DISTRIBUTION OF FILTER-FEEDING CALANOID COPEPODS IN THE EASTERN EQUATORIAL PACIFIC

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ABSTRACT

Zooplankton samples taken in the Eastern Equatorial Pacific between 5°N and 5°S by two Eastropac cruises (August-September 1967 and February-April 1968) were examined to determine the distribution of 21 species of epiplanktonic calanoid copepods. The distributions were considered relative to oceanographic conditions and circulations in the Eastern Equatorial Pacific Ocean. Distributional groups of species were defined by cluster analysis and correlation coefficients. The distributional groups were associated with waters influenced by the Peru Current, the warm equatorial and central waters, and the transition waters between them. The distribution patterns of the species varied in response to seasonal changes in the circulation of surface waters.

RESUMEN

Muestras de zooplancton tomadas en el Pacífico Ecuatorial Oriental entre 5°N y 5°S en dos cruceros Eastropac (agosto-septiembre 1967 y febrero-abril 1968) fueron examinadas para determinar la distribución de 21 especies de copépodos calanoídeos epipelágicos. Las distribuciones fueron consideradas en relación a las condiciones oceanográficas y a la circulación en el Océano Pacífico Ecuatorial Oriental. Los grupos de distribución estaban relacionados con masas de agua influenciadas por la corriente del Perú, aguas cálidas ecuatoriales y centrales, y masas de agua de trancisión entre ellas. Los patrones de distribución de las especies varían de acuerdo a cambios estacionales en la circulación de las aguas superficiales.

INTRODUCTION

This work focuses on the qualitative and quantitative distribution of herbivorous planktonic copepods of the mixed layer within the Eastern Equatorial Pacific (EEP), a complex region marked by surface currents, countercurrents, and undercurrents. The area studied lies off the coasts of Colombia, Ecuador, and northern Peru, and is part of the Panamic Province (Figure 1). It is overlain by tropical surface water and equatorial surface water of the Eastern Tropical Pacific (Wyrtki 1966).

Knowledge of the distribution of copepods in the EEP is relatively sparse. Works dealing with the taxonomy and geographical occurrence of calanoid copepods in this area have been published by Giesbrecht (1895) and Wilson (1950), from collections by the U.S. Fisheries steamer *Albatross*. Wilson (1942) lists species from the Carnegie expedition; later contributions to specific taxa include Bowman (1955) on *Mesocalanus*, Grice (1964) on five species from the Galápagos Islands, Fleminger (1967, 1975) on coastal-water *Labidocera*, Frost and Fleminger (1968) on *Clausocalanus*, Fleminger (1973) on *Eucalanus*, Bradford (1974) on *Euchaeta*, Fleminger and Hulsemann (1973) on *Pontellina*, and Mullin and Evans (1976) on *Neocalanus*. Of the very few descriptions and reports made for the coast of Ecuador, most are from the Gulf of Guayaquil (Johnson 1964; Fleminger 1975; Arcos 1978). Studies performed in waters

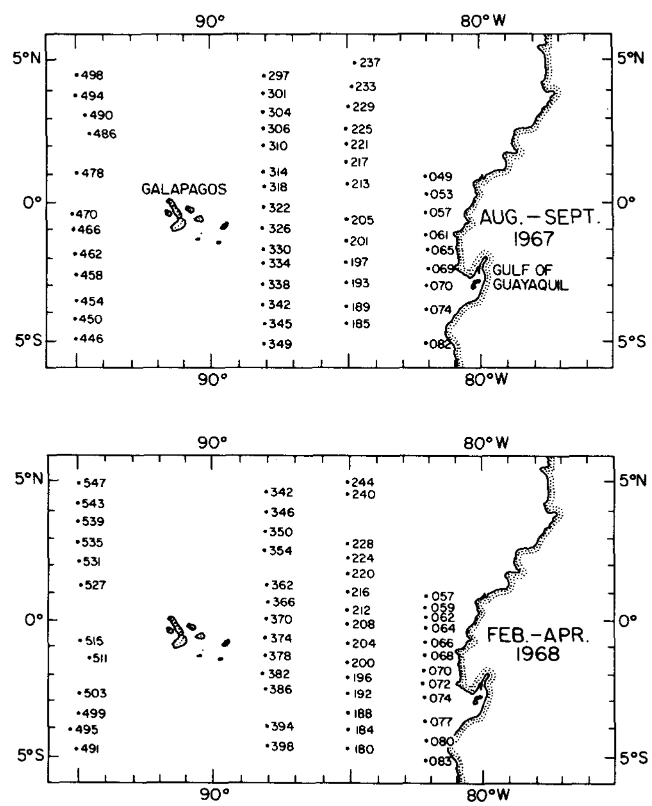

Figure 1. Stations sampled during R/V *Rockaway* cruise 47 (1967) and cruise 77 (1968), Eastropac Program in the Eastern Equatorial Pacific.

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adjacent to the area of our concern are by Heinrich (1960, 1973), who discusses horizontal distributions in the Equatorial Pacific (EP) and the Peru Current regions; by Timonin and Voronina (1977), who discuss vertical distribution related to the stratification of water masses on the equator between 100°W and 160°W; by Grice (1961), who reports on the systematics of copepods in the EP west of 120°W; by Gómez (1982), who refers to some calanoids at 9°S in the Peru Current; by Gueredrat (1971), who reports on the transpacific distribution of copepods in the upper 200 meters at the equator; by Lang (1964), who discusses systematics and distribution of the Eucalanidae in the Western and Central Pacific; by Manrique (1977), who discusses seasonal variation in the Gulf of California; and by Brinton et al. (1986), who review the plankton biota in the Gulf of California.

Of the more than 200 species of calanoids described in the literature cited above for the mixed layer in the EEP, 140 species have been reported from the area of this study (5°N-5°S and 82°W-95°W).

Here we establish the quantitative distribution of the individual species sampled by the Eastropac Program during R/V *Rockaway* cruises 47 (August-September 1967) and 77 (February-April 1968). A second objective is to determine whether the distributions display discernible patterns that are coherent with the major circulation systems of the study area.

MATERIALS AND METHODS

The zooplankton samples examined here were obtained from the region limited by 5°N and 5°S, and between 82° and 95°W, within the Eastern Equatorial Pacific. The samples were collected on two cruises of the Eastropac Program: 49 stations from R/V *Rockaway* cruise 47 in August-September 1967 and 52 stations from R/V *Rockaway* cruise 77 in February-April 1968 were examined (Figure 1). The distance between stations within the meridional lines was 70 km, and the distances between lines were 300 km east of the Galápagos, and 700 km west of the Galápagos.

The samples were taken by oblique hauls made with a 1-m zooplankton net constructed of nylon cloth (mesh aperture 0.505 mm), with approximately a 5:1 ratio (pore area to mouth area) of effective straining surface. Detailed description of the towing procedure is given by Love (1972a). The positions of the stations, as well as the numbers of organisms per 100 m^3 are given in an appendix that can be obtained by mail from either author. The estimated maximum depths of the 101 samples ranged from 100 to 266 m, with a mean of 200 m and a standard deviation of 24 m. The samples were taken at the time of arrival at the station, without regard for day or night.

The zooplankton samples were originally divided with the aid of a Folsom plankton sample splitter (McEwen et al. 1954), half of each sample being sent to the Smithsonian Institution in Washington and half deposited in the zooplankton collection of Scripps Institution of Oceanography (SIO). From the 50% fractions held by SIO, aliquots were taken using a Folsom splitter. Aliquots ranging in volume from 1/32 to 1/2 were taken in order to count at least 100 individuals of the most abundant species. In 80% of the cases, the two portions given by the splitter were counted independently. An overall difference of less than 10% was observed between the two portions.

The copepods analyzed and listed below were adult females of the 21 most abundant species. Two species were lumped under *Cosmocalanus* spp., and the copepodite stage V of *Calanus chilensis* was also counted because of its high abundance in some samples.

Calanus chilensis Brodsky
Calanus chilensis copepodites stage V
Centropages calaninus (Dana)
Centropages furcatus (Dana)
Centropages gracilis (Dana)
Cosmocalanus spp.
Eucalanus hyalinus (Claus)
Eucalanus inermis Giesbrecht
Mesocalanus tenuicornis (Dana)
Nannocalanus minor (Claus)
Neocalanus gracilis (Dana)
Neocalanus robustior (Giesbrecht)
Pareucalanus attenuatus (Dana)
Pareucalanus sewelli (Fleminger)
Rhincalanus nasutus Giesbrecht
Rhincalanus rostrifrons (Dana)
Subeucalanus pileatus (Giesbrecht)
Subeucalanus subcrassus (Giesbrecht)
Subeucalanus subtenuis (Giesbrecht)
Temora discaudata Giesbrecht
Undinula vulgaris (Dana)

Over 64,000 organisms were identified and counted under a dissecting microscope, the mean per sample being 634 individuals (range, 132 to 3879). Most of the species studied are easy to identify. In the case of eucalanids, when the identification was uncertain, the specimens were sorted for examination of the pore signature. This procedure, described by Fleminger (1973), readily permits one to distinguish species of Eucalanidae.

The number of organisms calculated for each sample was standardized to the volume of 100 m^3. The mean volume of water filtered during the field sampling was 620 m^3.

The samples were arranged into assemblages using the Ward method (Anderberg 1973) for cluster analysis from a pool of 2,020 values. The program forms successively fewer, larger, groups until the total number of samples has been reduced to a small number of assemblages (in the extreme, one assemblage consists of all samples). As the number of assemblages is allowed to decrease in this process by agglomeration of samples, the faunal variability included within each assemblage increases, but the spatial pattern of assemblages becomes easier to visualize and interpret. The method deals with the sum of Euclidean distances (SED) between stations; the same level of SED was used for the two cruises. Pearson's correlation coefficient (Sokal and Rohlf 1981) was used for evaluating the correlations between species.

Water temperatures were available at 1-m intervals from the surface to about 750-m depth for each station at which an STD determination of salinity and temperature was made. Since most of the copepods studied are distributed in the upper 50 m, the values of temperature and salinity were integrated for the 0-50-m water column. For the integration we used six values at 10-m intervals.

The Eastropac atlases (Love 1972a, b and 1975; Love and Allen 1975) presented the physical, chemical, and biological information of the region. M. Tsuchiya provided unpublished tabulated data of temperature and salinity.

SYSTEMATIC NOTE

There is general acceptance of the systematic status of most of the species observed, but we want to comment on the use of the genera *Subeucalanus* and *Pareucalanus*.

Fleminger (1973) divided the species of the genus *Eucalanus* s.l. Dana into four groups based on the pattern of integumental pore distributions. These are (1) the subtenuis group (*E. subtenuis, E. mucronatus, E. crassus, E. longiceps*, and *E. monachus*); (2) the pileatus group (*E. pileatus, E. subcrassus*, and *E. dentatus*); (3) the elongatus group (*E. elongatus, E. hyalinus, E. inermis, E. bungii*, and *E. californicus*); and (4) the attenuatus group (*E. attenuatus, E. sewelli, E. parki*, and *E. langae*). Geletin (1976) subsequently defined three genera based on the fifth legs of males, and abdomen morphology of females: *Eucalanus* s.s. represents the elongatus group, *Subeucalanus* the subtenuis and pileatus groups, and *Pareucalanus* the attenuatus group. This revision was further supported by Bjornberg's (1986) study of the morphological characteristics of the nauplii. Since these independent characters suggest the same taxonomical groupings, we accept Geletin's genera.

In the area of study there are two species of *Cosmocalanus*—*C. darwini* (Lubbock) and *C. caroli* (Giesbrecht)—that overlap in their distribution. There are morphological characteristics to separate the adult males, but not the females, so the two species were united together as *Cosmocalanus* spp.

Hydrography of Studied Area, 1967 and 1968

A number of oceanographic expeditions have studied the Eastern Equatorial Pacific and delineated its principal oceanographic features (e.g., Wooster and Cromwell 1958; Austin 1960; Knauss 1960, 1966; Bennett 1963; Wyrtki 1966, 1967, 1977; Tsuchiya 1968, 1970, 1972, 1974, 1985; Stroup 1969; Donguy and Rotschi 1970; Leetmaa 1982; Leetmaa et al. 1981; Lukas 1981; Moreano 1983).

The main surface current in our area of study is the South Equatorial Current (SEC) moving to the west, with the northern limit at 4°N and the southern at 10°S (Wyrtki 1977). This current is fed from the northeast by a branch of the North Equatorial Countercurrent (NECC) that flows to the east, strikes the coast of Central America, and advects water northward to Costa Rica, and southward from the Panama Bight to the south and west. From the southeast the SEC meets the Peru Current, which flows to the north along the coast of Peru and then turns west toward the Galápagos, forming the limit of the Equatorial Front as it encounters the warm surface tropical waters from the north (Wooster 1969).

