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THE NERITIC ZOOPLANKTON OF THE NORTHWESTERN GULF OF MEXICO

Texas A&M University PH.D. 1980

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THE NERITIC ZOOPLANKTON OF THE NORTHWESTERN GULF OF MEXICO

A Dissertation

by

THOMAS JOSEPH MINELLO

Submitted to the Graduate College of
Texas A&M University
in partial fulfillment of the requirement for the degree of

DOCTOR OF PHILOSOPHY

May 1980

Major Subject: Biology

THE NERITIC ZOOPLANKTON OF THE NORTHWESTERN GULF OF MEXICO

A Dissertation

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THOMAS JOSEPH MINELLO

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May 1980

ABSTRACT

The Neritic Zooplankton of the Northwestern
Gulf of Mexico. (May 1980)

Thomas Joseph Minello, B.S., Cleveland State University
M.S., Texas A&M University
Co-Chairmen of Advisory Committee: Dr. E. Taisoo Park
Dr. M. H. Sweet

Copepod species and major groups of zooplankton were identified from 513 samples taken at 20 stations on 5 transects in the coastal waters of the northwestern Gulf of Mexico. Monthly samples, using oblique tows and a GULF V sampler (approximately 200 μm mesh size), were taken over a 3-year period from 1963 to 1965. The bottom depths of the sampling stations ranged from 8 to 73 m. Temporal and spatial distributional patterns were examined in detail for major groups of zooplankton and common species of calanoid and cyclopoid copepods. The relationships between the densities of these groups and various physical and chemical factors were also examined.

Total zooplankton densities averaged over the entire sampling area peaked in April and September. The highest mean densities occurred in April (2870 organisms/m^3) and the lowest densities occurred in February (1124/m^3). Mean zooplankton densities decreased from 3412 organisms/m^3 at the 8 m stations to 1131/m^3 at the 73 m stations. The greatest mean densities occurred in 1964.

The dominant groups of zooplankton, determined by their average densities in the sampling area, were the copepods (61% of total zooplankton), larvaceans (7.7%), bivalve larvae (5.5), ostracods *(Euconchoecia)* (4.7%), and gastropod larvae (3.6%). All groups had density peaks in the spring although peaks also occurred during other seasons. Densities of all groups except the ostracods appeared to decrease with the bottom depth of the station. In general, the densities of the major groups of zooplankton showed little relationship with surface temperature, surface salinity, or the other physical factors examined.

Since the copepods dominated the zooplankton at all depths and times of the year, these organisms were identified to species and examined in greater detail. Overall, adult females were present in similar densities as immature forms (copepodids). The percentage of adult males generally remained around 15 to 20% of the copepods. Calanoid and cyclopoid copepods were abundant and harpacticoids were relatively rare.

A total of 134 species of adult female calanoid and cyclopoid copepods were identified. The dominant species, ranked in the order of their abundance based on mean densities over the entire sampling area, were *Paracalanus indicus, Acartia tonsa, Paracalanus quasimodo, Paracalanus crassirostris, Clausocalanus furcatus, Oncaea media, Oithona nana, Oithona plumifera, Temora turbinata* and *Oncaea venusta.* These ten species made up over 77% of the adult female copepods. When the temporal and spatial distributions of the abundant species were examined, the effect of bottom depth and month were frequently significant. Changes in density often appeared to be significantly related to surface temperature and surface salinity. Other physical variables, including runoff, were rarely significant in regression models. The mean number of species of adult female copepods increased with the bottom depth of the station reaching a maximum of 51 at the 73 m stations in January.

A species by species correlation matrix for 25 abundant species was used as a basis for graphically determining species clusters in the sampling area. This analysis revealed a distinct offshore group with many marginally linked members, an intermediate depth group, and an inshore group. These species groups were similar to groups reported in other studies on copepods from the coastal waters off Texas and the southeastern United States.

Since interspecific competition might be important in determining the distributions of closely related species, the temporal and spatial distributional patterns of common congeneric copepods were examined. Most congeners appeared to be distinctly separated by their sizes, distribution with station bottom depth, or by their temporal distributions. Apparent exceptions were seen in two common congeneric herbivorous species (*Paracalanus indicus* and *P. quasimodo*) which appeared to be separated vertically in the water column and in two carnivorous genera of cyclopoids. The lack of separation in these cyclopoid genera may be related to their predatory feeding habit.

ACKNOWLEDGMENTS

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INTRODUCTION

Zooplanktonic organisms are generally present in great numbers in marine environments. These animals establish a major link between the primary producers and the carnivores in the world's oceans. Since coastal waters over the continental shelf are among the most productive marine habitats, supporting a large percentage of the fisheries of the world, the zooplankton populations in these waters are ecologically and commercially important.

Although competition, predation, and a limiting food supply are significant factors affecting populations of organisms in marine habitats, the physical variability of the environment undoubtedly plays an important role in controlling the distribution and abundance of organisms in neritic waters. The physical characteristics of most coastal waters, including those in the northwestern Gulf of Mexico, are highly variable. Rapidly changing temperatures and salinities along with periodic upwelling and flushing of estuarine waters are common occurrences. The zooplankton populations in these areas are subsequently characterized by large numerical fluctuations both in time and space.

Despite their ecological importance, the coastal zooplankton populations in the Gulf of Mexico have not been extensively studied. A primary objective of this research is to examine the temporal and spatial variability of the zooplankton in the neritic waters of the Gulf of Mexico off Texas and western Louisiana. Changes in density will

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also be examined with respect to physical parameters such as surface temperature, surface salinity, runoff, and upwelling.

Due to the relatively homogeneous size distribution of the phytoplankton and the simplicity and similarity of feeding appendages in the most abundant planktonic animals, the copepods, the role of food in niche differentiation would appear to be limited in the marine planktonic environment as compared to terrestrial systems. Relatively little refuge from competition can be found by selective herbivory if the amount of food available is a limiting factor controlling zooplankton densities. It is expected that competition for the same food would frequently be indicated by differences in temporal and spatial distributions between morphologically similar species. A number of groups of similar congeneric species of copepods occur in the coastal waters of the northwestern Gulf of Mexico and a special effort will be made to examine the ecological separation between the species in these genera.

Most of the work done in the Gulf of Mexico has provided only a limited amount of information on the neritic zooplankton populations. Many studies simply report data with little or no analysis while others cover only a small geographic area or are limited to a few taxonomic categories. Samples taken for several years over a wide geographic range are necessary in order to determine general patterns of abundance and distribution for zooplankton populations in neritic areas. Usually, the collection and analysis of the great number of samples needed for a study of this type are beyond the capabilities of a single researcher. The opportunity to examine such a series of samples however was provided by the National Marine Fisheries Service Laboratory in Galveston, Texas. As part of a major project to study the biology and dynamics of shrimp populations (Kutkuhn, 1963), monthly zooplankton samples were collected from 1963 to 1965 at stations throughout the coastal waters of the northern Gulf of Mexico. The samples were taken from a modified shrimping vessel, the GUS III, and temperature and salinity data were also recorded. Zooplankton data from 11 of these stations (located off South Texas) were analyzed by Park (1976a, 1978). Data from nine other stations off the coasts of Texas and Louisiana were subsequently analyzed and the entire data set (513 samples from 20 stations) was used to examine the zooplankton populations in this area.

The present study therefore includes data from approximately 3 years of monthly samples taken at 20 stations on transects radiating off the coasts of Texas and western Louisiana. Many groups of zooplankton have been examined and copepods, the dominant organisms, have been identified to species. Temporal and spatial trends have been analyzed and the relationships between zooplankton densities and selected physical and chemical parameters have been examined. Correlated species groups have been identified and the distributions of the common congeneric copepods have been compared.

Literature Review

The zooplankton literature on the Gulf of Mexico has often been referred to as depauperate. There have been a number of studies, however, conducted on nearshore and continental shelf zooplankton populations in which some aspect of seasonality has been examined. None of these have covered the entire Gulf of Mexico, although Arnold

(1958) reported on settling volumes of planktonic fish eggs and larvae from a large portion of the Gulf, including coastal areas, from samples taken on ten cruises between March, 1951 and July, 1953.

In the Eastern Gulf, King (1950) studied zooplankton displacement volumes and identified copepods and other groups from monthly samples taken in 1949 at five stations on a transect off South Florida. Pierce (1951) worked on the chaetognaths of the western coast of Florida from 1948 to 1950. Grice (1957, 1960a) examined the calanoid and cyclopoid copepods from nearshore waters along the western coast of Florida from 1948 to 1955. At one station immediately offshore of Naples, Florida, Dragovich (1961, 1963) reported on zooplankton and phytoplankton samples taken five times per week from March, 1956 to August, 1957. Kelly and Dragovich (1967) studied macrozooplankton taken in monthly tows from September, 1961 to August, 1962 in the Tampa Bay area and the surrounding coastal waters. Also working in this area, Austin and Jones (1974) measured displacement volumes of total zooplankton at one station off Tampa, Florida from monthly samples taken between June, 1969 and August, 1970. The seasonal abundance and distribution of pink shrimp larvae have also been fairly extensively studied on the Tortugas Shelf and in the coastal waters off Tampa between the years 1959 and 1964 (Eldred et al., 1965; Munro et al., 1968; Jones et al., 1970). At coastal stations located between Horn Island and Tampa, Florida, Caldwell and Maturo (1976) examined the zooplankton, including some copepods, over three seasons in 1975 and 1976.

Most of the work done along the north central coast of the Gulf of Mexico has been conducted in the estuaries. Gonzalez (1957) however recorded seasonal abundances for the copepods of the Mississippi Delta region in 1956. Gillespie (1971) examined the zooplankton from monthly samples taken at 28 stations during 1968 and 1969 in the estuarine and coastal waters off Louisiana.

Many of the seasonal studies done in the western Gulf have been associated with samples taken by the National Marine Fisheries Service Laboratory in Galveston, Texas. Temple and Fischer (1965) examined the vertical distribution of larval penaeid shrimp over a 6-month period in 1963 at one station approximately 80 km south of Galveston. Other studies employing these samples include work on chaetognaths (Adelmann, 1967) and copepods (Allison, 1967). Temple and Fischer (1967) also reported on an extensive examination of the seasonal and spatial distribution of *Penaeus* spp. larvae in the shelf waters off Texas and Louisiana in 1961. Harper (1968) studied the seasonal distribution of *Lucifer faxoni* off the Texas coast from monthly samples taken in 1962. A limited amount of seasonal work on zooplankton populations has also been conducted off Freeport, Texas in 1973 (SEADOCK, 1975).

