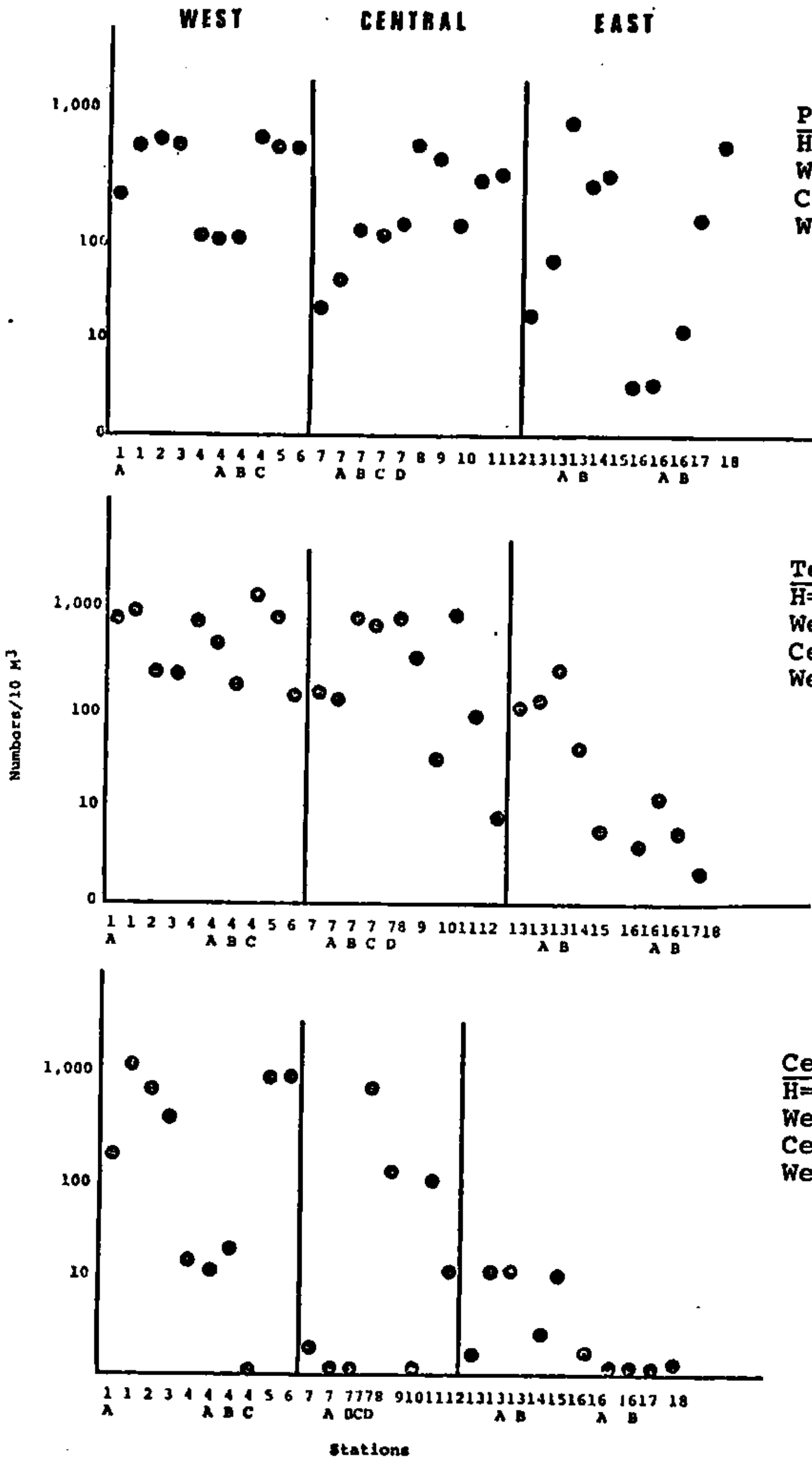


Fig. 12. Comparisons of the percentage occurrence of C. finmarchicus, P. minutus, and T. longicornis in summer at two depths inshore (0,10m) and four depths offshore (0,10,30,60m) in three coastal areas of the Gulf of Maine (West, Central, East).

Table 5. Relative abundance of copepods in Gulf of Maine coastal waters, Autumn, 1966.