The SEC carries a tremendous volume of water that is supplemented by water coming from the Equatorial Undercurrent (EU) in addition to that supplied by the NECC and the Peru Current (Wyrtki 1977). Tsuchiya (1972, 1975) describes the circulation of the subsurface currents, pointing out the presence of the EU, originally described by Cromwell et al. (1954), flowing eastward along the equator, and the presence of the north and south Equatorial Subsurface countercurrents having the same direction and lying at 3°-6°N and 4°-8°S, respectively.

Figures 2 and 3 show the surface temperature and salinity for August-September 1967 and February-April 1968. From these charts one can visualize the Equatorial Front (EF) defined by the 20° and 25°C isotherms. The EF is normally weak or absent in February-March, as can be seen in monthly average sea-surface temperature maps (e.g., Wyrtki 1964; Robinson 1976). In February-March 1968, the front was present east of the Galápagos Islands. The upper layer temperature off South America was lower than normal in this period, and the development of the cold water mass east of the Galápagos (Figure 2) was unusually strong, resulting in a fairly intense front.

In 1967 warmer and less saline water remained north of the EF, and cooler and more saline waters were to

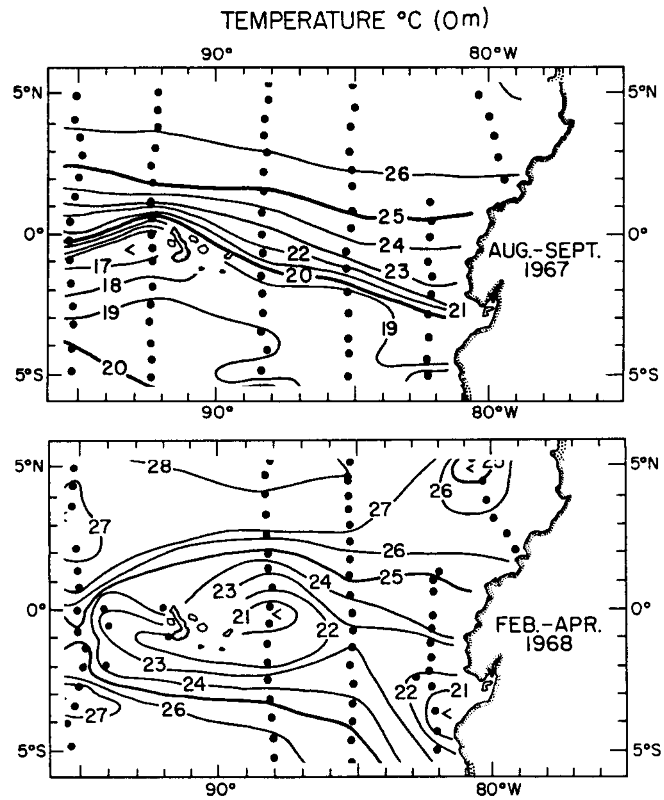

Figure 2. Distribution of surface temperature in the Eastern Equatorial Pacific in 1967 and 1968, reproduced from Love (1972a,b, 1975).

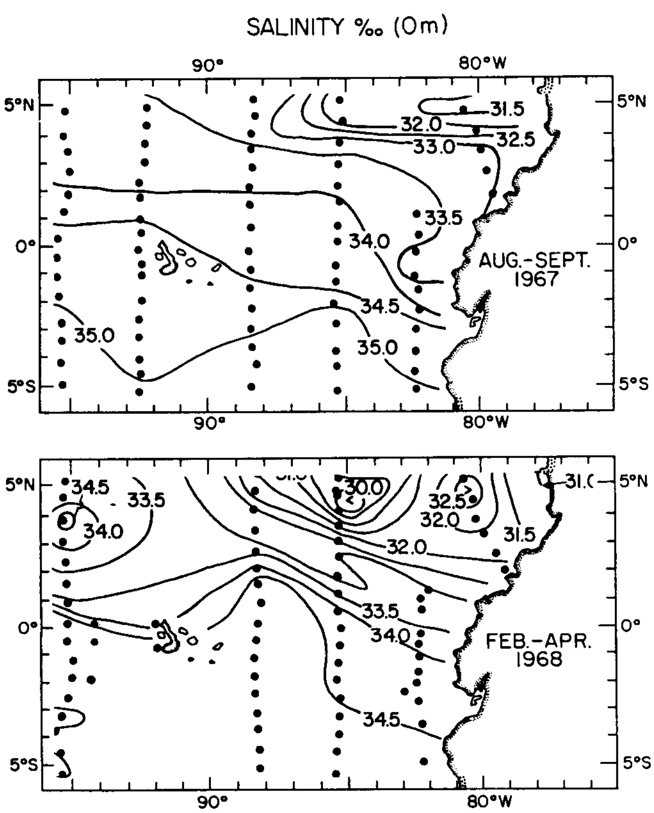

Figure 3. Distribution of surface salinity in the Eastern Equatorial Pacific in 1967 and 1968, reproduced from Love (1972a,b, and 1975).

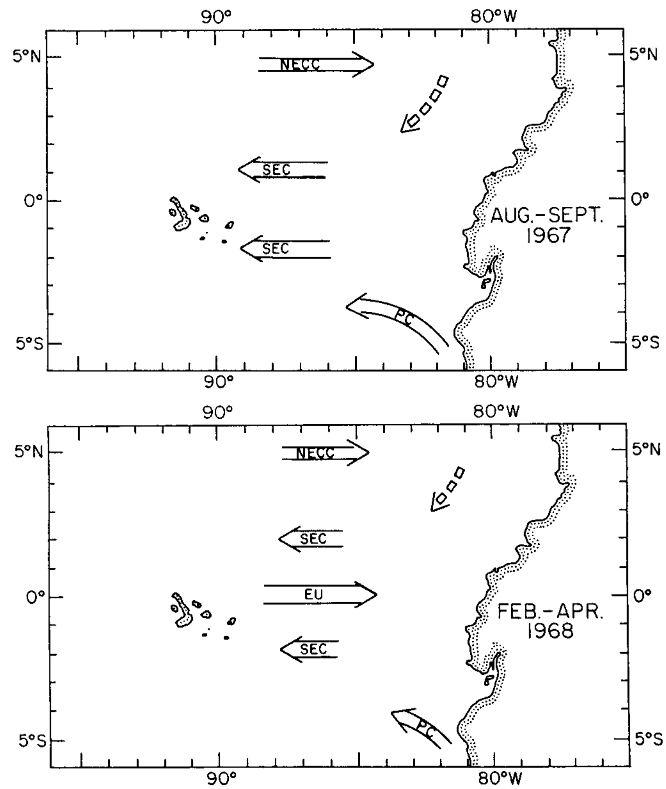

Figure 4. Trends of circulation of surface waters in the Eastern Equatorial Pacific in 1967 and 1968. See text for references.

the south. In 1968 temperatures lower than 21°C were not found; the 25°C isotherm was located at 1°N and 5°S in the east, and at 1°N and 2°S in the west. Waters warmer than 25°C were found north and south of the limits of that isotherm, with lower salinity to the north and higher salinity to the south.

In 1967 there was an indication of upwelling southwest of the Galápagos (Ahlstrom 1972), and in 1968 upwelling was evident east of the Galápagos and south of the Gulf of Guayaquil (Wyrtki et al. 1976; Moreano 1983).

The general trend of circulation (Figure 4) is based on data from Sverdrup et al. (1942), Wyrtki (1966, 1967), Tsuchiya (1972, 1975), Zambrano (1980), Sund et al. (1981), Moreano (1983), and Okuda et al. (1983). The North Equatorial Countercurrent, the South Equatorial Current and the Peru Current were stronger in 1967 than in 1968. Another primary difference between these two cruises is the surfacing in the latter of the Equatorial Undercurrent as it flows eastward along the equator (Jones 1969).

RESULTS

Abundance

Table 1 shows the mean abundance of species for all stations in each of the cruises. The most abundant species, exceeding 150 organisms (org.)/100m^3, for

TABLE 1
Mean Abundance of Individual Species (Org./100m^3) in August-September 1967 and February-April 1968

	1967	1968
Calanus chilensis	388	478
Calanus chilensis (stage V)	249	4,137
Centropages calaninus	1	0
Centropages furcatus	44	154
Centropages gracilis	—	2
Cosmocalanus spp.	188	150
Eucalanus hyalinus	—	1
Eucalanus inermis	11	74
Mesocalanus tenuicornis	34	29
Nannocalanus minor	249	495
Neocalanus gracilis	3	4
Neocalanus robustior	0	1
Pareucalanus attenuatus	9	4
Pareucalanus sewelli	66	50
Rhincalanus nasutus	260	116
Rhincalanus rostrifrons	12	8
Subeucalanus pileatus	39	20
Subeucalanus subcrassus	40	87
Subeucalanus subtenuis	374	202
Temora discaudata	71	144
Undinula vulgaris	14	12

TABLE 2
Occurrences of Individual Species for Each Cruise

	1967	1968	Total
Number of stations	49	52	101
Calanus chilensis	11	7	18
Calanus chilensis (stage V)	9	11	20
Centropages calaninus	8	2	10
Centropages furcatus	47	49	96
Centropages gracilis	16	14	30
Cosmocalanus spp.	47	45	92
Eucalanus hyalinus	9	12	21
Eucalanus inermis	18	27	45
Mesocalanus tenuicornis	45	47	92
Nannocalanus minor	49	52	101
Neocalanus gracilis	23	16	39
Neocalanus robustior	5	9	14
Pareucalanus attenuatus	18	17	35
Pareucalanus sewelli	48	48	96
Rhincalanus nasutus	34	41	75
Rhincalanus rostrifrons	33	31	64
Subeucalanus pileatus	34	30	64
Subeucalanus subcrassus	38	47	85
Subeucalanus subtenuis	49	51	100
Temora discaudata	46	45	91
Undinula vulgaris	27	24	51

the two cruises are *Calanus chilensis* (adults and stage V copepodites) (Figures 5 and 6), *Nannocalanus minor* (Figure 7), *Subeucalanus subtenuis* (Figure 8), *Rhincalanus nasutus* (Figure 9), and *Cosmocalanus* spp. (Figure 10). Intermediate abundance values, between 40 and 150 org./100m^3, are found for *Temora discaudata* (Figure 11), *Centropages furcatus* (Figure 12), *Pareucalanus sewelli* (Figure 13), *Eucalanus inermis* (Figure 14), and *Subeucalanus subcrassus* (Figure 15). Species showing the lowest abundance, below 40 org./100m^3, are *Mesocalanus tenuicornis* (Figure 16), *Subeucalanus pileatus* (Figure 17), *Undinula vulgaris* (Figure 18), *Rhincalanus rostrifrons* (Figure 19), *Pareucalanus attenuatus* (Figure 20), *Neocalanus gracilis* (Figure 21), *Centropages gracilis* (Figure 22), *Eucalanus hyalinus* (Figure 23), *Neocalanus robustior* (Figure 24), and *Centropages calaninus* (Figure 25).

Frequency

Table 2 shows the number of occurrences of each species from the total of samples studied and from each cruise. Species represented in more than 50% of the samples are *Nannocalanus minor, Subeucalanus subtenuis, Pareucalanus sewelli, Centropages furcatus, Cosmocalanus* spp., *Mesocalanus tenuicornis, Temora discuadata, Subeucalanus subcrassus, Rhincalanus nasutus, Subeucalanus pileatus, Rhincalanus rostifrons,* and *Undinula vulgaris*. Species represented in less than 20% of the samples are *Calanus chilensis* (adults and juveniles), *Neocalanus robustior,* and *Centropages calaninus*.