Monthly data from 11 of the GUS III stations sampled off South Texas from 1963 to 1965 have been recorded by Park (1976a, 1978). Temple (1976) examined larval penaeids from these samples and from other monthly samples taken off Texas from 1962 to 1965. Seasonal data on ichthyoplankton from 12 stations sampled in 1974 and 1975 off South Texas have been recorded by Finucane (1976). Park (1976b, 1977, 1979) also analyzed seasonal and some monthly data from these 12 stations and reported on the copepods and other zooplankton from 1974 to 1977. These data were analyzed in more detail by Park and Turk (1980).

There are several other studies on copepods in the coastal areas of the Gulf of Mexico which did not include seasonal data but did provide useful information. Davis (1950) reported on the copepods off West Florida in 1947 and 1948, Fleminger (1956) examined the distributions of calanoids in the epiplanktonic waters throughout the Gulf, and Grice (1960b) recorded occurrences of five species of *Oithona* in the Gulf. Livingston (1974) examined recurrent groups of calanoids from the open ocean and coastal areas of the Gulf of Mexico.

The faunal assemblages within the zooplankton along the southeastern coast of the United States appear to be similar to those found in the Gulf of Mexico (Fleminger, 1956). Bowman (1971) examined the seasonal distributions of calanoid copepods in the coastal waters between Cape Hatteras and South Florida. In the more northern areas along the eastern coast, a large amount of seasonal data has been analyzed from the waters off of New York by Malone (1977). He also summarized other work done in this area.

Hydrography and Physiography of the Northwestern Gulf of Mexico

The continental shelf off Texas and Louisiana extends to approximately the 100 m depth contour. Its width ranges from about 75 km near Port Isabel, Texas to approximately 177 km near the mouth of the Sabine River on the border of Texas and Louisiana (Lynch, 1954; Uchupi, 1975). The waters over this shelf owe a great deal of their characteristics to the flow of the Mississippi River which turns westward and moves along the coast.

Hedgpeth (1953) noted that in the coastal waters off Texas and Louisiana surface salinities became higher and seasonal salinity ranges became narrower as the distance from the Mississippi River increased. He also reported that surface water temperatures were generally related to air temperatures and seasonal differences were similar over the area.

Temperature and salinity measurements taken with the samples used in this study were analyzed by Harrington (1966), Temple and Martin (1976), and Temple, Harrington, and Martin (1977). These studies also showed that surface water temperatures varied with air temperatures and seasonal changes decreased with station depth and with latitude. Subsurface water temperatures over the outer shelf reached their maximum levels in the fall and minimum levels in the spring. An analysis of vertical temperature profiles indicated that upwelling was occurring at offshore stations through much of the spring and summer and at times this upwelling extended to the nearshore stations (Temple and Martin, 1976). Surface salinities were found to increase with the distance from shore and again with the distance from the freshwater input off the Louisiana coast. Seasonally, surface salinities were closely related to this freshwater runoff from Louisiana rivers with a lag time of approximately 1 to 1½ months. River flows along the entire coast were relatively low in the fall and winter and increased dramatically in the spring. The mean outflow of Louisiana rivers was at least an order of magnitude greater than the mean riverflow of Texas.

Drift bottle studies were conducted over the entire shelf area from the Mississippi River to Port Isabel in order to measure surface currents in 1962 and 1963. The results of this work have been reported by Kimsey and Temple (1964) and Temple and Martin (1979). The surface current patterns were similar for the 2 years and can be divided into four different seasonal types.

1. September-February. Surface currents generally flowed down the coast, i.e., west off Louisiana and southwest off Texas. Velocities ranged from 4-19 km/hr.
2. March-May, Transitional Period. The flow off Louisiana was to the west in March but changed to the north and in toward the shore by May. An area of convergence was noted off the Texas coast where southwest currents met northwest currents. This area of convergence moved northward as the season progressed. In general, velocities decreased from March to May as currents moved more onshore.
3. June-July. Flow was reversed from the winter. Coastal surface currents flowed northward along the Texas coast and averaged around 7 km/day. Off Louisiana currents were to the north (ave. vel. 3 km/day) or east. Most of the eastward movement was restricted to the deeper waters over the shelf.
4. August, Transitional. Currents were onshore along the Texas coast with velocities slowing to 2-3 km/day.

Current patterns for the coastal waters off Texas from 1963 to 1965 were inferred by Armstrong (1976) from vertical temperature and salinity profiles and densities. His results were similar to those from the drift bottle study. Over the outer shelf flow was to the north and east (along the coast) from mid-March through September and to the west and south from October through February. In nearshore waters from Galveston, Texas to Port Aransas, Texas flow was typically to the southwest from October to June and northwest in July and August.

METHODS AND MATERIALS

All of the samples analyzed in this study were collected by the staff of the National Marine Fisheries Service Laboratory in Galveston, Texas. The location of all of the GUS III stations examined is shown in Figure 1 and the bottom depths for each station are indicated in Figure 2. I assisted in the analysis of samples from the stations on Transects I-III and these data have been reported by Park (1976a, 1978). The additional stations on Transects IV and V were subsequently analyzed and the data from all 20 GUS III stations were then used to examine the spatial and temporal distributions of organisms and the relationships between the densities of these organisms and the chemical and physical factors examined.

At each GUS III station, one sample was collected approximately once a month for 3 years from 1963 to 1965. Table 1 is a summary of the location and number of samples collected during each year. The samples were taken with a Gulf V net having a mouth diameter of 40.5 cm and a mesh size of approximately 200 μm (Arnold, 1958). Tows were of the step oblique type from just off the bottom to the surface. Tow durations were approximately 20 minutes and the amount of water filtered was estimated from a flowmeter positioned in the center of the net mouth.

Larval penaeids were removed by the staff of the National Marine Fisheries Service (NMFS) before the samples were received. In the laboratory the samples were split using a Folsom Plankton Splitter. The size of the aliquot examined varied to allow at least 1000 total

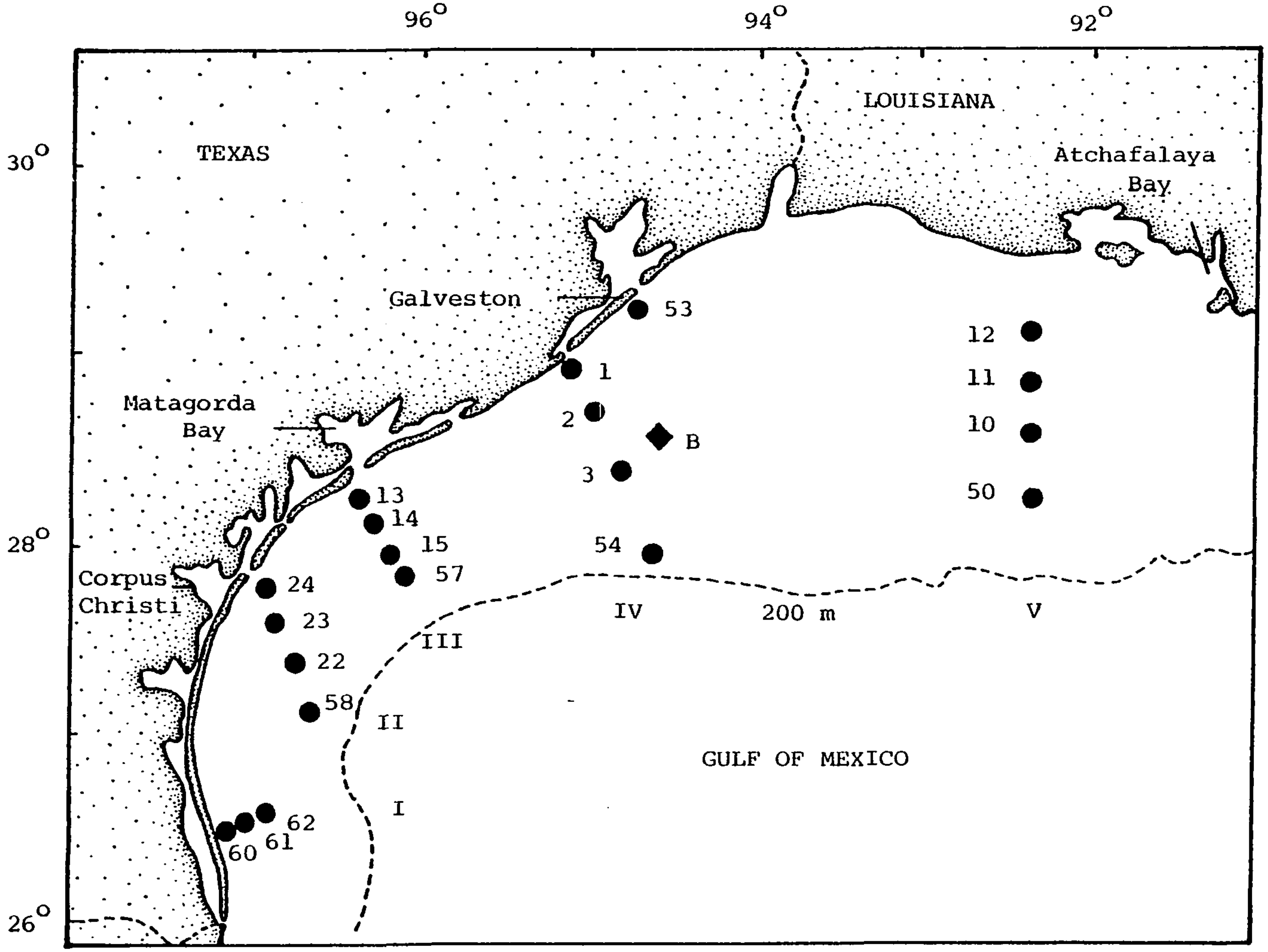


Figure 1. Location of GUS III stations used in this study. Transects are indicated by Roman numerals. Vertical distribution data were obtained from Station B.