	Mean Rank	Dominance	Abundance Range			Std. Dev.	Dispersion	Frequency of Occurrence	% Occurrence
			Range	Median	Mean				
Pseudocalanus minutus	18.68	9/30	5-3841	317	757.6	29.90	.847	30/30	100
Temora longicornis	18.03	7/30	3-3839	366	604.2	27.97	.772	29/30	96.67
Centropages hamatus	16.17	0	1-610	63	100.2	11.43	.767	29/30	96.67
Acartia longiremis	15.40	0	1-383	21	76.8	10.74	.666	27/30	90.00
Calanus finmarchicus	14.50	0	1-280	39	60.6	8.80	.783	26/30	86.67
Acartia clausi	13.90	0	1-180	10	28.6	6.92	.599	26/30	86.67
Centropages typicus	13.65	2/30	1-3925	31	456.3	31.02	.474	22/30	73.33
Metridia lucens	11.05	0	1-44	15	9.17	3.46	.764	17/30	56.67
Tortanus discaudatus	10.72	0	1-36	15	8.8	3.50	.718	16/30	53.33
Oithona spinirostris	9.90	0	1-37	8	6.6	3.28	.615	16/30	53.33
Eurytemora herdmani	7.90	0	1-13	3	1.2	1.63	.463	9/30	30.00
Metridia longa	7.18	0	1-14	9	1.2	1.83	.357	5/30	16.67
Harpacticoid sp.	7.15	0	1-5	3	0.5	1.08	.397	5/30	16.67
Cyclopoid sp.	7.08	0	1-5	1	0.3	0.99	.341	5/30	16.67
Oithona similis	7.00	0	1-7	1	0.4	1.14	.306	5/30	16.67
Euchaeta norvegica	6.43	0	1-2	1	0.1	0.63	.253	2/30	6.67
Calanoid spp. imm.	6.42	0	1-18	9	0.6	1.80	.196	2/30	6.67
Eurytemora affinis	6.40	0	243-243	243	8.1	6.60	.186	1/30	3.33
Eurytemora lacustris	6.33	0	47-47	47	1.6	2.90	.186	1/30	3.33
Anomalocera pattersoni	6.12	0	1-1	1	.03	0.42	.186	1/30	3.33



Pseudocalanus minutus
H=5, P< 0.05
West-East, U=22, P< 0.025
Central-East, U=33, P> 0.05
West-Central, U=35, P> 0.05

Temora longicornis
H=14.21, P< 0.001
West-East, U=4, P< 0.001
Central-East, U=14, P< 0.01
West-Central, U=33, P> 0.05

Centropages typicus
H=9.72, P< 0.01
West-East, U=8.5, P< 0.001
Central-East, U=46.5, P> 0.05
West-Central, U=21.5, P< 0.025

Fig. 13. Comparisons of densities ($N/10M^3$) of P. minutus, T. longicornis, and C. typicus in autumn among three coastal areas of the western Gulf of Maine. Kruskal-wallis one-way analysis of variance H and P values are given for each of the species comparisons among areas. Mann-Whitney U and P values are given for between area comparisons.