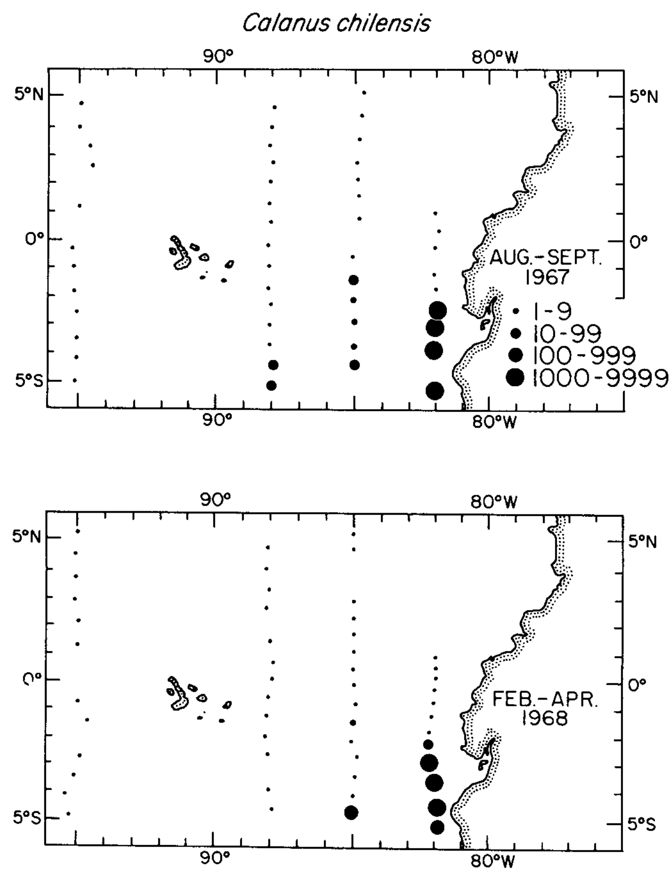

Figure 5. Distribution of abundance of adult females of *Calanus chilensis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

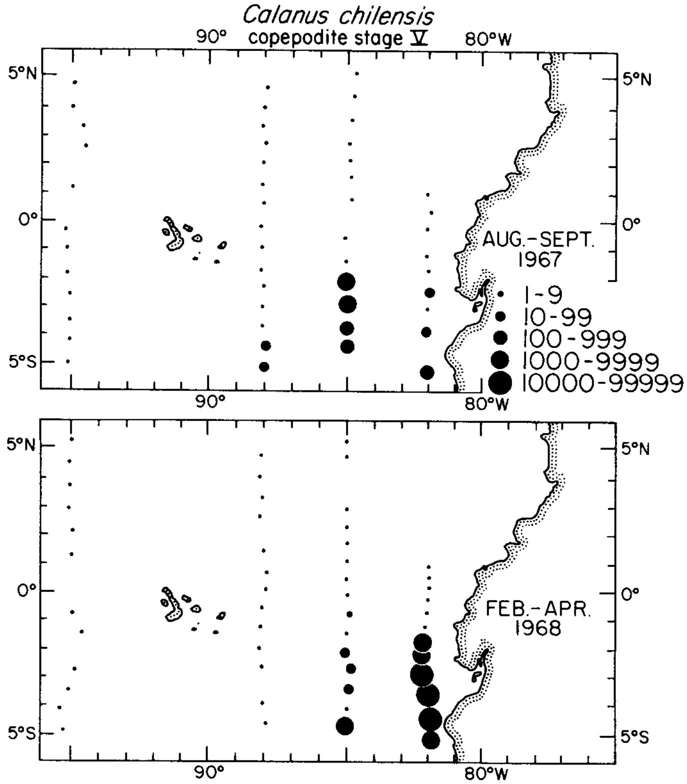

Figure 6. Distribution of abundance of *Calanus chilensis* stage V copepodites in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

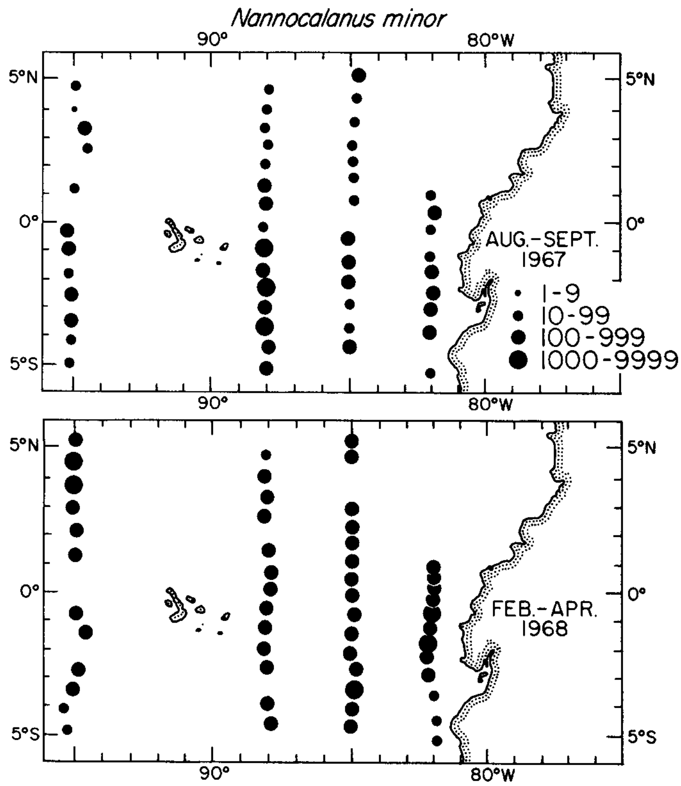

Figure 7. Distribution of abundance of adult females of *Nannocalanus minor* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

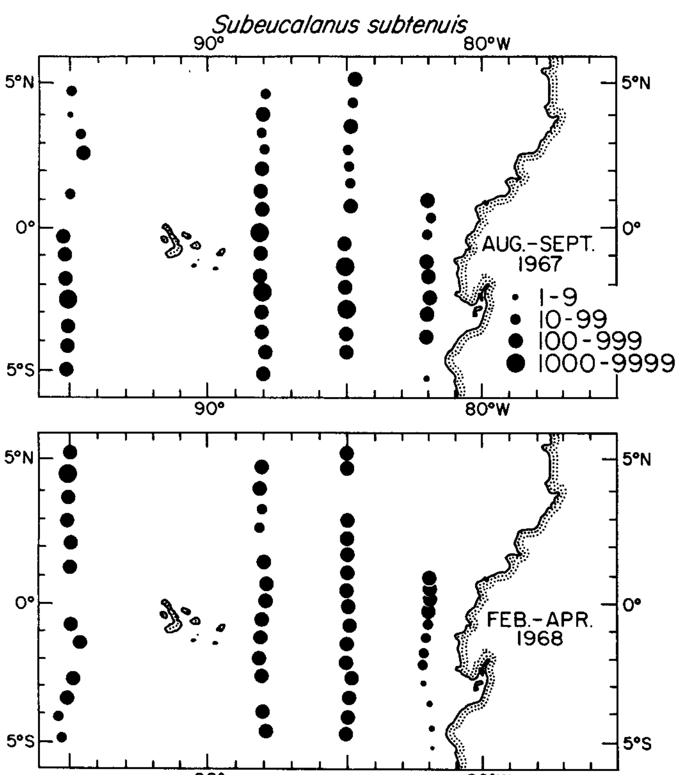

Figure 8. Distribution of abundance of adult females of *Subeucalanus subtenuis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

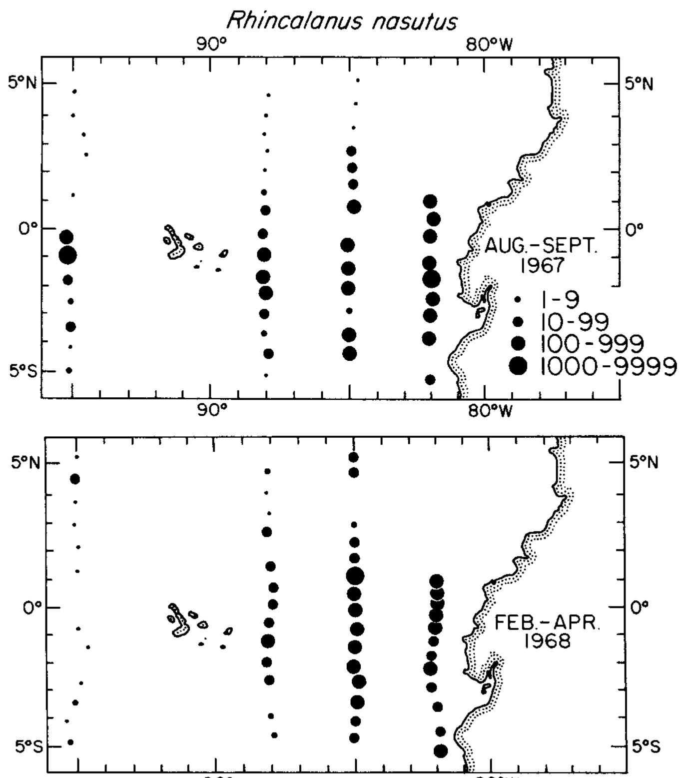

Figure 9. Distribution of abundance of adult females of *Rhincalanus nasutus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

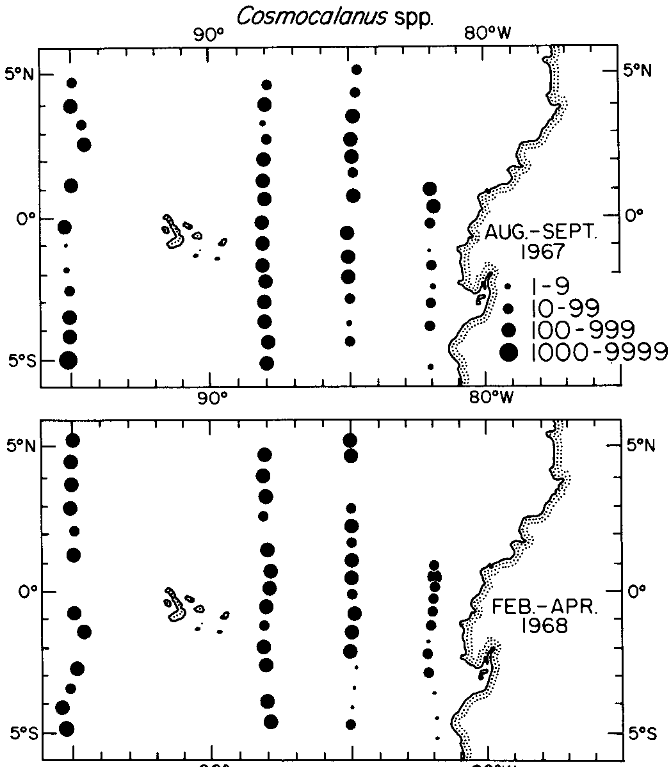

Figure 10. Distribution of abundance of adult females *Cosmocalanus* spp. in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

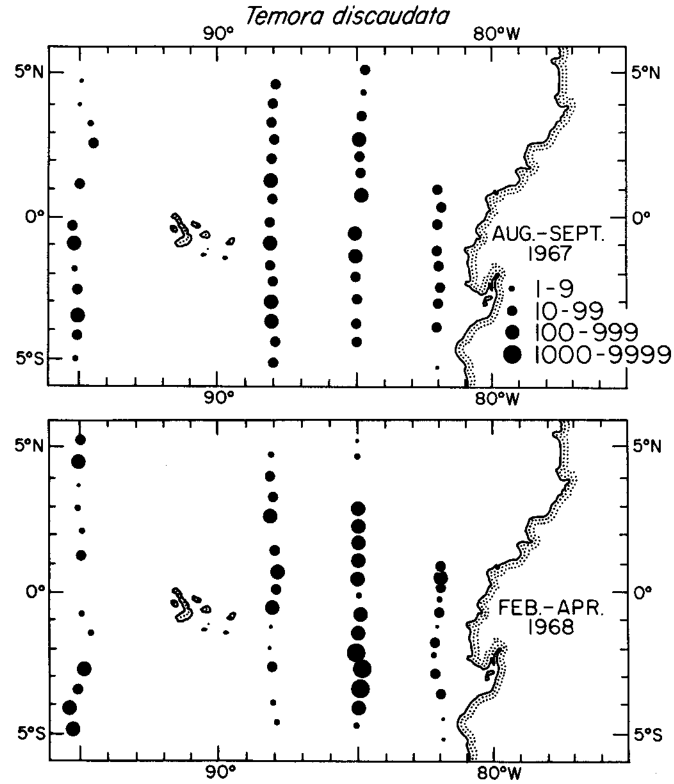

Figure 11. Distribution of abundance of adult females of *Temora discaudata* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

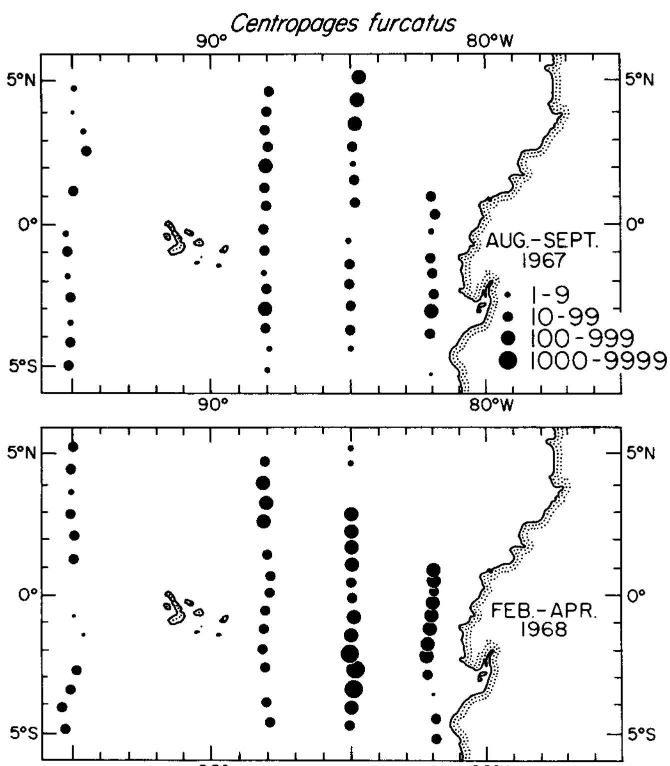

Figure 12. Distribution of abundance of adult females of *Centropages furcatus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