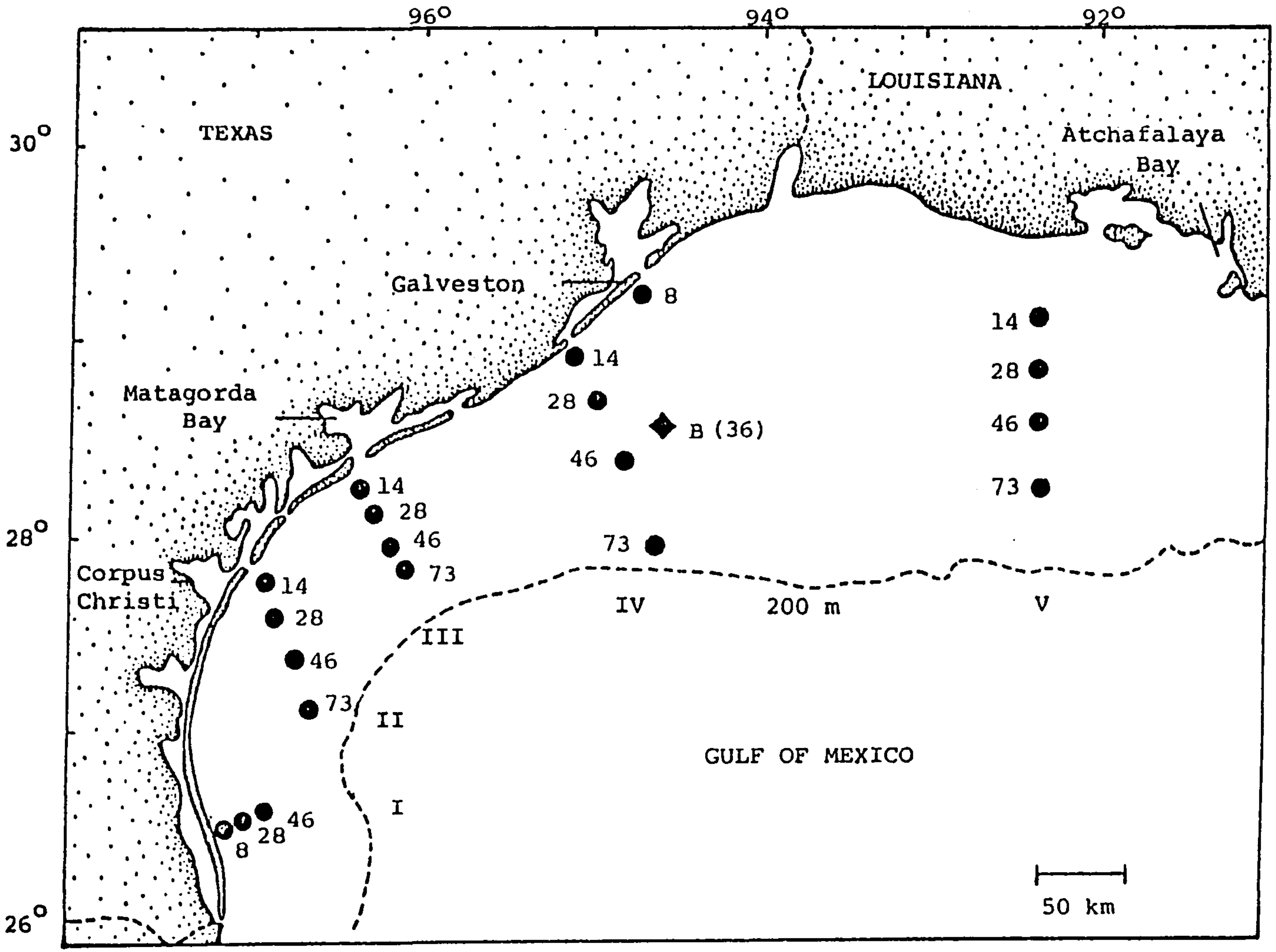


Figure 2. GUS III stations identified by bottom depth (m) and transect (Roman numerals).

Table 1. Summary of sampling information. The number of samples examined from different combinations of bottom depth, transect, and year are listed.

Bottom Depth	Transect	Station	1963	1964	1965	Sums	
8 m	I	60	9	12	8	29	53
	IV	53	9	10	5	24	
14 m	II	24	9	10	9	28	95
	III	13	9	10	7	26	
	IV	1	11	8	· ·	19	
	V	12	10	6	6	22	
28 m	I	61	8	11	8	27	128
	II	23	9	9	9	27	
	III	14	9	12	7	28	
	IV	2	10	12	· ·	22	
	V	11	11	7	6	24	
46 m	I	62	9	11	7	27	132
	II	22	10	12	7	29	
	III	15	10	12	9	31	
	IV	3	9	11	· ·	20	
	V	10	11	8	6	25	
73 m	II	58	11	12	8	31	105
	III	57	11	12	9	32	
	IV	54	9	11	· ·	20	
	V	50	9	7	6	22	
All	I		26	34	23		83
	II		39	43	33		115
	III		39	46	32		117
	IV		48	52	5		105
	V		41	28	24		93
							513

individuals to be counted per sample. The organisms present were then identified and grouped into various taxonomic categories. Since the copepods dominated the zooplankton, adult female copepods were identified to the species level. Abundances were calculated as average densities (#/m^3) in the water column using the flowmeter readings supplied by the NMFS.

The samples used to examine vertical distributions of *Paracalanus indicus* and *P. quasimodo* were taken at Station B (Fig. 1, p. 11) located approximately 80 km south of Galveston, Texas. These samples were also supplied by the National Marine Fisheries Service Laboratory in Galveston. Temple and Fischer (1965) originally used the samples to examine the vertical distribution of penaeid shrimp larvae. Subsequently, Adelman (1967) has examined the chaetognaths and Allison (1967) has identified many of the copepods. The sampling gear consisted of a modified Clarke-Bumpus sampler that carried two 330 µm mesh nets. Each net had a mouth area of 120.6 cm^2. Only the samples taken over a 2-day period in July of 1963 were used in this study. The collections were made every 4 hr at 2, 18, and 34 m (Temple and Fischer, 1965). In the laboratory, I removed four 5 ml subsamples from each sample with a Stempel pipette. The sample volume was adjusted in relation to the volume of water filtered in the tow so that the subsample volume (20 ml) always represented 1 m^3 of water.

The relationships between the zooplankton densities in the GUS III samples and seven chemical and physical variables were examined in this analysis. These variables included surface temperature, surface salinity, local runoff, Mississippi runoff, upwelling, stability of the water column, and the cross shelf component of the water currents. Temperatures and salinities were measured at each station when the zooplankton tows were taken (Temple, Harrington, and Martin, 1977). Temperatures were measured with mechanical bathythermographs. Salinities were measured from water samples taken with Nansen bottles. The salinities were calculated from chlorinities determined in the laboratory by the Knudsen method. Temperature and salinity measurements were taken at the surface, 3, 11, 24, 43, and 70 m depending on the water depth at the station. Temperatures were also taken at the bottom of the water column.

Local runoff was calculated as mean river flow in m^3/sec from statistics collected by the U.S. Geological Survey (1969). The local runoff for each transect was a combined mean river flow from all major rivers located near that transect. The previous month's Mississippi runoff was also chosen as a variable (PMMSROFF). Although the lag time for the movement of water from the mouth of the Mississippi to each transect was undoubtedly not constant, 1 month appeared to be a reasonable estimate. Temple, Harrington, and Martin (1977) showed a relationship between the previous month's runoff from the Mississippi and the surface salinities at these stations.

Periods of upwelling were estimated from surface and bottom temperature charts for each station. When surface temperatures were rising and bottom temperatures were dropping, upwelling or movement of deeper colder water into the area was assumed. When bottom temperatures dropped faster than surface temperatures this also was taken as an indication of upwelling (Reed Armstrong, personal communication, NMFS, Northeast Fisheries Service, Narragansett, Rhode Island). Subjective values for no upwelling (0), moderate (1), and strong upwelling (2) were assigned to each sample.

The stability or resistance to mixing was also estimated from the difference between surface and bottom temperatures. This difference was used directly as a measure of stability. During periods when upwelling was occurring, however, the stability was assigned a value of 0.

The cross shelf current component was estimated from current charts constructed for each cruise by Armstrong (1976). Movement of water towards or away from the coast was considered to be an important factor possibly controlling the distributions of organisms. When net movement was away from the coast the cross shelf current component (CSCURR) was assigned a value of +1, when it was towards the coast it was assigned a value of -1. When current patterns were strictly parallel to the coast CSCURR was equal to 0.

Counts of organisms in each subsample were punched on data cards and FORTRAN computer programs were constructed to correct abundances to $\#/m^3$, calculate percentages, and tabularize the zooplankton counts. Programs were also used to check for normality in the data. The analysis of the frequency distributions of a number of the groups and species of zooplankton indicated that the data were not normal and that a natural log transformation, ln (density + 1), was sufficient for normalization. All statistical analyses were done on transformed data.

Densities of the most abundant zooplankton groups and species of copepods were entered into a Statistical Analysis System (SAS) data set along with physical and chemical variables and other attributes for each sample. Through SAS, graphs of densities versus various factors were constructed and simple univariate statistics were calculated. The analysis of variance, analysis of covariance, simple and multiple regressions, and the correlation analysis were also calculated through the use of the SAS language and procedures.

The Analysis of Variance

The analysis of variance (AOV) was used as a basis for examining temporal and spatial variability in the various groups and species of zooplankters. The main effects of Depth, Transect, Month, and Year were included in the analysis. Transects were considered to be whole plots and a split-plot design was used (Charles Gates, personal communication, Institute of Statistics, Texas A&M University). Depth, Transect, and Month were considered to be fixed effects and Year was considered to be a random effect. Main effects and first order interactions were tested. The second and third order interactions were pooled and used as the residual error term. The design resulted in Year and Transect being tested over the Transect*Year interaction, Depth being tested over the Depth*Year interaction, and Month being tested over the Month*Year interaction.

Significant effects in the analysis of variance were examined graphically. Interactions were examined first if they were significant at the 1% level. Main effects were examined separately only if the effect did not interact with another. Emphasis was not placed on Month*Year interactions which were frequently significant. The delay of seasonal abundance peaks would strongly influence this interaction.

Since the AOV was calculated on log transformed densities using a linear method to fill in missing data cells, which were numerous, it was not completely compatible with the graphical methods used to examine the significant effects in more detail. The means used in the graphical analyses of spatial and temporal distributions are based on untransformed data and are often influenced by missing data. Although I felt it was important to examine the data in this unadulterated form, care must be taken in interpreting the AOV results through these methods. One deceptive distributional trend was due to the presence of 8 m stations only on Transects I and IV. Comparing mean densities on these transects with other transects often was misleading when depth related trends were significant (a frequent occurrence). The low number of samples from 1965 on Transect IV (Table 1, p. 13) also caused the mean densities on this transect to be affected by yearly variability.

The Effect of Sampling Time

Zooplankton tows were taken whenever the research vessel arrived on station. The effect of this variability in sampling time during the day appeared to be significant for some organisms. Theoretically, oblique tows taken to near the bottom should eliminate sampling variability caused by the diel vertical migrations of planktonic animals. In practice, however, tows seldom reach the water close to the bottom and the time during the day in which the sample is taken can still be an important source of variability in estimating densities of migrating species. In this analysis, days were divided into three periods and numerically coded: (1) day (0900-1659 hrs); (2) twilight (0500-

0859 and 1700-2059 hrs); and (3) night (2100-0459 hrs). References to sampling times throughout this paper refer to these time periods.

When the frequency of sampling times at each station was examined most stations had a fairly even distribution for the three periods. A notable exception was found on Transect IV where most of the samples from the 8 and 14 m stations were taken during the day or twilight. Most of the samples taken at the 28 and 46 m stations were taken at night. This frequency distribution was considered when interpreting results on spatial differences for organisms.