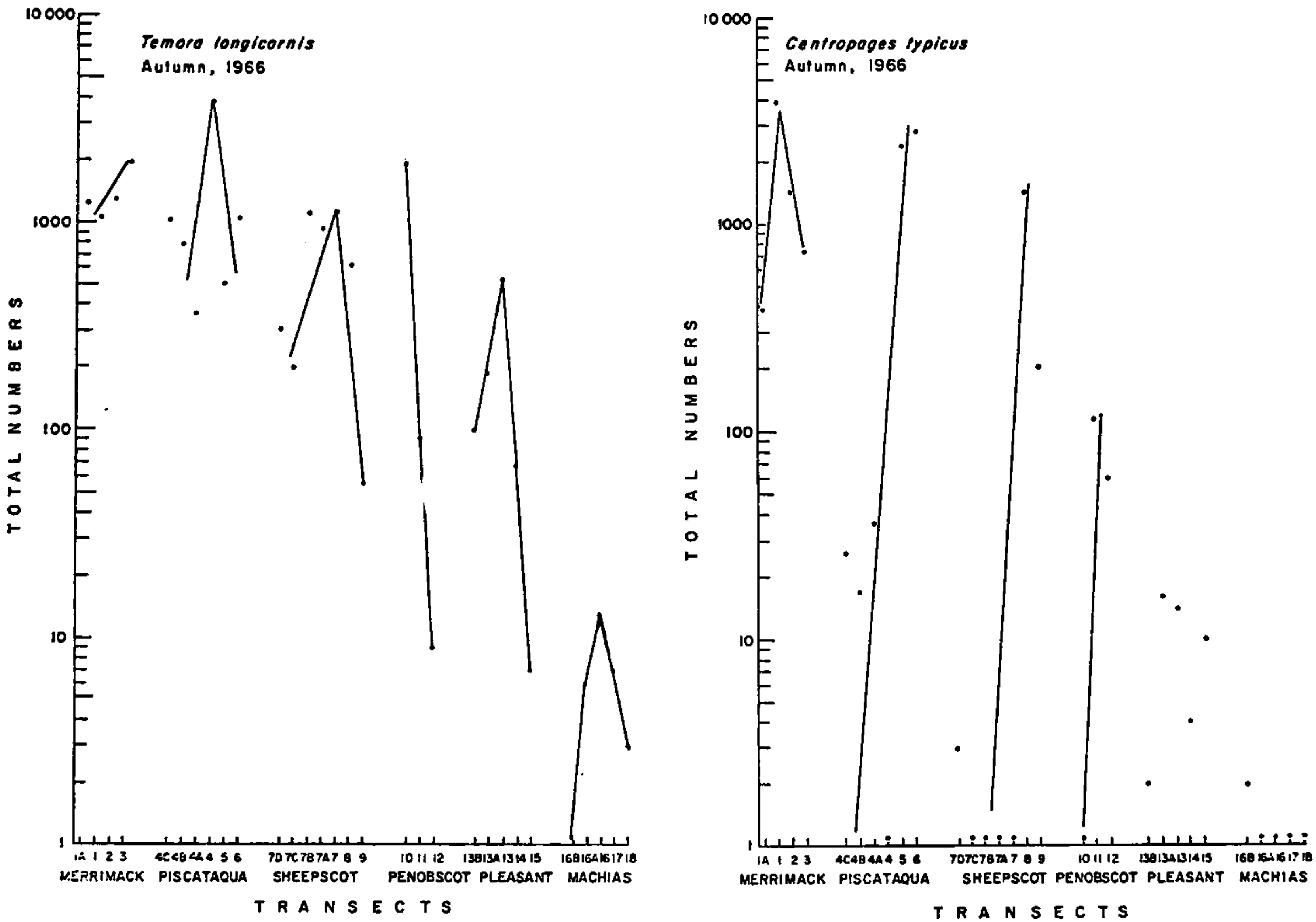


Fig. 14a. Changes in the inshore-offshore densities of T. longicornis and C. typicus ($N/10M^3$) in autumn along six transects in coastal waters of the western Gulf of Maine. Spearman rank correlation coefficients for each species are given in Table 2.