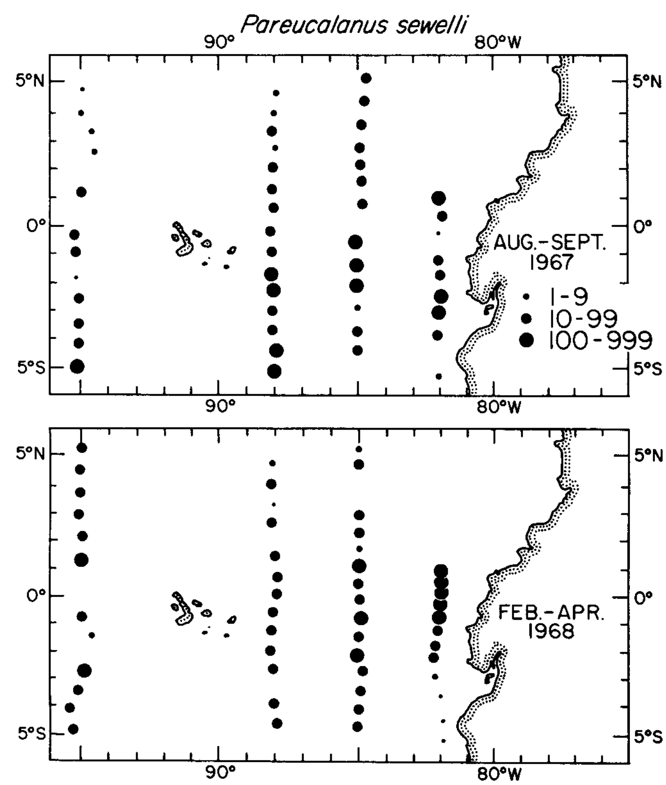

Figure 13. Distribution of abundance of adult females of *Pareucalanus sewelli* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

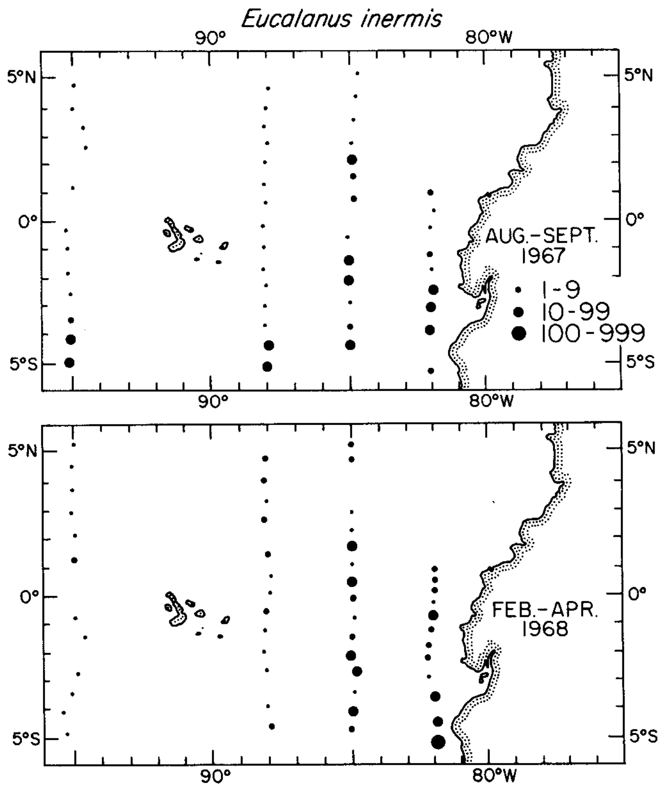

Figure 14. Distribution of abundance of adult females of *Eucalanus inermis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

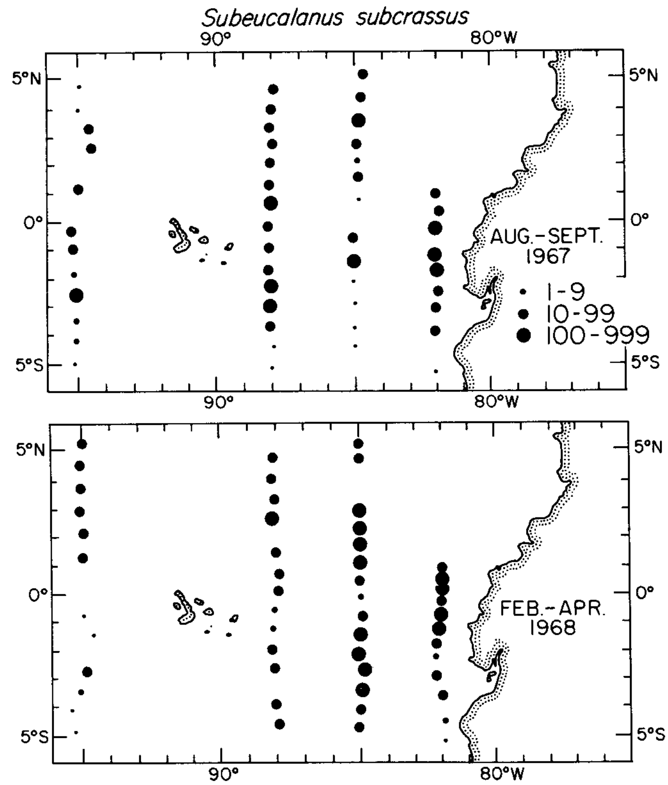

Figure 15. Distribution of abundance of adult females of *Subeucalanus subcrassus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

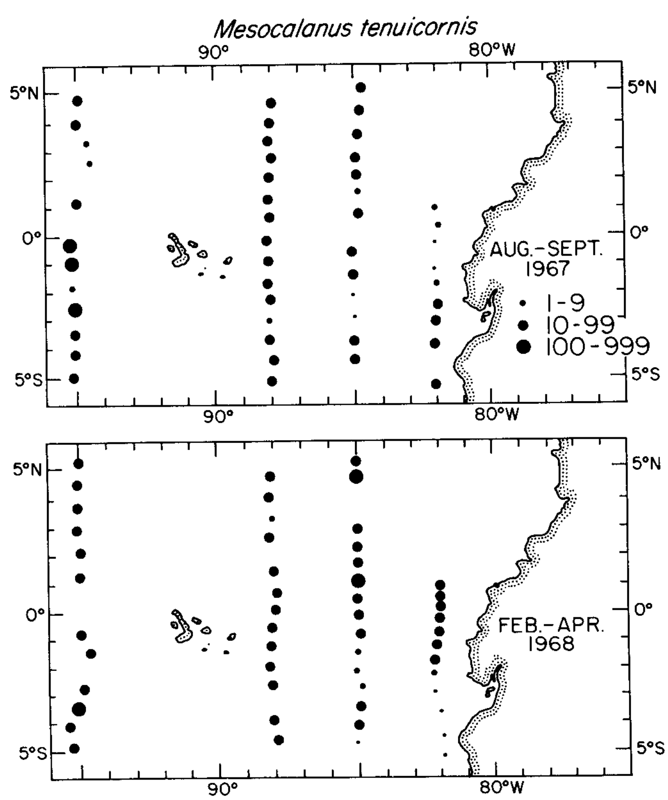

Figure 16. Distribution of abundance of adult females of *Mesocalanus tenuicornis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

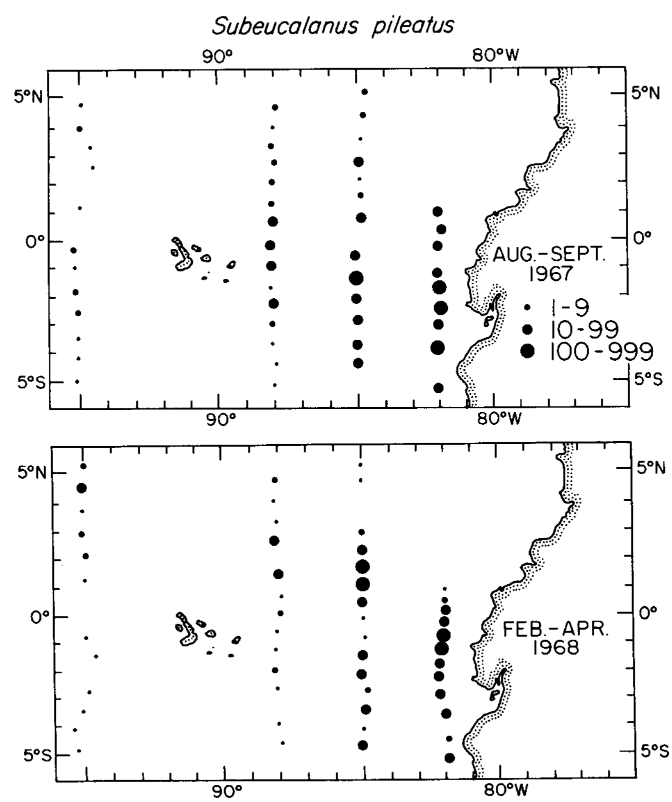

Figure 17. Distribution of abundance of adult females of *Subeucalanus pileatus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

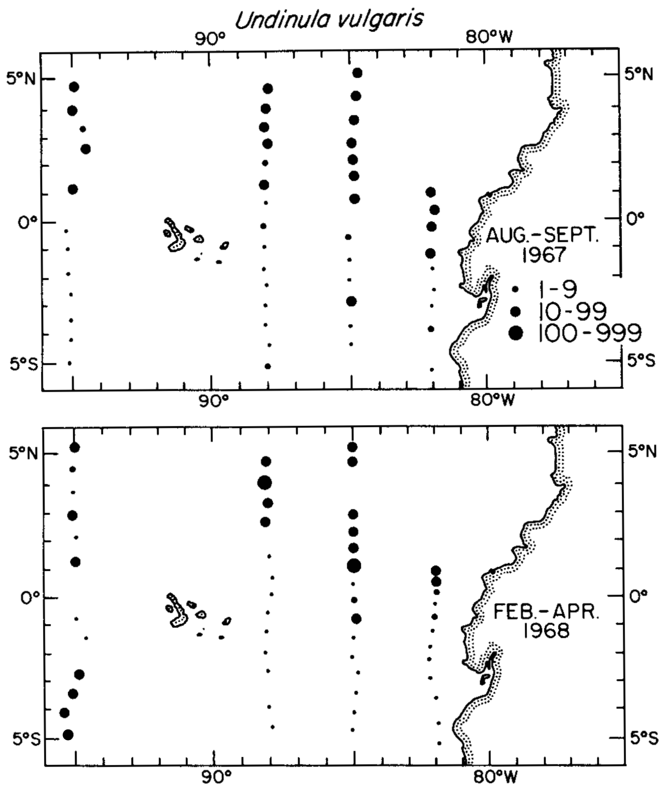

Figure 18. Distribution of abundance of adult females of *Undinula vulgaris* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

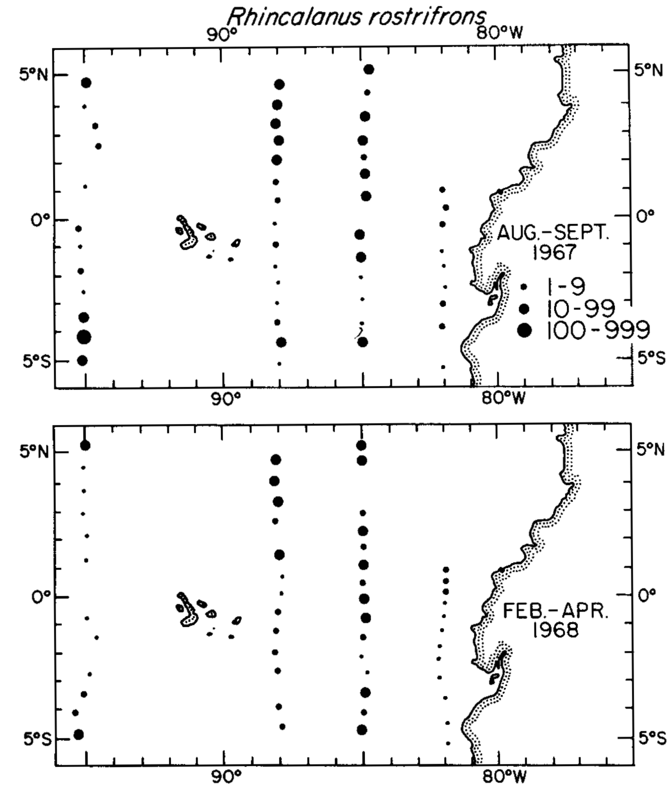

Figure 19. Distribution of abundance of adult females of *Rhincalanus rostrifrons* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