Since vertical migration patterns can be expected to differ for various species, the relationship between density and sampling time was examined for each zooplankton group or species separately. Mean densities were plotted for each time period. Since most organisms that showed some relationship between density and sampling time exhibited intermediate density values during the twilight hours, linear correlations were also calculated. If highly significant correlation coefficients were found between the log of the density and sampling time or the graphical relationship appeared significant, an analysis of covariance (AOCOV) was calculated on the spatial and temporal effects using sampling time as a covariate.

Relationships with Physical and Chemical Factors

Simple linear regressions were calculated on the log of the density for each species or group versus the various physical and chemical parameters measured. These factors included surface temperature, surface salinity, local runoff, previous month's Mississippi runoff (PMMSROFF), the stability of the water column, the cross shelf current, and a measure of upwelling. Multiple regressions were also calculated for all combinations of two factor models, three factor models, etc. The R^2 values from these regression models were considered to be a measure of the percentage of the variability in the log density of the organism which could possibly be explained by the particular regression model under consideration. The relationships between density and surface temperature and salinity were also examined with the use of histograms. The bars of these histograms represent mean log densities for each organism over different temperature and salinity intervals. Since no measure of variance is included around these means, these charts should be interpreted with the regression results.

Histograms were also used to examine densities at different temperature and salinity combinations. Surface temperatures were divided into two ranges, below 21°C and above 21°C, and the relationship between density and salinity was examined over each temperature range. Salinities were divided into three ranges, (1) below 30°/oo, (2) 30-35°/oo, and (3) above 35°/oo. The relationship between density and temperature was then examined over these salinity ranges.

A more detailed regression analysis was used to examine seasonal and spatial effects on the relationship between the density of five common copepods and surface temperature and salinity. Regressions for these species were calculated for each month and depth separately. These copepods included the three most abundant species in the sampling area, *Paracalanus indicus*, *Acartia tonsa*, and *P. quasimodo* (all calanoids) and two abundant congeneric cyclopoids, *Oithona nana* and *O. plumifera*.

Subsampling Error

The Folsom Plankton Splitter has been used extensively in zooplankton research. This device allows samples to be split in half in succession until an aliquot small enough to examine is achieved. In an attempt to statistically examine the error involved in this splitting process, McEwen, Johnson, and Folsom (1954) split artificial samples of amphipods and euphausiids and determined that the subsampling error was random. Using mixed natural zooplankton samples, Miller, C. B. (unpublished) determined that 95.4% of the splits were random.

The reasons for a nonrandom distribution of Folsom splits probably are related to the clumping of organisms in the subsampling device. This could occur through the hooking of spines or setae or through the entanglement of organisms in gelatinous material in the samples. Nonrandomness in zooplankton subsamples therefore should be related to the composition of the sample being split. This makes the derivation of a universal estimate or a correction factor for subsampling error very difficult. Since this error term will vary for each sample examined, it should be determined separately for each sample. This is not feasible in most plankton studies due to the large number of subsamples that need to be examined.

Snider (1975) showed that the Folsom Splitter was very inaccurate for samples of pteropods taken in the Gulf of Mexico. These heavy shelled organisms fall out of suspension rapidly and are not split adequately. For this reason, results on shelled molluscs in this study should be viewed with caution.

Most of the trends examined in this study are based on mean densities from a large number of samples. This should tend to reduce the effect of subsampling error on the results. Basing conclusions on small differences in zooplankton densities or on results from a small number of samples should generally be avoided in studies of this type due to the unknown magnitude of the error involved with subsampling.

RESULTS AND DISCUSSION

Physical and Chemical Factors in the Sampling Area

Surface Temperature

Surface temperature fluctuations over the sampling area were examined with respect to depth, month, and transect. The monthly variability of mean surface temperature for each depth, averaged over transects and years is shown in Figure 3. The highest temperatures were observed during June, July, and August. The lowest temperatures were recorded during February at the deepest stations and during January at the shallowest stations (8 and 14 m). During the spring and fall the temperature profiles were similar at each depth. During the winter, however, surface water temperatures became colder as water depth increased. Mean summer temperatures exhibited a decrease during July (apparently due to upwelling) at stations of all depths except 73 m, which had a mean surface temperature peak during July.

Figure 4 shows the monthly variability of mean surface temperature at each transect, averaged over depths and years. Although confounded by the fact that each transect does not have stations at all depths, it appears that Transects IV and V had the highest summer temperatures and the lowest winter temperatures. Transect V did not have the July drop in temperature exhibited at the other transects. The factors affecting these temperature profiles probably include:

1. Distance from shore. The width of the shelf was considerably greater at Transects IV and V and it became narrower at the southern transects (Fig. 5).

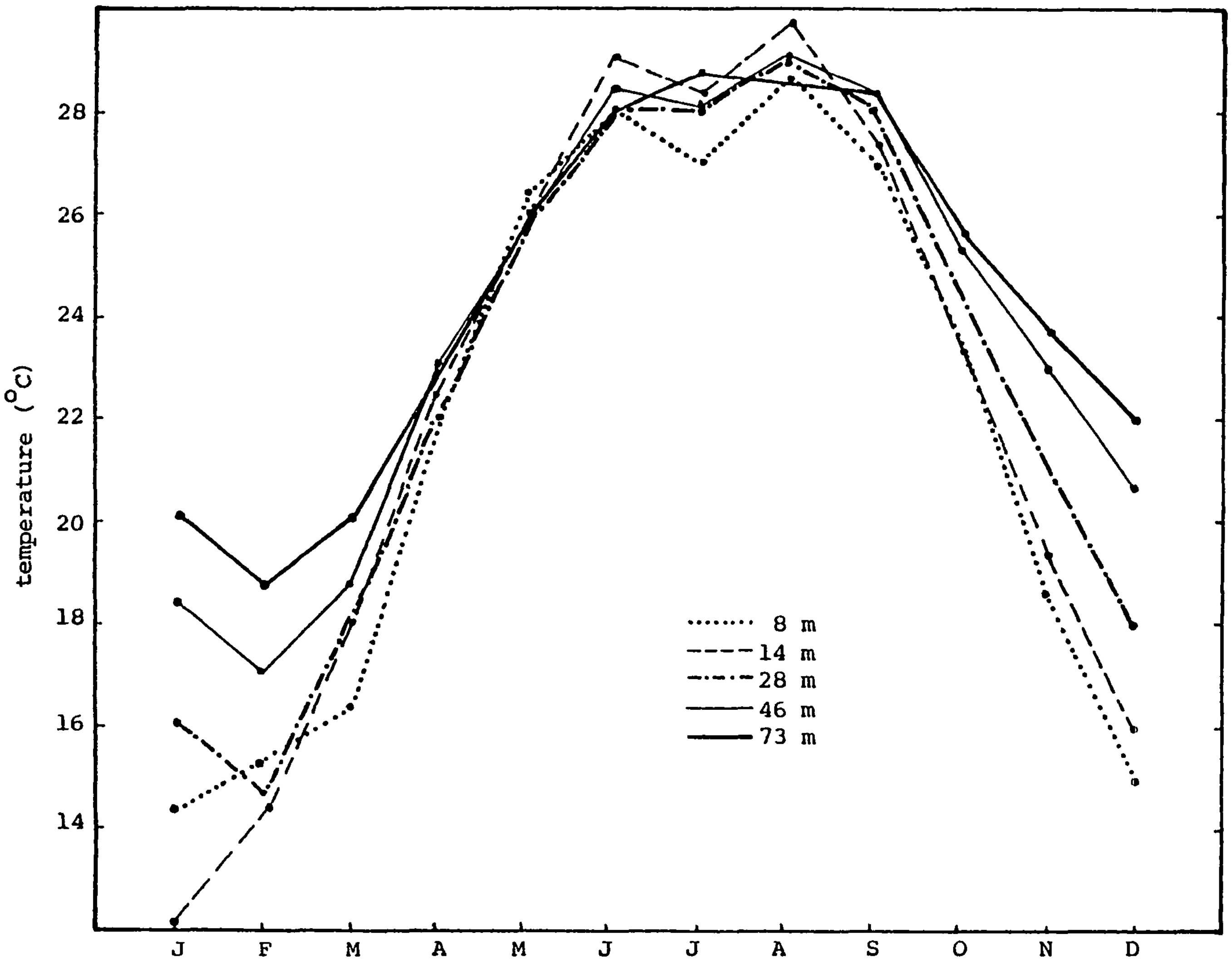


Figure 3. Monthly mean surface temperatures at each bottom depth sampled. Values are averaged over transects and years.