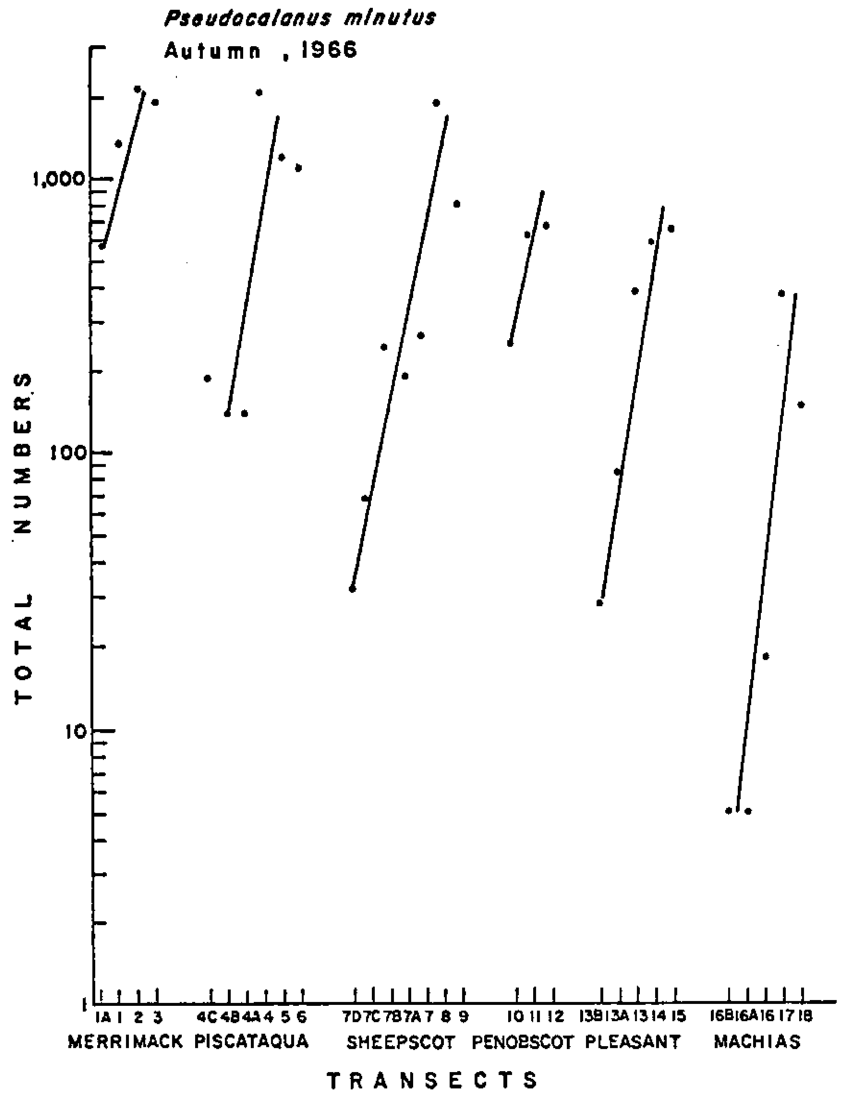


Fig. 14b. Changes in the inshore-offshore densities of P. minutus ($N/10M^3$) in autumn along six transects in coastal waters of the western Gulf of Maine. Spearman rank correlation coefficients are given in Table 2.