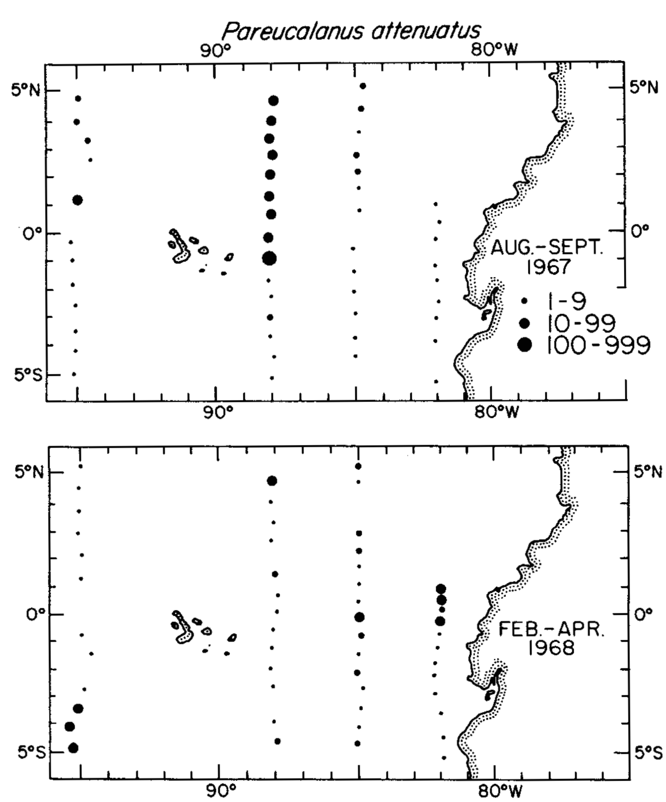

Figure 20. Distribution of abundance of adult females of *Pareucalanus attenuatus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

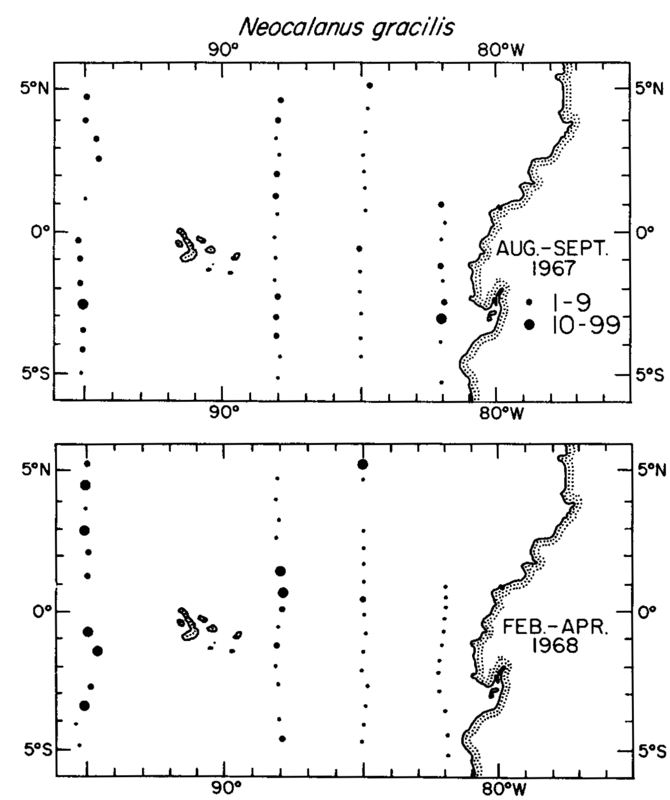

Figure 21. Distribution of abundance of adult females of *Neocalanus gracilis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

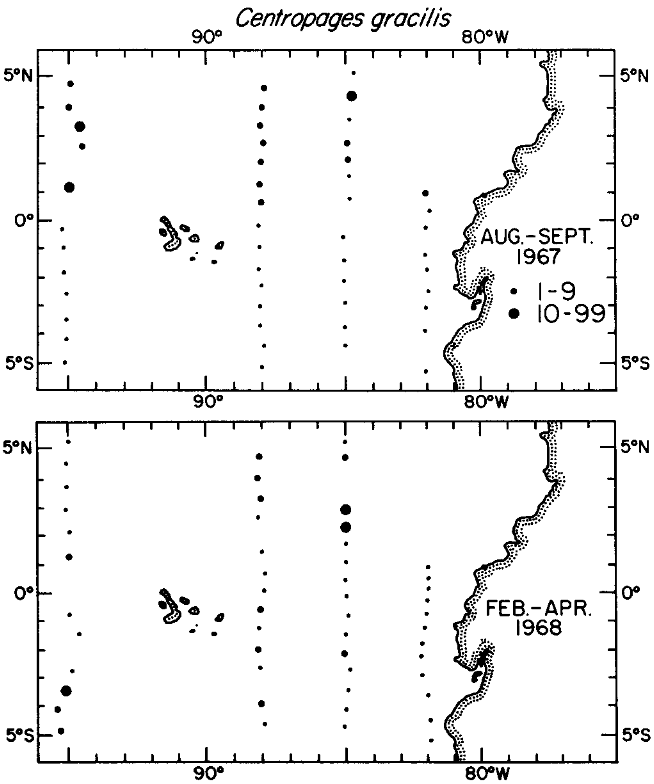

Figure 22. Distribution of abundance of adult females of *Centropages gracilis* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

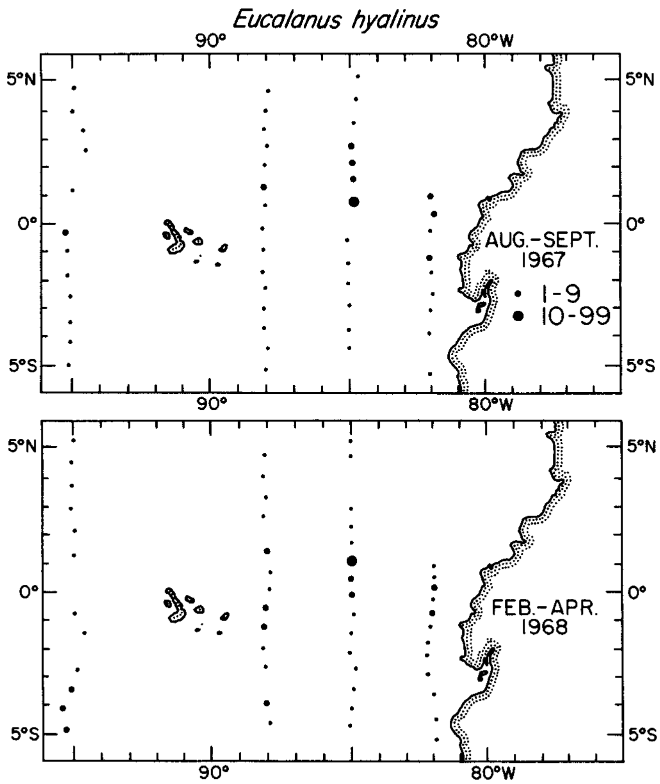

Figure 23. Distribution of abundance of adult females of *Eucalanus hyalinus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

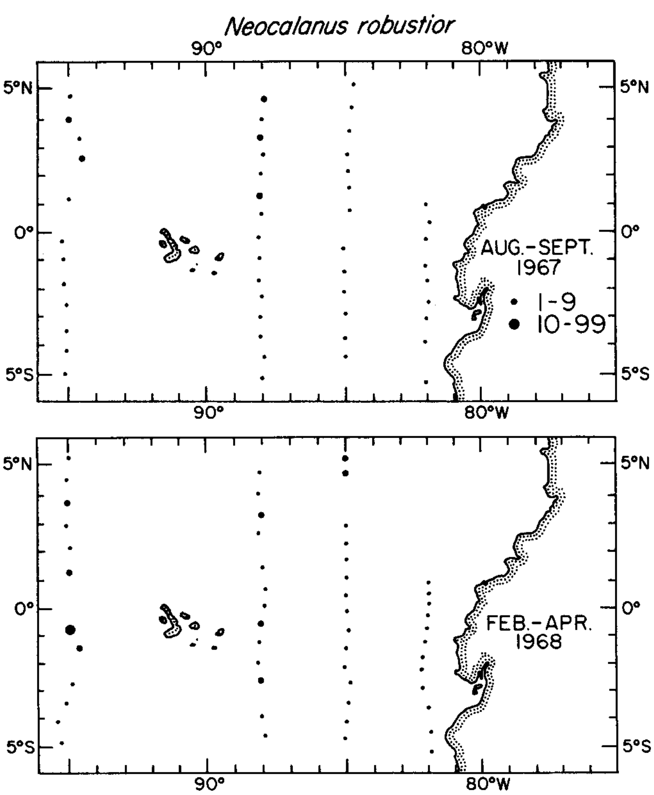

Figure 24. Distribution of abundance of adult females of *Neocalanus robustior* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

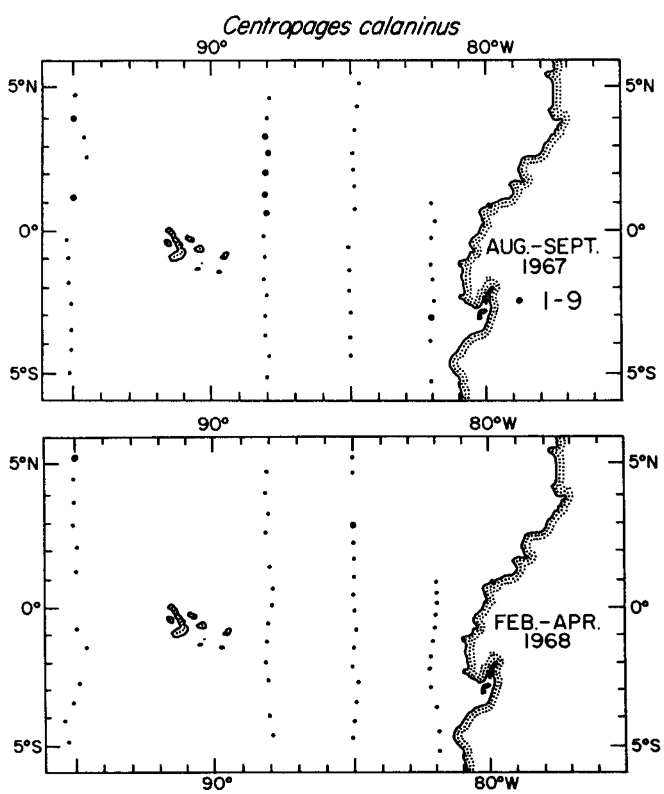

Figure 25. Distribution of abundance of adult females of *Centropages calaninus* in the Eastern Equatorial Pacific during August-September 1967 and February-April 1968. Dots represent numbers of individuals per 100 m^3.

TABLE 3
Mean Abundance (Org./100m³) in Night and Day Samples

	Night	Day
Calanus chilensis	270	111
Calanus chilensis (stage V)	639	853
Cosmocalanus spp.	248	176
Centropages calaninus	1	1
Centropages furcatus	120	104
Centropages gracilis	1	3
Eucalanus hyalinus	1	1
Eucalanus inermis	25	10
Mesocalanus tenuicornis	39	37
Nannocalanus minor	511	319
Neocalanus gracilis	4	4
Neocalanus robustior	1	1
Pareucalanus attenuatus	9	6
Pareucalanus sewelli	70	58
Rhincalanus nasutus	289	144
Rhincalanus rostrifrons	13	11
Subeucalanus pileatus	38	20
Subeucalanus subcrassus	80	49
Subeucalanus subtenuis	360	306
Temora discaudata	126	147
Undinula vulgaris	17	14

Day-Night Observations

Stations were divided according to day (0600-1759 h) and night (1800-0559 h) time of sampling, yielding 49 and 52 stations, respectively. Table 3 shows the mean abundance of each species in day and night samples. As expected, there were more organisms caught during the night. The overall difference of the total number of organisms between day and night was 19%. The day-night variability is less than station-to-station variability, and the diurnal variation of organisms shows no effect on the spatial coherence of the areas grouped in the analysis described below.