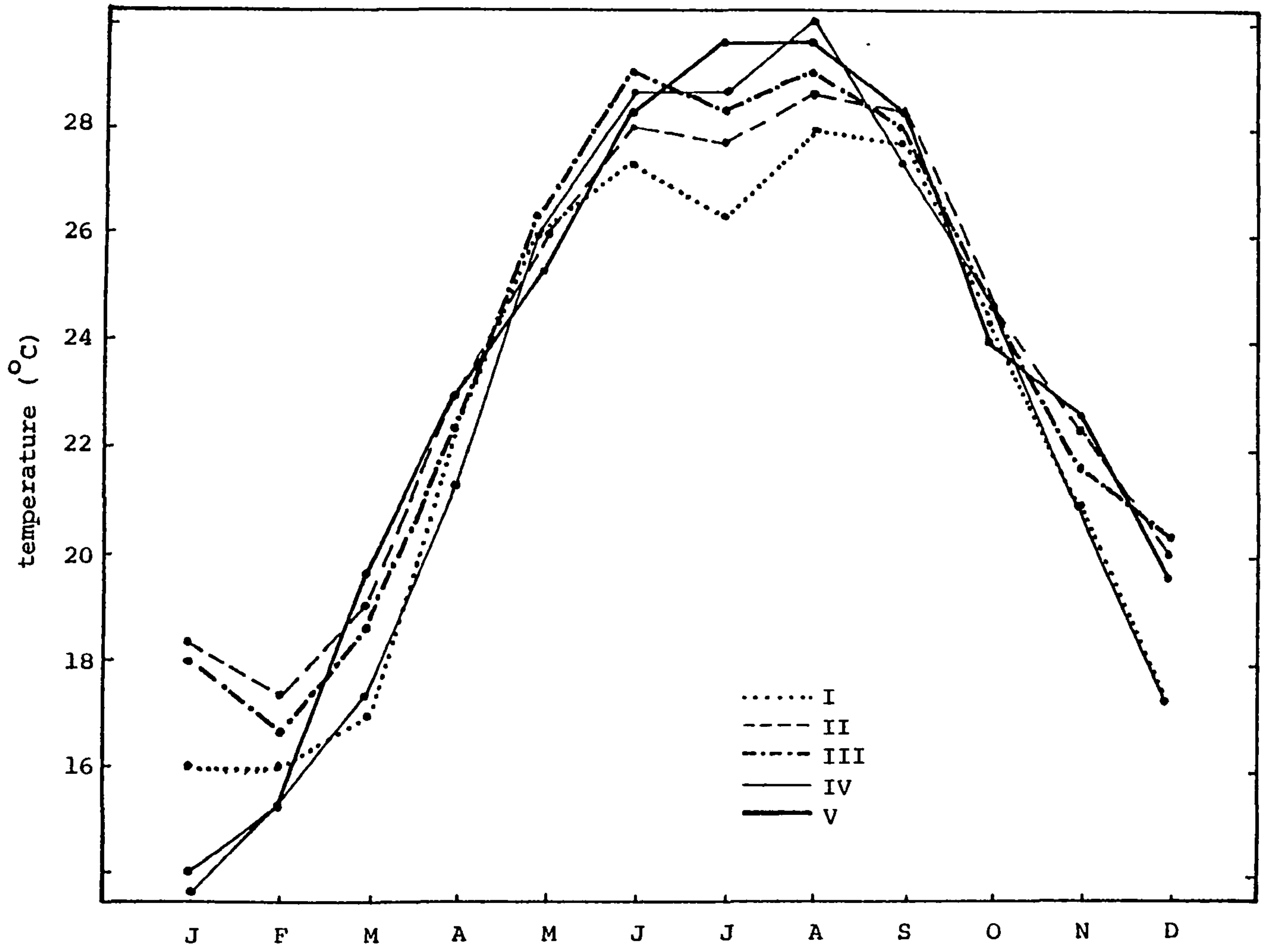


Figure 4. Monthly mean surface temperatures on each transect. Values are averaged over bottom depths and years.

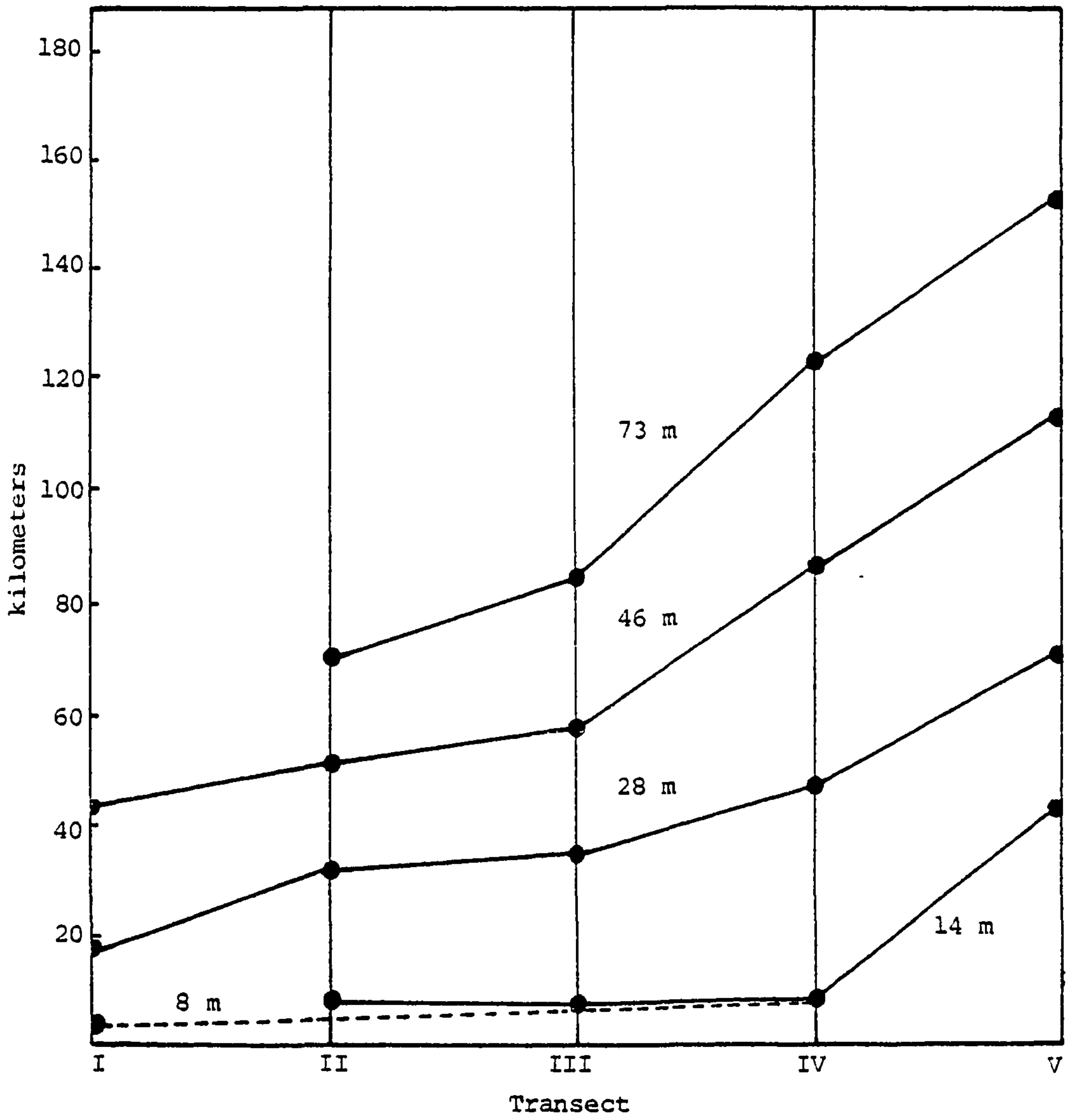


Figure 5. Distance from shore for each sampling station. Dots representing stations with similar bottom depths are connected. The dashed line connecting the 8 m stations indicates that these bottom depths were not sampled on every transect. Distances were measured perpendicular to the coastline.

2. Latitude
3. The absence of some depths on some of the transects. Transects II, III, and V did not have an 8 m station, and the 14 m and 73 m stations were absent on Transect I.

Seasonal variability, measured by the difference between mean monthly minimum and maximum temperatures was lowest on Transect I (lowest latitude) and highest on Transects IV and V.

When temperatures were averaged over all of the samples taken at a particular station (Fig. 6), the increase in mean temperature with depth, already seen in Figure 3 (p. 24), was again visible. The difference between mean temperatures at the shallow stations and the deeper stations was greatest at the northern transects. Again, this may have been due to the variability in the distance from shore for each depth.

The frequency of various surface temperatures taken with samples is shown in Figure 7. Most temperature values were between 14 and 30°C. Temperatures around 29 and 30°C were most frequently recorded. The frequency of temperatures for three salinity classes is shown in Figure 8.

Surface Salinity

The monthly variability of mean surface salinity at each depth is shown in Figure 9. Stations at 8 and 14 m appeared similar with a high seasonal variability characterized by a large decrease in salinity during April and May and relatively high values during the summer months.

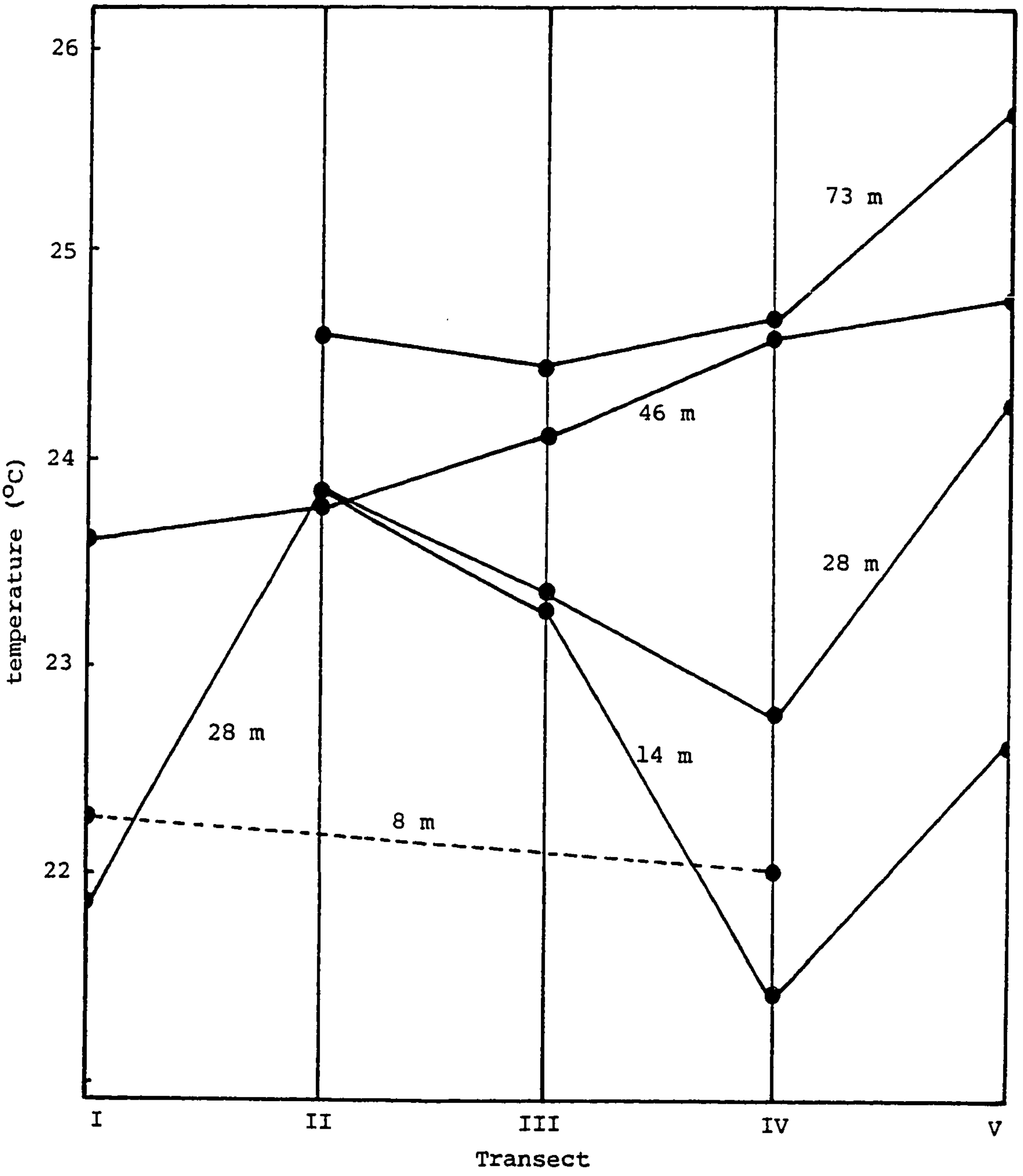


Figure 6. Mean surface temperature values at each station. Values are averaged over months and years. Dots representing stations with similar bottom depths are connected. The dashed line connecting the 8 m stations indicates that these bottom depths were not sampled on every transect.