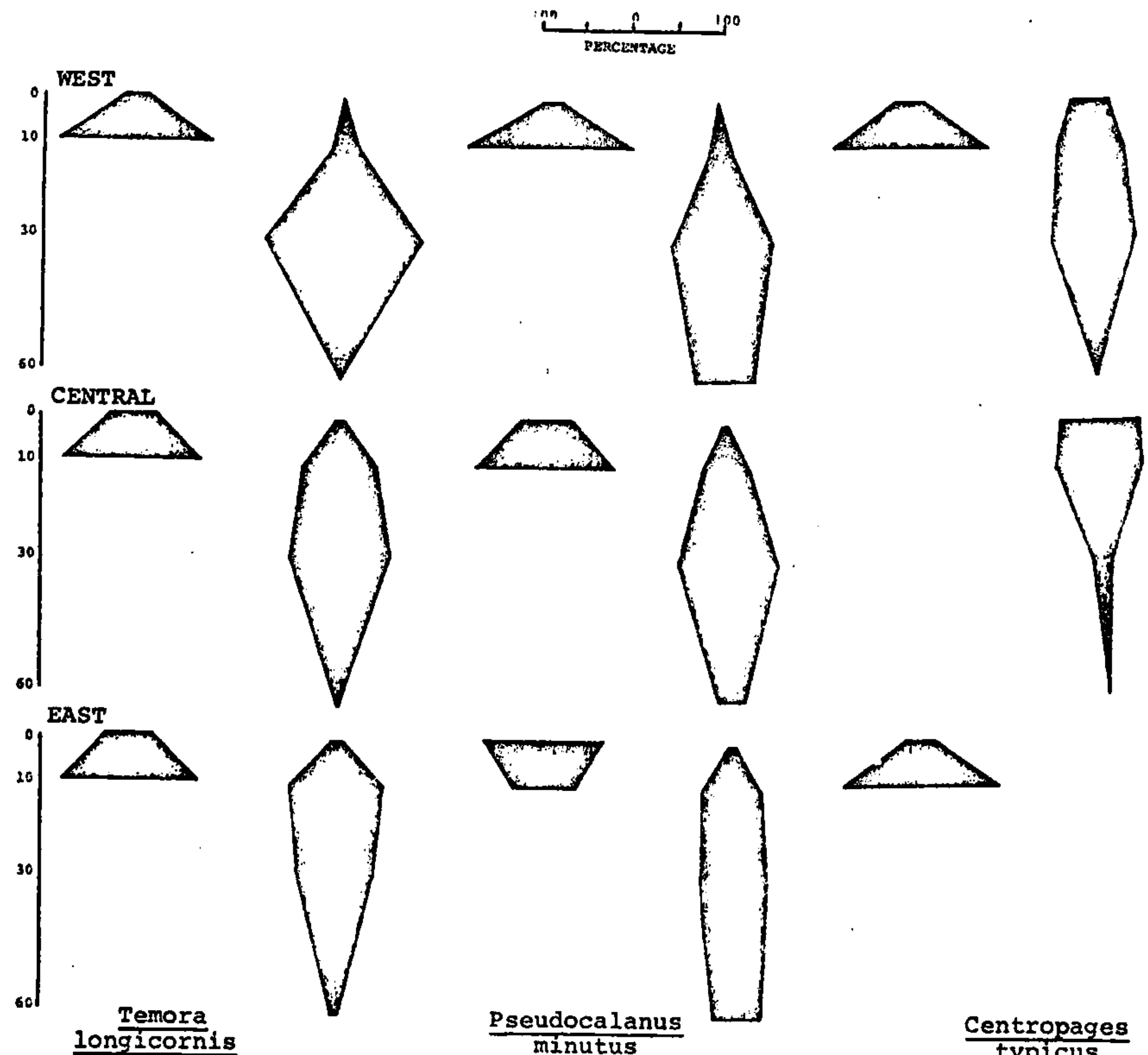


Fig. 15. Comparisons of the percentage occurrence of T. longicornis, P. minutus, and C. typicus in autumn at two depths inshore (0,10m) and four depths offshore (0,10,30,60m) in three coastal areas of the Gulf of Maine (West, Central, East).

coastal gulf in late spring, reaches a peak in summer, and declines in autumn and winter (Fig. 2 and 3); changes in copepod abundance also follow this seasonal sequence. Between late April and the first half of May, the copepod fauna changes from a low abundance level of essentially adult individuals to swarms of nauplii and copepodites (Bigelow, 1926; Sherman, 1970). This follows the onset of the vernal phytoplankton bloom, which is dependent on the initiation of thermal stratification (Bigelow et al., 1940). The close relationship between phytoplankton blooms and copepod swarming has been reported for at least two of the more numerous calanoids, C. finmarchicus and P. minutus, which undergo maximal breeding activity in response to increases in temperature and food abundance (Marshall and Orr, 1964; McLaren, 1965). Both species breed most intensively in the Gulf during the warm months of the year (Fish, 1936a,b).

The general decline in copepod abundance from west to east in spring, summer, and autumn is consistent with similar differences found for the coastal zooplankton assemblage in both the early decades of the century (Bigelow, 1926), and more recently from 1963 to 1968 (Sherman, 1970). The differences result from the dissimilar hydrography along the coast. In the east, the unstable water column and the lack of appreciable influx of zooplankton from the north and east lead to minimal conditions for population growth. The higher spring, summer, and autumn temperatures in the western and central areas, where the waters are relatively stable and stratified, provide an increasingly favorable environment for growth and development of zooplankton from Mt. Desert to Cape Ann (Bigelow, 1926; Fish and Johnson, 1937; Sherman, 1968). The lack of significant differences in abundance among the areas in winter is not clear. This may be a reflection of the low abundance of copepods, lack of significant breeding activity, and similarity of hydrographic conditions along the coast in this season.

The changes in copepod distributions on the inshore-offshore transects reflect differences resulting from the mixing of gradients of abundance rather than simply changes in the presence or absence of species. A. clausi, A. longiremis, and harpacticoids are most numerous inshore, and C. finmarchicus and C. typicus are abundant offshore. The distributions of P. minutus and T. longicornis are more variable. T. longicornis is concentrated inshore when moderately numerous; however, in summer as abundance increases, swarms are common throughout the coastal zone. The abundant P. minutus appears to be the species most tolerant of environmental differences within the sampling zone; concentrations tend to decrease from offshore to inshore in spring, summer, and autumn, but swarms occasionally occur inshore, particularly in winter.