Differences between Cruises

Although some differences both in abundance and frequency are observable within the cruises, the numerical relationships among the species are very similar for both; that is, species correlated in 1967 were also correlated in 1968. Pearson's correlation coefficients were obtained, and the positive correlations between species with a significance of .01 or .001 are shown in Figure 26. There was almost total consistency of correlations within cruises. Of the 46 and 48 significant positive correlations in 1967 and 1968, all but 6 occurred during both years.

Dendrograms of Ward's Cluster Analysis

The sum of Euclidean distances (SED) provides information on differences between samples of relative rather than absolute abundance of species. The dendrograms of SED between stations grouped the stations in three major clusters (Figures 27 and 28). The stations grouped by the clusters have been plotted in the maps in order to determine the areas formed for each of the clusters. The three areas defined for each cruise are referred to as areas A, B, and C (Figure 29). The clusters were formed by the same species in both cruises, bearing out the correlations between species for the two cruises.

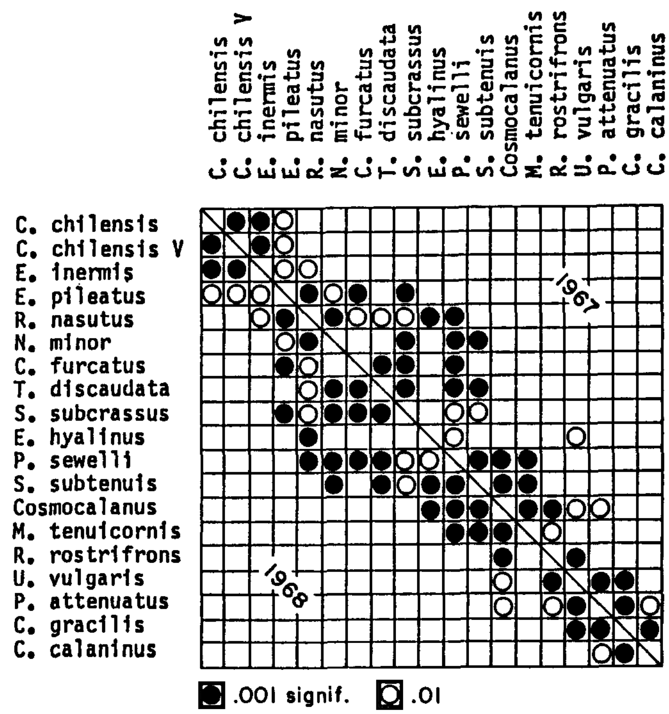

Figure 26. Significant positive Pearson's correlation coefficients between species in 1967 and 1968.

Area A is restricted to the southeast of the sampled area in both cruises; in 1967 this area extends farther westward than in 1968.

Area B in 1967 is almost parallel to area A, extending up to the equator. In 1968 area B is somewhat U-shaped, with the base facing the coast and the branches extending westward north and south of the equator; the northern branch extends farther westward. The northwest patch of area B is characterized by the species *Subeucalanus pileatus* and *Rhincalanus nasutus*, which share the highest abundance in both portions of area B.

Area C in 1967 occupies the northern region, limited zonally at the south by area B. In 1968, area C is found at the north, west, and southwest, surrounding most of area B, and meeting area A in the southeast.

Dendrograms of SED and Areas Formed by Deleting Neritic Species

To test the possibility that species of neritic origin may obscure the groups given by Ward's cluster

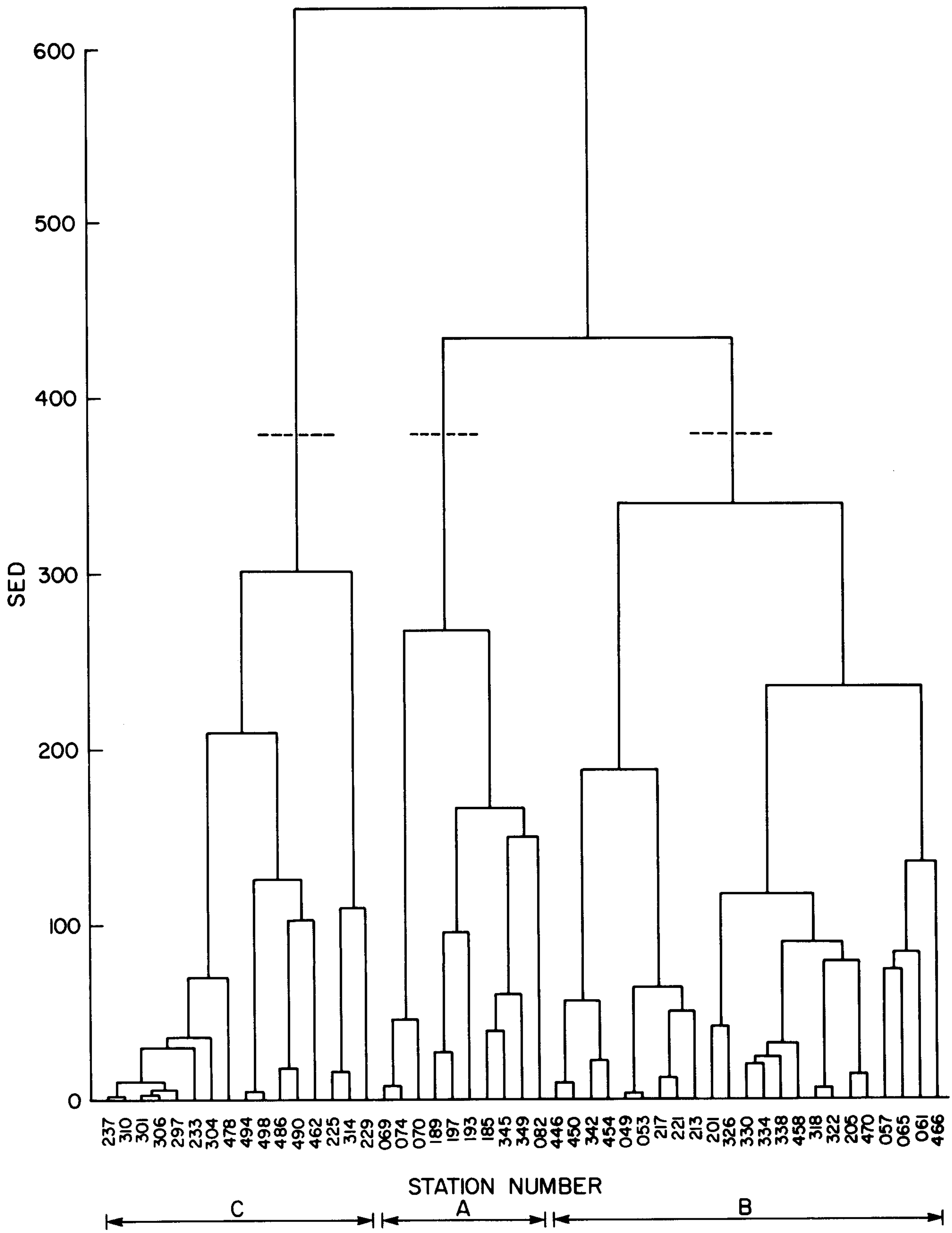

Figure 27. Dendrogram of the sum of Euclidean distances of 21 species for the stations in 1967.

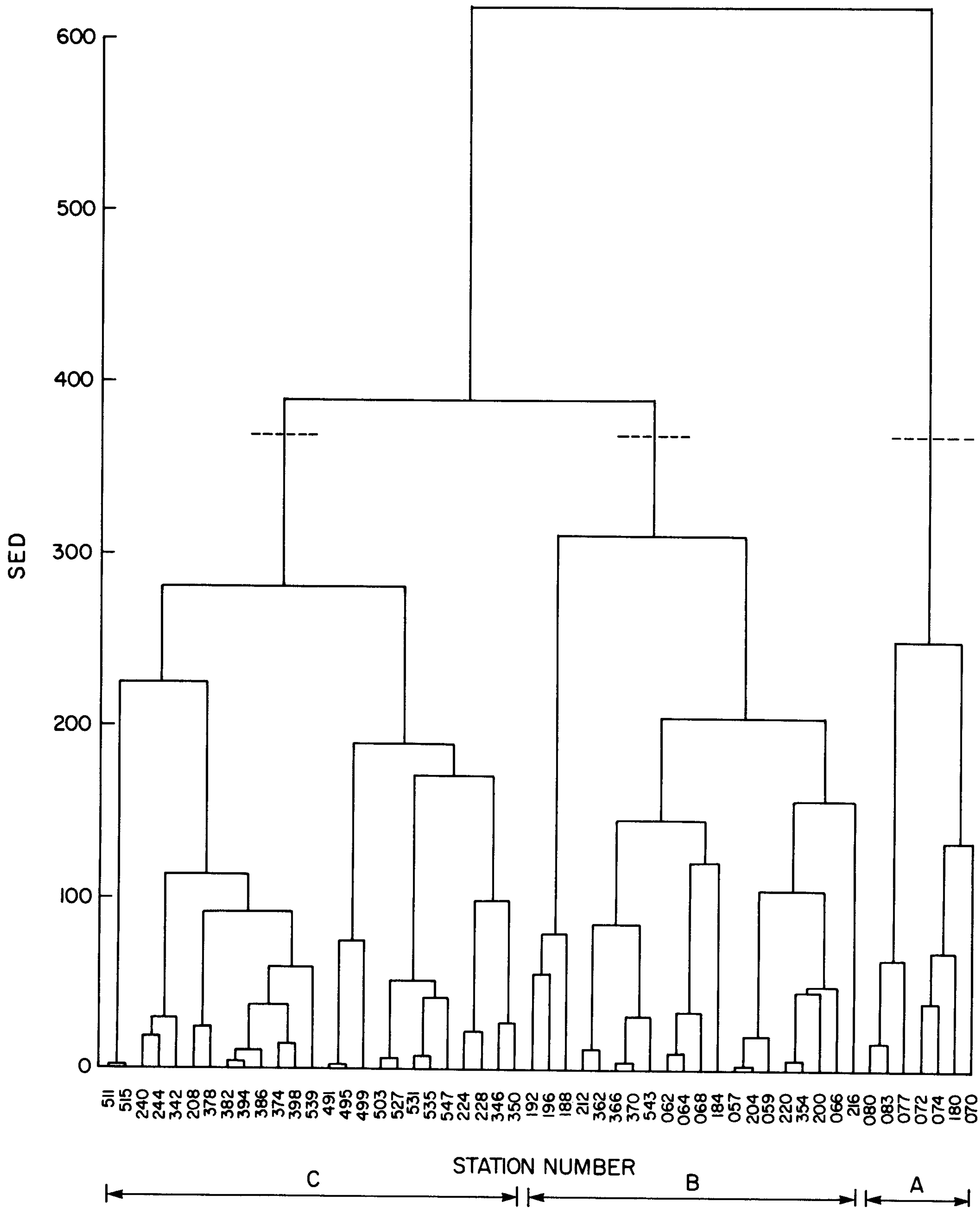

Figure 28. Dendrogram of the sum of Euclidean distances of 21 species for the stations in 1968.

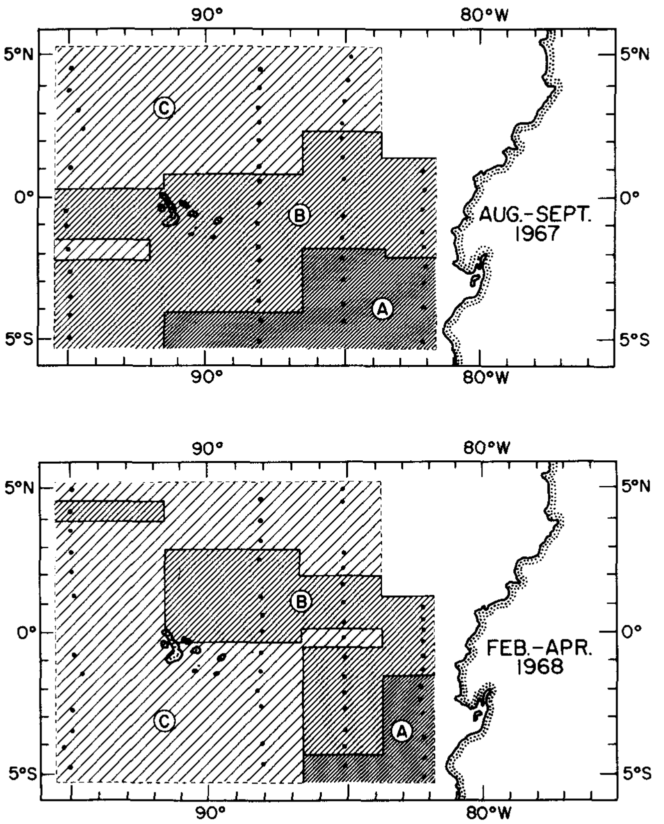

Figure 29. Areas of association defined by Ward's cluster analysis with 21 species in the Eastern Equatorial Pacific.

analysis, we reran the analysis excluding the neritic species, namely, *Undinula vulgaris, Subeucalanus pileatus, S. subcrassus, Temora discaudata,* and *Centropages furcatus* (Fleminger 1975, Fleminger and Hulsemann 1973). These neritic species succeed offshore, probably because of the large quantities of food in the upper mixed layer produced by the equatorial divergence system (see Discussion, below). The new areas formed by the clusters are substantively the same as those obtained with the full list of 21 species.