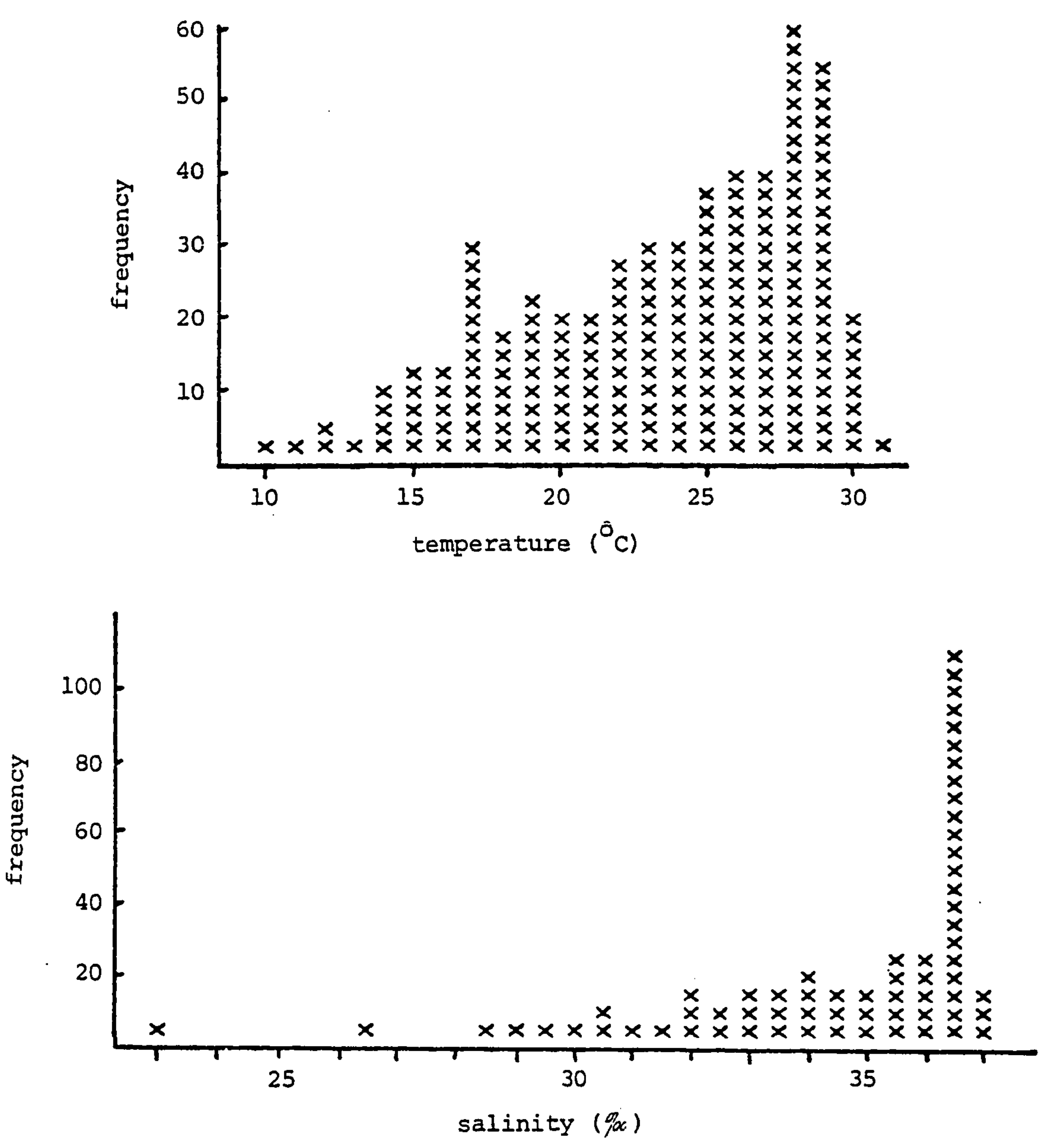


Figure 7. Frequency distribution of surface temperature and surface salinity in samples analyzed. The height of the bars indicates the number of samples examined for 1°C temperature intervals and 0.5 ‰ salinity intervals.

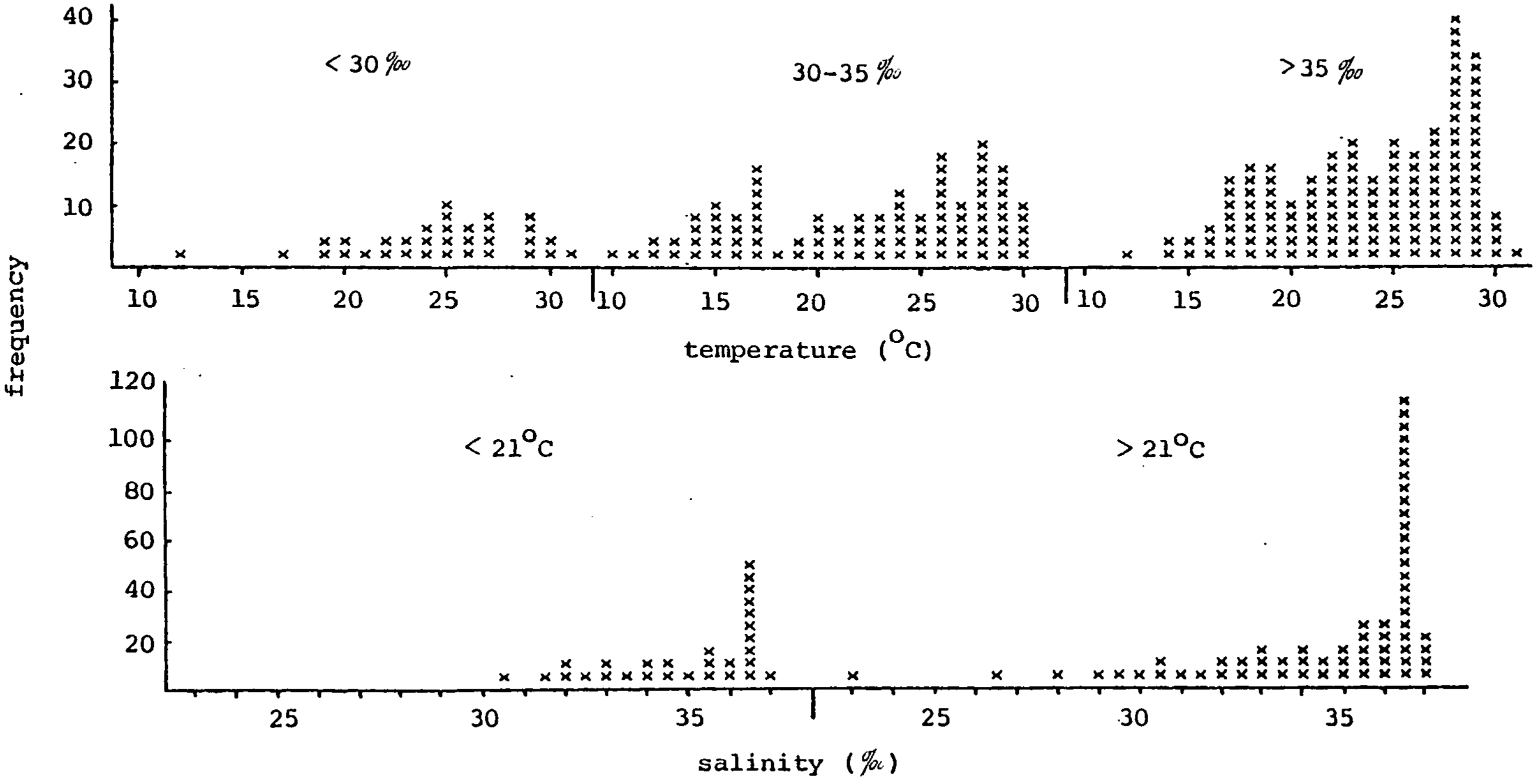


Figure 8. Frequency distribution of various combinations of surface temperature and surface salinity for the samples analyzed. The height of the bars indicates the number of samples examined for 1°C temperature intervals over three salinity ranges and for 0.5 °/oo salinity intervals over two temperature ranges.

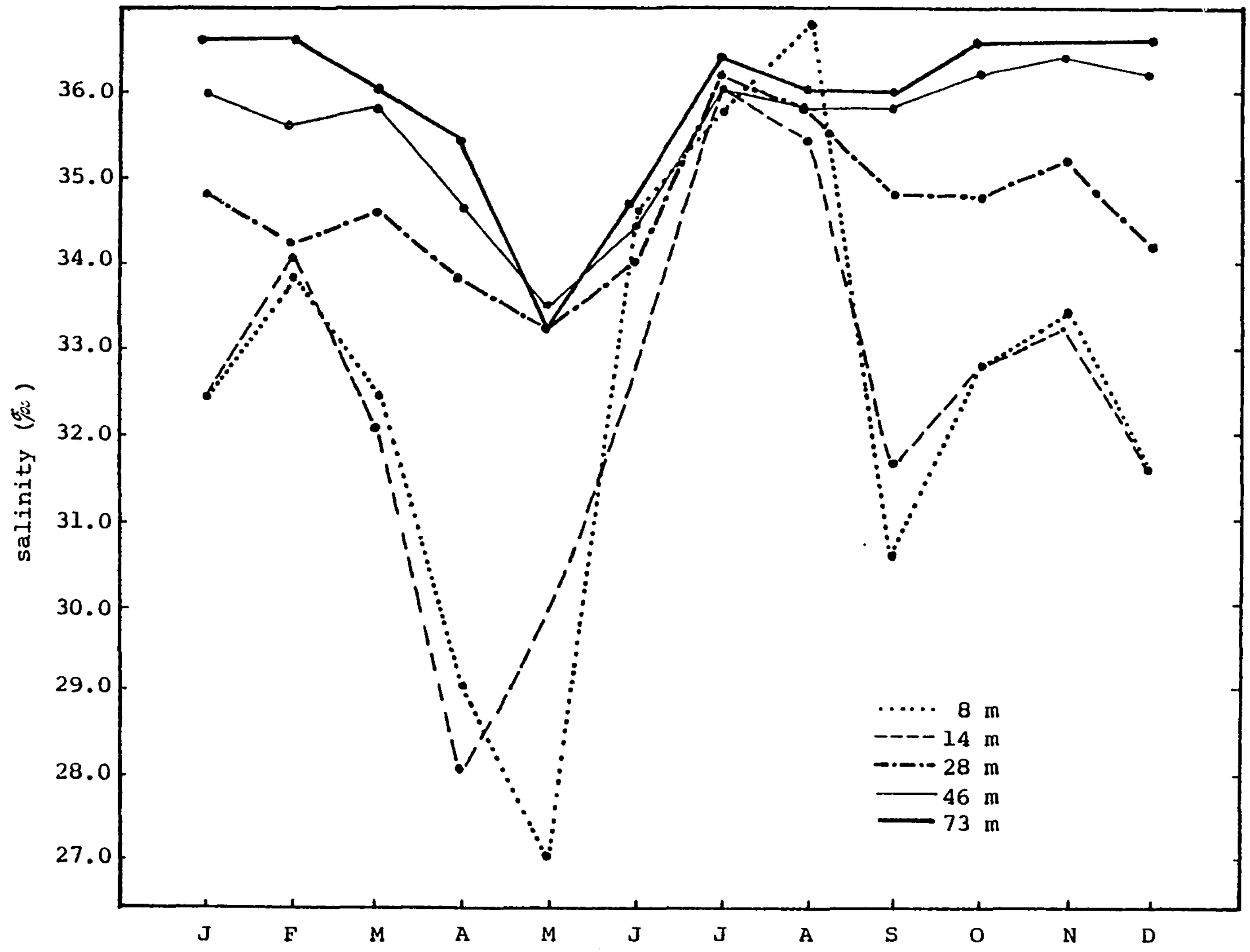


Figure 9. Monthly mean surface salinities at each bottom depth sampled. Values are averaged over transects and years.