Differences in the gradients of abundance of the dominants are in agreement with observations made earlier by Bigelow (1926) who, in his classical study of Gulf of Maine plankton, reported that A. clausi, A. longiremis, and T. longicornis were more abundant in the coastal belt and over shoal water than over the deeper basins during the colder half of the year and more widely distributed in the warmer months as their abundance increased. He classified C. finmarchicus as the dominant calanoid in waters outside the immediate coastal zone, and C. typicus as widespread, with its chief center of abundance off Massachusetts Bay north of Cape Cod, but also numerous out to the edge of the continental shelf off southern New England: P. minutus was considered to have a wider distribution in the Gulf of Maine over both shoal and deep water areas, and T. discaudatus and the harpacticoids, Zaus abbreviatus and Harpacticus uniremis, were found in abundance only in the shoal waters of the embayments.

The differences in the gradients of abundance of the more numerous species from inshore to offshore are more closely associated with changes in depth of the bottom than with a specific temperature or salinity regime. Trends in the inshore-offshore gradients of abundance persist in all seasons regardless of the area of the coastal zone occupied by cold or warm water or by low salinity inner coastal water (> 32 o/oo) that bathes most of the region sampled in spring and summer and the higher salinity (> 32 o/oo) outer coastal water that predominates in autumn and winter.

The biological and ecological factors that may influence the changes in abundance of copepods with depth have been discussed by several investigators, but have not been clearly defined. Bigelow (1926) in commenting on this relationship for T. longicornis remarked "...why Temora (and this applies to many other neritic members of the plankton) should be so closely confined to the comparatively shoal regions, irrespective of the physical state of the water within wide limits, when it has no connection with the bottom at any stage in its existence but is pelagic throughout its life, is a question to which no answer can yet be given..." Other contemporary investigators have reported similar conclusions. Fleminger (1956), in discussing biological faciation of copepods in the Gulf of Mexico, concluded that calanoid facies were most directly influenced by the land mass and its contribution to the marine environment; a view previously held by Clarke, et al.(1943), whoppostulated that chemical substances from the shore or bottom may control the distribution of holoplanktonic species. This conclusion was based, in part, on the differential distributions of chaetognaths and calanoid copepods on Georges Bank, where they found the chaetognath Sagitta elegans and Pseudocalanus minutus concentrated on the Bank, with S. serratondentata, S. enflata, and Calanus finmarchicus numerous over the deeper water around the periphery of the Bank. More recently, Pavshtics and Gogoleva (1964) reported that T. longicornis and P. minutus were concentrated on Georges Bank when C. finmarchicus was abundant over the adjacent deeper water. In the waters immediately south of Cape Cod, Grice and Hart (1962) found that four of the species that are predominant in coastal waters of the Gulf of Maine, P. minutus, C. typicus, T. longicornis, and C. finmarchicus, decreased in abundance from the shoal neritic to deeper slope waters and two of this group. P. minutus, and C. typicus, remained moderately abundant in slope water, but none were in the Gulf Stream or Sargasso Sea. In more northern waters, however, C. finmarchicus is distributed across the North Atlantic (Matthews, 1970). The persistence of P. minutus in the deeper slope waters is not consistent with other reports of its differential distribution on Georges Bank and in adjacent waters. Apparently this species has wide tolerance to ecological changes offshore in the outer shelf waters as well as in coastal waters.