Abundance and Frequency by Cluster Area

This analysis includes all the species studied. Tables 4 and 5 show the mean abundance of each species and their occurrences in each of the areas (A, B, and C) for 1967 and 1968. Both abundance and frequency of some species characterize the areas, as discussed below.

Temperature and Salinity by Cluster Area

The mean values of temperature and salinity in the integrated 0-50-m water column for each of the areas is given in Table 6. This table shows the values to be consistently different for each area in both cruises. The lowest value of temperature and the highest of salinity are found in area A. The values are intermediate in area B. In area C, the temperature is the highest and the salinity is lowest.

TABLE 4
Distribution of the Mean Abundance (Org./100m^3) and Occurrence (in Parentheses) of Species in Groups Formed by the Ward Cluster Analysis, August-September 1967

	Area					
	A		B		C	
Number of stations per group		10		24		15
Calanus chilensis	1,164	(10)	1	(1)	0	(0)
Calanus chilensis (stage V)	747	(9)	0	(0)	0	(0)
Eucalanus inermis	27	(9)	6	(8)	0	(0)
Subeucalanus pileatus	74	(10)	44	(20)	2	(9)
Rhincalanus nasutus	246	(10)	514	(23)	1	(2)
Pareucalanus sewelli	108	(10)	73	(22)	18	(15)
Subeucalanus subtenuis	446	(10)	557	(24)	119	(15)
Cosmocalanus spp.	75	(10)	309	(20)	179	(15)
Temora discaudata	43	(9)	122	(24)	49	(13)
Nannocalanus minor	311	(10)	363	(24)	72	(15)
Subeucalanus subcrassus	17	(3)	64	(22)	38	(13)
Centropages furcatus	43	(9)	26	(24)	60	(14)
Mesocalanus tenuicornis	23	(8)	48	(22)	32	(15)
Rhincalanus rostrifrons	7	(4)	15	(14)	14	(13)
Undinula vulgaris	2	(3)	9	(9)	31	(15)
Neocalanus gracilis	3	(2)	3	(12)	2	(9)
Pareucalanus attenuatus	0	(0)	11	(5)	17	(13)
Eucalanus hyalinus	0	(0)	2	(6)	1	(2)
Centropages gracilis	0	(0)	1	(3)	2	(13)
Centropages calaninus	1	(1)	1	(1)	1	(6)
Neocalanus robustior	0	(0)	0	(0)	1	(5)

The species are ordered numerically by areas.

TABLE 5
Distribution of the Mean Abundance (Org./100m^3) and Occurrence (in Parentheses) of Species in Groups Formed by the Ward Cluster Analysis, February-April 1968

	Area					
	A		B		C	
Number of stations per group		7		20		25
Calanus chilensis	1,425	(6)	10	(1)	0	(0)
Calanus chilensis (stage V)	12,047	(7)	364	(4)	0	(0)
Eucalanus inermis	210	(6)	10	(13)	12	(5)
Subeucalanus pileatus	14	(7)	41	(17)	5	(13)
Rhincalanus nasutus	66	(7)	234	(20)	47	(14)
Pareucalanus sewelli	4	(4)	104	(20)	41	(25)
Subeucalanus subtenuis	8	(6)	363	(20)	236	(25)
Cosmocalanus spp.	9	(3)	187	(17)	253	(25)
Temora discaudata	12	(5)	343	(19)	76	(21)
Nannocalanus minor	301	(7)	780	(20)	403	(25)
Subeucalanus subcrassus	8	(6)	211	(20)	43	(21)
Centropages furcatus	58	(6)	353	(20)	52	(23)
Mesocalanus tenuicornis	2	(2)	43	(20)	41	(25)
Rhincalanus rostrifrons	1	(1)	10	(12)	15	(11)
Undinula vulgaris	0	(0)	15	(9)	20	(21)
Neocalanus gracilis	0	(0)	4	(4)	7	(9)
Pareucalanus attenuatus	1	(1)	4	(7)	7	(8)
Eucalanus hyalinus	0	(0)	2	(5)	2	(7)
Centropages gracilis	0	(0)	1	(1)	4	(13)
Centropages calaninus	0	(0)	0	(0)	1	(2)
Neocalanus robustior	0	(0)	0	(0)	2	(9)

The species are ordered numerically by areas.

Characteristics of the Cluster Areas

Area A is a region strongly influenced by waters from the Peru Current and is characterized by low mean temperature and high salinity. The species positively correlated in abundance (r = .001) are *Calanus chilensis* and *Eucalanus inermis*. *C. chilensis* (adults and stage V copepodites) is very important numerically, reaching up to 18,000 org./100m^3. The northern limit of distribution is south of the equator in both seasons (Figures 5 and 6). This species has been previously reported from the coast of Chile and Peru (Brodsky 1959; Herman and Mitchell 1981; Gómez 1982). Arcos (1978) reported the presence of *C. chilensis* (as *Calanus* sp.) in the Gulf of Guayaquil, associated with a tongue of cold and saline water from the Peru Current. This study confirms that the northern limit of the species is related to the northernmost influence of the Peru Current south of the equator. *E. inermis* (Figure 14) was more frequent and had more than 80% of its individuals in Area A in both cruises.

Species significantly correlated in area B (r = .001) were *Rhincalanus nasutus*, *Subeucalanus subtenuis*, *Temora discaudata*, *Nannocalanus minor*, and *Mesocalanus tenuicornis*. *R. nasutus* (Figure 9) has its maximum mean abundance in this area (Table 4); it was present in all but one station in 1968. The distribution of this species partially explains the shape of area B in both seasons.

Area C shows the largest amount of geographical variability between cruises. The species correlated by abundance and occurrence in this area are *Undinula vulgaris*, *Pareucalanus attenuatus*, *Centropages gracilis*, and *Neocalanus robustior*.

TABLE 6
Mean Temperature and Salinity of the Integrated 0-50 m in Groups Formed by the Ward Cluster Analysis, 1967 and 1968

	Area	Temperature	Salinity
1967	A	17.68	35.01
	B	19.33	34.64
	C	22.96	34.02
1968	A	17.43	34.80
	B	19.30	34.55
	C	22.17	34.25

DISCUSSION

The results demonstrate that groups of species were indeed related to the hydrography of the system. Ward's cluster analysis provided evidence that stations grouped by similarities in species and abundances encompassed coherent geographical areas affected by different circulation systems. Relative mean abundance and frequency analysis showed consistent patterns in the areas formed by the cluster analysis for both cruises, as seen in Tables 4 and 5. Pearson's correlation coefficients indicated highly significant positive correlations between pairs of species. With the positive correlations arranged along the diagonal axis in Figure 26, the species became ordered in such a manner that there is a trend from cool-water to warm-water species.

The numerically important filter-feeding calanoid copepod species in the Eastern Equatorial Pacific, as seen in Table 1, are *Nannocalanus minor* (Figure 7), *Subeucalanus subtenuis* (Figure 8), and *Cosmocalanus* spp. (Figure 10). The species best defining the limits of biologically different water masses of the region are *Calanus chilensis* (Figure 5 and 6), *Rhincalanus nasutus* (Figure 9), and *Neocalanus robustior* (Figure 24); these are likely indicator species for areas affected by different water masses of the EEP. *C. chilensis* indicates the northernmost influence of the Peru Current in area A; *R. nasutus* is most abundant in the transition zone (area B) and is apparently supported by equatorial upwelling; and *N. robustior*, although extremely low in abundance, appears to be an indicator of equatorial warm waters.

Area A is related to the Peru Current with hydrographic characteristics of low temperature and high salinity. The area is identified by the numerically dominating occurrence of *C. chilenis* (Figures 5 and 6) and *Eucalanus inermis* (Figure 14). The seasonal variation in shape and size of this area can be explained by the strength of the Peru Current's flow, shown by the altered extent of the low surface temperatures off the Gulf of Guayaquil (Figure 2). The presence of this area has been shown to be associated with several species of euphausiids (Antezana and Cornejo de Gonzáles 1979) and with high values of zooplankton biomass (Cajas 1982). Fleminger (1975) indicates a sharp break in the distribution of neritic calanoids at the south of the Gulf of Guayaquil.

Area C is related to warm tropical waters. It shows high geographical variation between cruises, probably in response to a breakdown of the circulation during February-April 1968. In 1967, the species grouping representing this area appears to originate from and be maintained by the North Equatorial Countercurrent as it contributes to the South Equatorial Current moving to the west. Weakening of the westward flow, and dominance of equatorial waters flowing to the east along the equator (Tsuchiya 1970; Lukas 1981) allowed warm waters found only in the north in 1967 to be present west and south in the sampled area in 1968.

The populations of neritic species *Temora discaudata* (Figure 11), *Centropages furcatus* (Figure 12), and *Undinula vulgaris* (Figure 18)—in the judgment of Jones (1962) and Fleminger and Hulsemann (1973)—are probably supported offshore by high standing stocks of phytoplankton and by the shallow mixed layer found in the area during the two periods of this study (Blackburn et al. 1970). An example of offshore maintenance of a neritic fine-particle feeding copepod population related to food supply is given by Checkley (1980a,b). He studied *Paracalanus parvus* in the California Current system and found that its offshore distribution and breeding was associated with high concentrations of chlorophyll *a*. Neritic copepods extending into the EEP in general originate from the coasts of Panama, Ecuador, and Colombia. The consistent presence of these species north of the equator and towards the continent in both years could be associated with the flow to the west. In February-April 1968, intermediate to high numbers of individuals of the same neritic species were found in the southwestern stations (Figures 11, 12, and 18). High numbers of individuals of the neritic copepod *Canthocalanus pauper* were also found in those stations but not in surrounding waters. This suggests that the populations of neritic copepods offshore southwest of the Galápagos in 1968 were independent of those north of the equator and that the southern populations may originate far west of the Galápagos (e.g., the Marquesas Islands) and be transported by an eastward surface flow. Eldin (1983) has called attention to the South Equatorial Countercurrent located between latitudes 7° and 14°S moving at <10 cm/sec and passing through the Marquesas Islands. Jones (1962) showed the presence of *U. vulgaris* 180 km downstream of the Marquesas Islands. He related its presence to enhanced productivity associated with the wake of the islands. There is also evidence of a weak eastward flow along about 10°S from 112°W to 90°W in February-March 1967 and February-April 1968, as discussed by Tsuchiya (1974). This flow is too far south to account for the occurrence of *U. vulgaris* east of the Marquesas.

Area B, having intermediate values of temperature and salinity, is transitional between the two previously discussed groupings. It also is an area of biotic transition between species supported by the Peru Current and those of the central and equatorial waters to the east; an increase in the EC in 1968 is suggested by the westward reduction in the distribution of *R. nasutus* in 1968 (Figure 9). The populations maintained in this region, including neritic species, could be supported by high phytoplankton productivity resulting from equatorial upwelling. Vingradov and Voronina (1963) observed maximum concentrations of zooplankton along the equator in the Central Pacific associated with upwelling events. From the Eastropac atlases one can observe that in both seasons covered by this study the higher values of zooplankton standing stocks are related to areas A and B where the main upwellings occur. This agrees with Fleminger's (in press) findings in the Indo-Australian region. He describes *R. nasutus* as an upwelling species related to low surface temperatures and high displacement volumes of zooplankton biomass.

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LITERATURE CITED

Ahlstrom, E.H. 1972. Kinds and abundance of fish larvae in the Eastern Tropical Pacific on the second multivessel Eastropac survey, and observations on the annual cycle of larval abundance. Fish. Bul. 70(4):1153-1242.

Anderberg, M.R. 1973. Cluster analysis for applications. Academic Press, New York, 359 p.

Antezana, T., and M. Cornejo de Gonzáles. 1979. Distribución de los eufáusidos epipelágicos del Ecuador y su validez como indicadores de masas de Agua (Crustácea: Zooplancton). Publ. INOCAR (C.M.) 3(1): 1-30.

Arcos, F. 1978. Distribución de la biomasa plantónica y copépodos en la parte interior del Golfo de Guayaquil. Rev. Com. Perm. Pacífico Sur 9:41-50.