The profiles at the deeper stations showed less seasonal variability but the spring salinity minimum was still apparent.

The mean monthly salinity profiles for each transect (averaged over depths and years) were highly variable and the only distinct pattern seen was the spring decrease in salinity (Fig. 10). The interpretation of these data is subject to the same problems encountered with the temperature data represented in similar fashion. Anomalously, no distinct spring decrease in salinity was apparent on Transect V although this transect was located near the outflow of the Atchafalaya and the Mississippi Rivers which had high spring flows. This anomaly might be partially explained by the relatively large distance from shore of the stations on Transect V and the absence of an 8 m station. When the seasonal salinity profiles at each depth on this transect were examined, it was apparent that a large decrease in salinity during the spring was present only at the shallowest station (14 m). The drift bottle studies of Temple and Martin (1979) showed that surface currents were onshore and to the west during April and May of 1962 and 1963. If these same current patterns were present throughout the study period (1963-1965), high salinity water may have been moving in from offshore in this area during the spring.

Mean surface salinities at each station averaged over time (Fig. 11) generally showed an increase in salinity with depth. The difference between salinities at the inshore and offshore stations was lowest on the southern transects (I and II).

The frequency of occurrence of surface salinity values recorded with the zooplankton samples is shown in Figure 7 (p. 29). Salinity

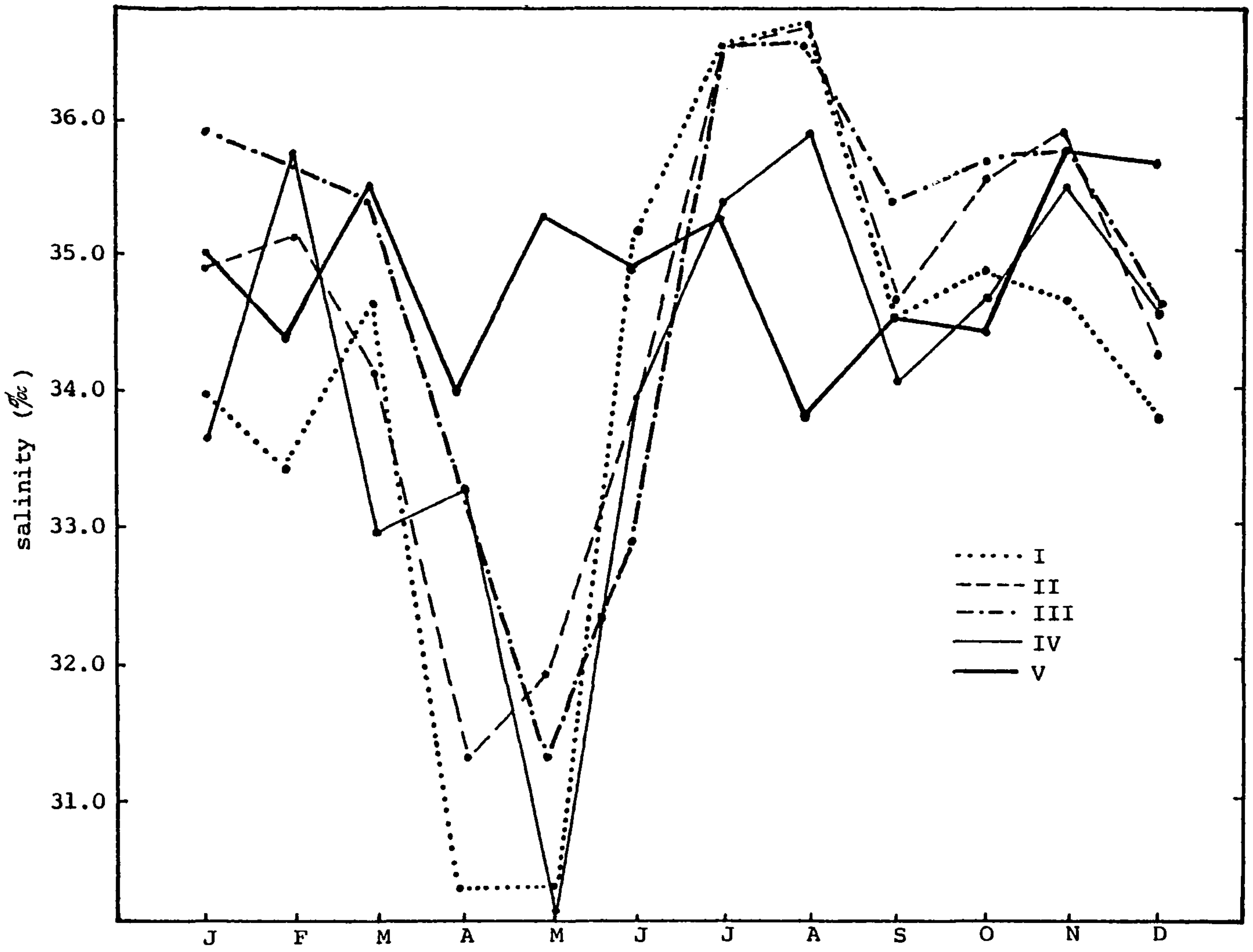


Figure 10. Monthly mean surface salinities on each transect. Values are averaged over bottom depths and years.

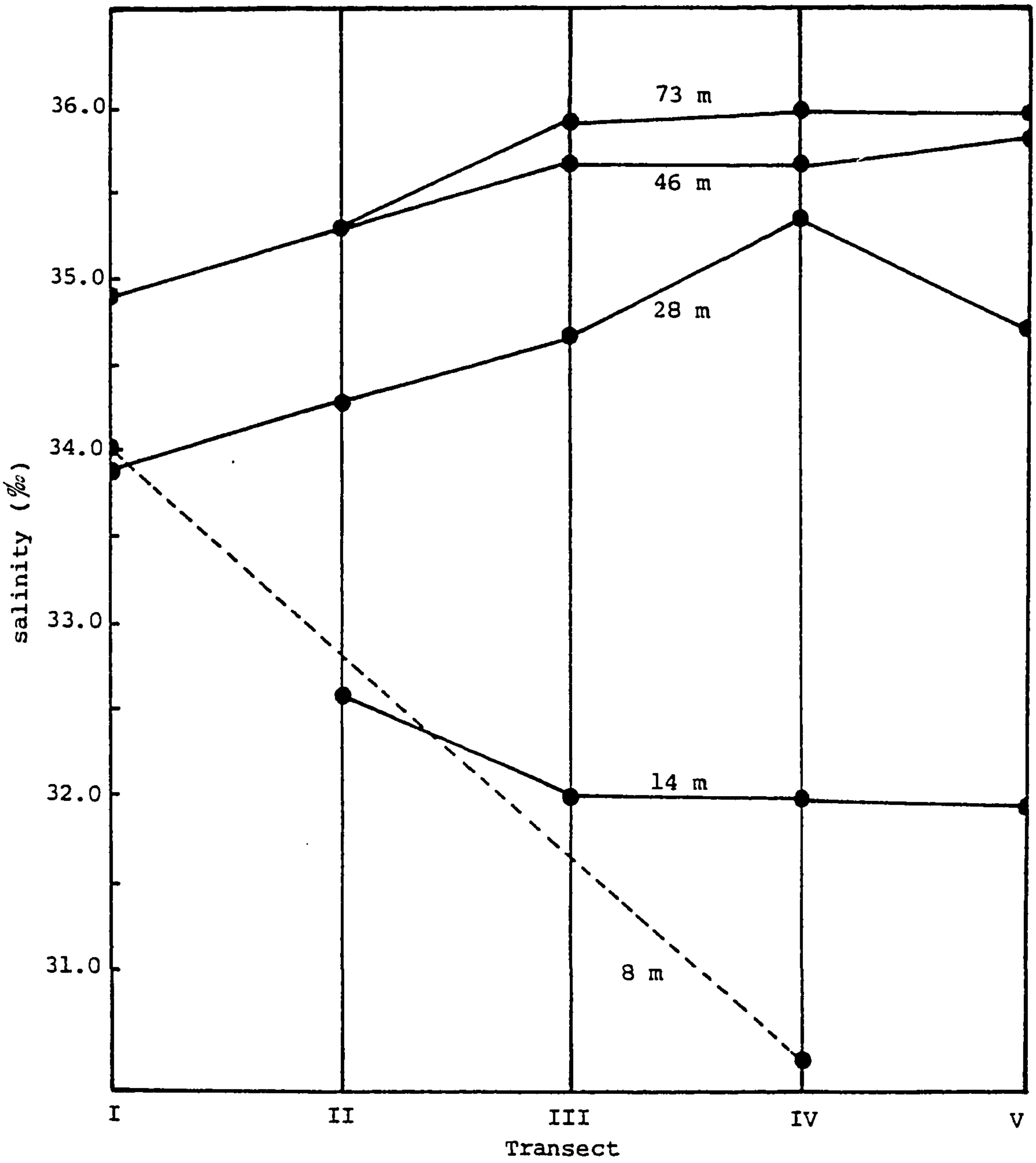


Figure 11. Mean surface salinity values at each sampling station. Values are averaged over months and years. Graphed as in Figure 6 (p. 28).

frequencies for two different temperature ranges (below 21°C and above 21°C are shown in Figure 8 (p. 30).