In the northeast Atlantic where neritic, shelf, and oceanic waters mix near the coast, the relationship of the holoplanktonic copepods to the bottom and/or discrete water bodies is more complex than in the coastal waters of the Gulf of Maine. The relationships between surface water bodies and species associated with them are not dependent on temperature or salinity, but rather on a "unique and Honey, 1970). Other small copepods important in the larval diet in winter include harpacticoids, T. longicornis, A. longiremis and A. clausi, all species that are more numerous over the shoal inshore spawning areas than in the deeper outer coastal waters. A similar observation was made by Deevey (1960), who found that small copepods were the predominant species in Long Island Sound, which she considered a nursery area for fishes; the larger calanoids were more numerous in the adjacent deeper coastal waters. In this regard, it is possible to speculate on the importance of concentrations of small copepods over the offshore banks for the survival of commercially important fish stocks. Concentrations of P. minutus, Acartia spp., and T. longicornis that have been observed over the shallow areas of the banks in outer coastal waters that are also frequented by spawning fish, would provide a readily available source of food if the fish larvae and their planktonic food were maintained on the banks. The presence of eddy systems over a shoal area of Georges Bank, as reported by Clarke et al., (1943) for the chaetognath, Sagitta elegans, suggests that concentrating mechanisms for fish larvae and their forage could also be present on the Bank, where several important commercial species spawn, including herring.

Although adult herring are known to undergo migrations in outer coastal and shelf waters, information on the movements of adults on the Gulf coast is scanty. Adults are fished on Jeffreys Ledge and adjacent shoal areas by vessels of several nations. Adult fish collected in autumn from Jeffreys area were feeding heavily on C. typicus (Sherman, unpublished data); and it is possible that they may aggregate over the rich feeding grounds in the western Gulf, where the large calanoids, C. finmarchicus and C. typicus, are concentrated in summer and autumn. It is unlikely that in a feeding migration adults preying on large calanoids, which are most numerous in outer coastal waters, would move into the coastal embayments.

property" of the water as yet undefined (Bary, 1963). How these relationships may relate to changes in the depth of the bottom is not clear. Other investigators who examined the changing distributions of copepods and other zooplankters among a wide range of areas and depths in the northeast Atlantic, have reported that changes in gradients of abundance of several plankters, including copepods, are correlated with the 100 fathom curve; some species are abundant over deep water and absent over the shelf, and others abundant over the shelf but decline abruptly at the 100-fathom isobath (Colebrook et al., 1961).

The differential distributions of copepods in coastal waters of the Gulf of Maine can only be considered as trends that are indicative of directions of change in abundance of the dominant species between the shoal and deeper waters of the coast. Correlation coefficients (r_s) were significant ($P < 0.05$) for only four of the species: A. longiremis in winter; C. finmarchicus on three transects in winter and spring, and on all of them in summer; harpacticoids on single transects in winter and spring; and P. minutus on a single transect in winter, two in spring and summer and one in autumn. The r values for T. longicornis and T. discaudatus were non-significant ($P > 0.05$) in each of the seasons, largely because of their concentrations at the mouths of the estuaries and sharp reductions both within the estuaries and offshore; the r values for A. clausi were low because of its limited abundance (Table 2).

Copepod Distributions and Herring Ecology

The survival, growth, and distribution of herring in coastal waters of the northwest Atlantic are affected by differences in the availability and abundance of copepods, their predominant food source. Pavshtics (1963) and Zenkevitch (1967) have reported that movements of commercial aggregations of adult herring in outer coastal waters between the mid-Atlantic Bight and Georges Bank are correlated with copepods and other zooplankters that are concentrated in seasonally formed frontal zones between coastal and slope waters. By monitoring the formation and movement of these frontal zones it may be possible to develop short-term forecasts of herring availability in the Georges Bank region. In coastal waters of the Gulf of Maine, where the fishery for immature herring is centered, it is likely that short term availability forecasts based on hydrographic and plankton conditions can be made. Preliminary findings, based on tag returns, indicate that one and two year old herring, the age groups preferred by the "sardine" industry, do not undergo extensive migrations (Watson, J.E., Bur. Comm. Fish., Boothbay Harbor, unpublished data), suggesting that local feeding conditions will have a dominant influence on survival and growth. This influence is reflected in differences in the increased length of herring west of Penobscot Bay, by about 2 cm, over fish in the eastern area of the coast (Watson, J.E., unpublished data); conditions for feeding and growth are better in the warm waters in the western area with their high standing stock of copepods, than in the cooler less productive waters of the eastern coastal region.

In addition to providing a vital food source for juveniles, copepods are also the predominant food of larval herring in coastal waters of the Gulf (Sherman and Honey, 1968). One of the smaller but abundant copepods, P. minutus is a species that serves as a primary food source for herring larvae in coastal waters during the critical period of low zooplankton abundance in winter (Sherman

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