Austin, T.S. 1960. Oceanography of the east central equatorial Pacific as observed during expedition Eastropic. Fish. Bull. 60:257-284.

Bennett, E.B. 1963. An oceanographic atlas of the eastern equatorial Pacific Ocean, based on data from EASTROPIC Expedition, October-December 1955. Bull. Inter-Am. Trop. Tuna Comm. 8:31-165.

Bjornberg, T.K.S. 1986. The rejected nauplius: a commentary. *In* G. Schriever, H.K. Schminke, and C.-t. Shih (eds.), Proceedings of the Second International Conference on Copepoda, Ottawa, Canada, 13-17 August, 1984. Syllogens 58:232-236.

Blackburn, M., R.M. Laurs, R.W. Owen, and B. Zeitzschel. 1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the Eastern Tropical Pacific. Mar. Biol. 7(1):14-31.

Bowman, T.E. 1955. A new copepod of the genus *Calanus* from the northeastern Pacific with notes on *Calanus tenuicornis* Dana. Pac. Sci. 9(4):413-422.

Bradford, J.M. 1974. *Euchaeta marina* (Prestandrea) (Copepoda, Calanoida) and two closely related new species from the Pacific. Pac. Sci 28(2):159-162.

Brinton, E., A. Fleminger, and D. Siegel-Causey. The temperate and tropical planktonic biotas of the Gulf of California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:(this volume).

Brodsky, K.A. 1959. Concerning phylogenetic relationships of several species of *Calanus* (Copepoda) of the northern and southern hemispheres. Zool. Zhurn. T. 38(10):1537-1553. (In Russian)

Cajas, L.C. de. 1982. Estudios del zooplankton marino en aguas ecuatorianas, Eastropac 1, 2 y 3. Revista de Ciencias del Mar y Limnología, INP 1(2):147-163.

Checkley, D.M. 1980a. The egg production of a marine planktonic copepod in relation to its food supply: laboratory studies. Limnol. Oceanogr. 25(3):430-446.

———. 1980b. Food limitation of egg production by a marine, planktonic copepod in the sea off southern California. Limnol. Oceanogr. 25(6):991-998.

Cromwell, T., R.B. Montgomery, and E.D. Stroup. 1954. Equatorial Undercurrent in Pacific Ocean revealed by new methods. Science 119:648-649.

Donguy, J.-R. and H. Rotschi. 1970. Sur un courant Est dans le Pacifique central tropical Sud. C.R. Acad. Sci. Paris B 271:869-872.

Eldin, G. 1983. Eastward flows of the South Equatorial Central Pacific. J. Phys. Oceanogr. 13(8):1461-1467.

Fleminger, A. 1967. Taxonomy, distribution and polymorphism in the *Labidocera jollae* group with remarks on evolution within the group (Copepoda; Calanoida). Proc. U.S. Nat. Mus. 120(3567):1-61.

———. 1973. Pattern, number, variability and taxonomic significance of integumental organs (sensilla and glandular pores) in the genus *Eucalanus* (Copepoda, Calanoida). Fish. Bull. 71(4):965-1010.

———. 1975. Geographical distribution and morphological divergence in American coastal-zone planktonic copepods of the genus *Labidocera*. *In* Estuarine research, Vol. 1. Academic Press, New York, p. 392-419.

———. In press. The Pleistocene equatorial barrier between the Indian and Pacific oceans and a likely cause for Wallace's Line. Proceedings of the International Conference on Pelagic Biogeography, May-June, 1985. UNESCO Press, Amsterdam, Netherlands.

Fleminger, A., and K. Hulsemann. 1973. Relationship of Indian Ocean epiplanktonic calanoids to the world oceans. *In* B. Zeitzschel (ed.), Ecological studies: analysis and synthesis, 3. Springer-Verlag, Berlin, p. 339-347.

Frost, B., and A. Fleminger. 1968. A revision of the genus *Clausocalanus* (Copepoda:Calanoida) with remarks on distributional patterns in diagnostic characters. Bull. Scripps Inst. Oceangr. 12:1-235.

Geletin, Yu. V. 1976. The ontogenetic abdomen formation in copepods of genera *Eucalanus* and *Rhincalanus* (Calanoida, Eucalanidae) and new system of these copepods. Issled Fauna Morye 17(26):75-93. [In Russian]

Giesbrecht, W. 1985. Reports on the dredging operations off the west coast of Central America to the Galápagos, to the west coast of Mexico and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S.F.C. steamer Albatross, during 1891. XVI. Die Pelagischen Copepoden. Bull. Mus. Comp. Zool. Harv. 25(12):243-263.

Gómez, O. 1982. Los copépodos planctónicos del mar peruano. Boletín de Lima, No. 23:1-17.

Grice, G. 1961. Calanoid copepods from equatorial waters of the Pacific Ocean Fish. Bull. 61:171-246.

———. 1964. Two new species of calanoid copepods from the Galápagos Islands with remarks on the identity of three other species. Contr. WHOI 1332:255-264.

Gueredrat, J.A. 1971. Evolution d'une population de copépodes dans le système des courants equatoriaux de l'Ocean Pacific. Zoogéographie, ecologie et diversité specifique. Mar. Biol. 9(4):300-314.

Heinrich, A.K. 1960. Horizontal distribution of copepods in the central part of the Pacific Ocean and their determining factors. Acad. Nauk. SSSR, Trudy Inst. Okeanol. 41:31-41. [In Russian]

———. 1973. Horizontal distribution of copepods in Peru Current region. Oceanology 13(1): 94-103. [In Russian]

Herman, A.W. and M.R. Mitchell. 1981. Counting and identifying copepod species with an in situ electronic zooplankton counter. Deep-Sea Res. 28(7):739-755.

Johnson, M. W. 1964. On a new species of *Pseudodiaptomus* from the west coast of Mexico, Costa Rica and Ecuador (Copepoda). Crustaceana 7(1):33-40.

Jones, E.C. 1962. Evidence of an island effect upon the standing crop of zooplankton near the Marquesas Islands, Central Pacific. J. du Conseil 27(3):223-231.

Jones, J.H. 1969. Surfacing of Pacific Equatorial Undercurrent: direct observation. Science 163:1449-1450.

Knauss, J.A. 1960. Measurements of the Cromwell Current. Deep-Sea Res. 6:265-286.

———. 1966. Further measurements and observations on the Cromwell Current. J. Mar. Res. 24:206-239.

Lang, B.T. 1964. Taxonomic review and geographical survey of the genera *Eucalanus* and *Rhincalanus* in the Pacific Ocean. Ph.D. dissertation, University of California, San Diego, 248 p.

Leetmaa, A. 1982. Observations of near-equatorial flows in the eastern Pacific. J. Mar. Res. 40(Suppl):357-370.

Leetmaa, A., J.P. McCreary, and D.W. Moore. 1981. *In* B.A. Warren and C. Wunsch (eds.), Evolution of physical oceanography. Equatorial currents: observations and theory. M.I.T. Press, Cambridge, Mass., p. 184-196.

Love, C.M. (ed.). 1972a. Physical oceanographic and meteorological data from principal participating ships, second survey cruise, August-September 1967. Eastropac atlas, vol. 5.

———. 1972b. Biological and nutrient chemistry data from principal ships, second survey cruise, August-September 1967. Eastropac atlas, vol. 6.

———. 1975. Physical oceanographic and meteorological data from principal participating ships, third survey cruise, February-March 1968. Eastropac atlas, vol. 9.

Love, C.M., and R.M. Allen (eds.). 1975. Biological and nutrient chemistry data from principal participating ships, third survey cruise, February-March, 1968. Eastropac atlas, vol. 10.

Lukas, R. 1981. The termination of the Equatorial Undercurrent in the Eastern Pacific. Ph.D. dissertation, University of Hawaii, 127 p.

Manrique, F.A. 1977. Seasonal variation of zooplankton in the Gulf of California. *In* Proc. Symp. on Warm Water Zooplankton, Dona Paula, Goa, India, 14-19 Oct. 1976. UNESCO/NIO Spec. Publ., p. 242-249.

McEwen, G.F., M.W. Johnson, and T.R. Folsom. 1954. A statistical analysis of the performance of the Folsom plankton sample splitter, based upon test observations. Arch. Meteor. Geoph. Bioklimat. Ser. A, 7:502-527.

Moreano, H.R. 1983. Interacción océano-atmósfera sobre la zona costera del Ecuador. Acta Oceanográfica del Pacifico. INOCAR 2(1):1-11.

Mullin, M.M., and P.M. Evans. 1976. Distribution, morphometry, and seasonal biology of the planktonic copepods *Neocalanus robustior* and *Neocalanus gracilis* in the Pacific Ocean. Pacific Science 30(2):33-40.

Okuda, T.R. Trejos de Suescum, M. Valencia, and A. Rodriguez. 1983. Variación estacional de la posición del Frente Equatorial y su efecto sobre la fertilidad de las aguas superficiales ecuatorianas. Acta Oceanográfica del Pacífico 2(1):53-84.

Robinson, M.K. 1976. Atlas of North Pacific Ocean monthly mean temperatures and mean salinities of the surface layer. Naval Oceanographic Office, N00 RP-2, 19 p. + 137 figs.

Sokal, R., and F.J. Rohlf. 1981. Biometry. Second edition. W.H. Freedman and Company, San Francisco, 859 p.

Stroup, E.D. 1969. The thermostad of the 13°C water in the Equatorial Pacific Ocean. Ph.D. dissertation, Johns Hopkins University, Baltimore, 202 p.

Sund, P.N., M. Blackburn, and F. Williams. 1981. Tunas and their environment in the Pacific Ocean: a review. Oceanogr. Mar. Biol. Ann. Rev. 19:443-512.

Sverdrup, H.U., M.W. Johnson, and R.H. Fleming. 1942. The oceans: their physics, chemistry and general biology. Prentice-Hall, New York, 1087 p.

Timonin, A.G., and N.M. Voronina. 1977. Net plankton distribution along the equator in the Eastern Pacific Ocean. Pol. Arch. Hydrobiol. 24 Suppl.:281-305. [In Russian]

Tsuchiya, M. 1968. Upper waters of the intertropical Pacific Ocean. Johns Hopkins Oceanogr. Stud. 4. 50 p.

———. 1970. Equatorial circulation in the South Pacific. *In* W.S. Wooster (ed.), Scientific exploration of the South Pacific. Natl. Acad. Sci., Wash., D.C., p 69-74.

———. 1972. A subsurface north equatorial countercurrent in the eastern Pacific Ocean. J. Geophys. Res. 77: 5981-5986.

———. 1974. Variation of the surface geostrophic flow in the eastern intertropical Pacific Oean. Fish. Bull. 72(4):1075-1086.

———. 1975. Subsurface countercurrents in the eastern equatorial Pacific Ocean. J. Mar. Res. Suppl. 33:145-175.

———. 1985. The subthermocline phosphate distribution and circulation in the far eastern equatorial Pacific Ocean. Deep-Sea Res. 32(3):299-313.

Vinogradov, M.E., and N.M. Voronina. 1963. Distribution of plankton in the waters of the equatorial currents in the Pacific Ocean. I. The distribution of the plankton biomass and the horizontal distribution of some species. Transactions of the Institute of Oceanology 71:22-58. [In Russian]

Wilson, C.B. 1942. Copepods of the plankton gathered during the last cruise of the Carnegie. Carnegie Institute, Washington, Pub. 536, 237 p.

———. 1950. Copepods gathered by the U.S. Fisheries steamer Albatross from 1887 to 1909, chiefly in the Pacific Ocean. Contr. to the Biology of the Philippine Archipelago and adjacent regions. Bull. U.S. Nat. Mus. 100:141-441.

Wooster, W.S. 1969. Equatorial front between Peru and Galápagos. Deep-Sea Res. 16 (Suppl.): 407-419.

Wooster, W.S., and T. Cromwell. 1958. An oceanographic description of the eastern tropical Pacific. Bull. Scripps Inst. Oceanogr. 7:169-282.

Wyrtki, K. 1964. The thermal structure of the eastern Pacific Ocean. Deut. Hydrogr. Zeit. Erlag. Reihe A, No. 6, 84 p.

———. 1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Ann. Rev. 4:33-68.

———. 1967. Circulation of water masses in the Eastern Equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1:117-147.

———. 1977. Advection of the Peru Current as observed by satellite. J. Geophys. Res. 82:3939-3943.

Wyrtki, K., E. Stroup, W. Patzert. R. Williams and W. Quinn. 1976. Predicting and observing El Niño. Science 191(4225):343-346.

Zambrano, E. 1980. Distribución de la temperatura superficial en el Pacífico ecuatorial oriental (1974–1976). Acta Oceanográfica del Pacífico 1(1): 1-9