Runoff

Mean monthly river flow values were combined for the major rivers located near each transect in the study area. These rivers are listed in the following table.

Transect	Rivers
I	Rio Grande
II	Nueces, San Antonio, Guadaloupe
III	San Antonio, Guadaloupe, Lavaca, Colorado
IV	San Bernard, Brazos, Oyster Creek, Buffalo Bayou, San Jacinto, Trinity, Village Creek
V	Atchafalaya

Mean monthly local river flow values for each transect, averaged over the 3 years, are shown with the Mississippi River flow in Figure 12. Generally the flow from the Mississippi was between one and two orders of magnitude greater than any of the local flows at the transects. The Atchafalaya River (Transect V) also had a significantly higher flow than the other rivers. Local river flow near Transect I (Rio Grande River) was negligible.

Seasonally, the Mississippi and the Atchafalaya exhibited peak flows during April. The flow rates at the transects off the Texas coast (I-IV) generally peaked during the winter and early summer. Although the annual variability for the 3 years of the study was low for the Mississippi River, Texas rivers generally had the greatest runoff during 1965.

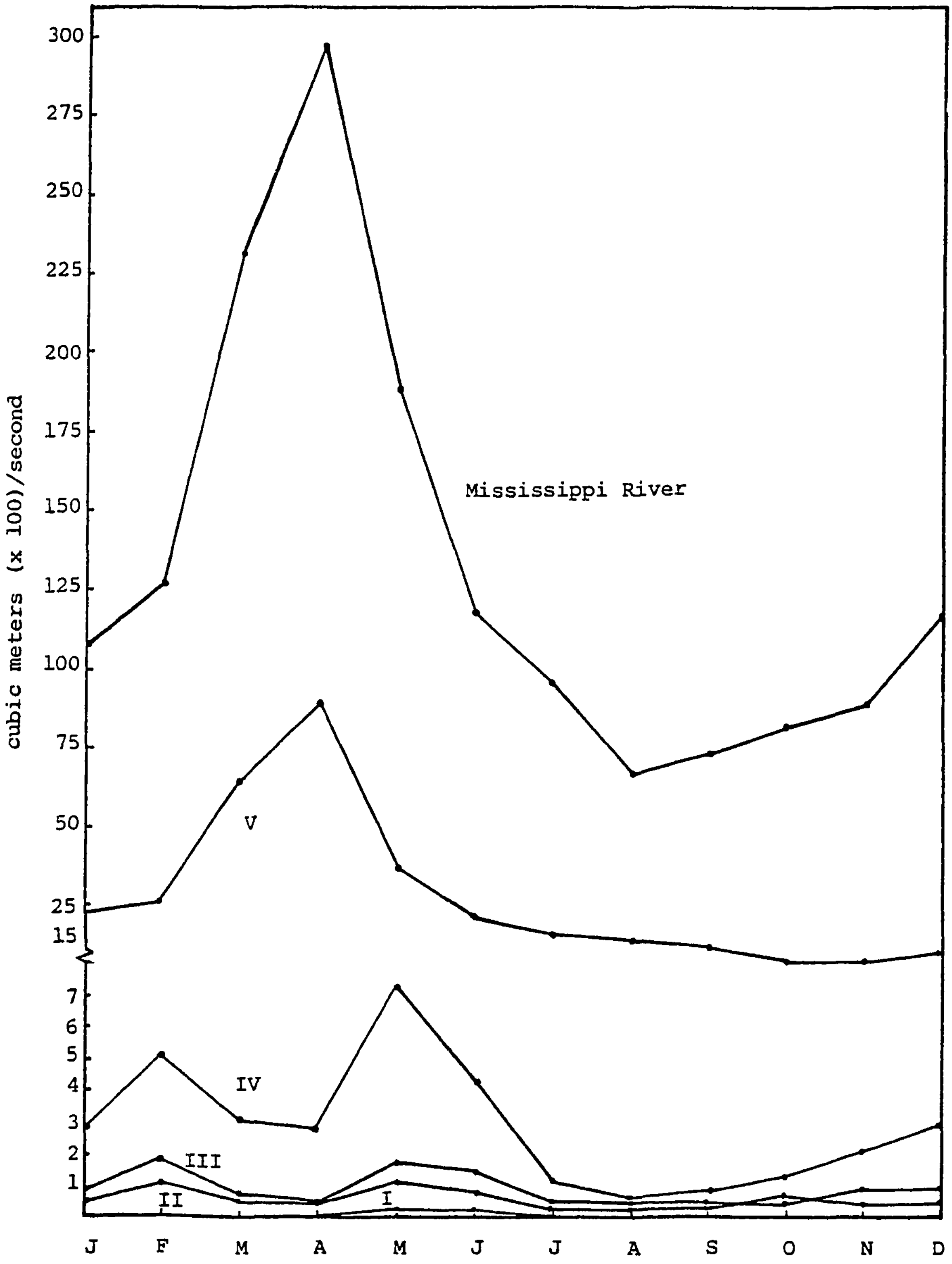
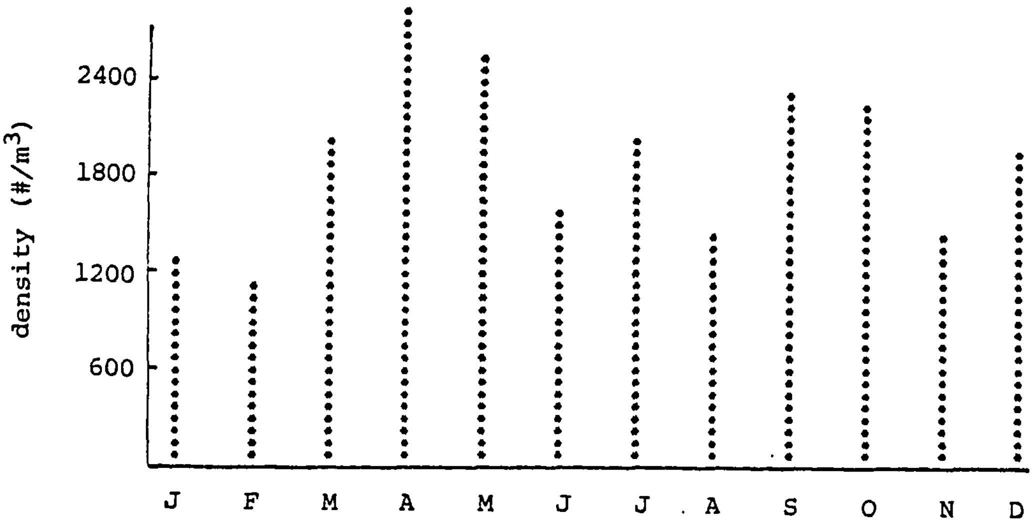


Figure 12. Mean monthly runoff values from the Mississippi River and the rivers located near each transect in the study area.

The relationship between river flow and surface salinity can be examined by comparing Figures 9 (p. 31) and 12. At four out of the five bottom depths, surface salinity minimums occurred during May. This coincided with the peak river flows from the Texas coast. If a 1-month lag time was used, these salinity minimums also coincided with peak Mississippi River flow. This lag time corresponds approximately to the time it would take for Mississippi River water to reach the Texas coast. When local runoff and the previous month's Mississippi runoff were plotted against surface salinity at each station, Mississippi flow appeared to influence the salinity at every station except the deeper stations on Transect V. The high salinities at these stations have already been discussed. Local runoff only appeared to be related to salinity at some of the shallower stations. These data along with the large springtime decrease in salinity on Transect I (Fig. 10, p. 33) which occurred although there was only negligible runoff in the immediate area, would seem to indicate that the flow of the Mississippi River is more of a controlling factor for surface salinity in the study area than local river flow. Local flows probably have an effect on the salinity at some of the nearshore stations.

Total Zooplankton

Zooplankton densities peaked in April and May and again in September and October (Fig. 13), with the largest mean density occurring in April (2870 organisms/m^3). The lowest mean monthly densities occurred in January (1301/m^3) and February (1124/m^3). Densities decreased with depth from 3412 organisms/m^3 at 8 m to 1131/m^3 at 73 m.



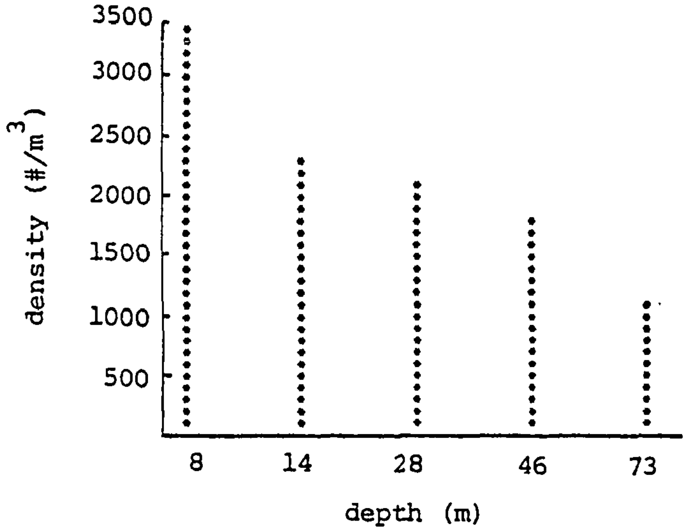


Figure 13. Mean density of zooplankton for each month and bottom depth. Monthly means are averaged over transects, bottom depths and years. Means for each bottom depth are averaged over transects, months, and years.

The greatest mean densities occurred in 1964 (Fig. 14). The analysis of variance indicated that no interactions were significant at the 1% level (Table 2). The main effects of Month and Depth were significant.

There was some evidence that the time of day when the tows were taken may have affected the total zooplankton counts. A negative correlation was obtained by correlating the log of the density with the three time categories. The analysis of covariance results, however, were similar to the results from the AOV. The Month*Year interaction became significant. This was probably the result of the high spring density peaks which occurred during 1964 (Fig. 14).

Simple regression models on the log of the density versus the physical and chemical factors examined, indicated that there was a negative relationship with salinity that explained 7.8% of the variability in the zooplankton density. Combining salinity and the cross shelf current explained 10.5% of the variability in a multiple regression model. The other physical factors did not appear to be significant. The histogram of density versus salinity showed some indication of this negative relationship (Fig. 15). No relationship with temperature was apparent and temperature salinity interactions also did not appear significant (Fig. 16).

Density trends reported off the South Texas coast by Park (1979) were similar to those found in this study. At the two stations sampled monthly by Park with comparable bottom depths, density peaks occurred in 1976 and 1977 during the spring and early summer and the late summer and fall. The highest density was found in May and June when a mean number of 5768 organisms/m^3 was reported over the 2 years.

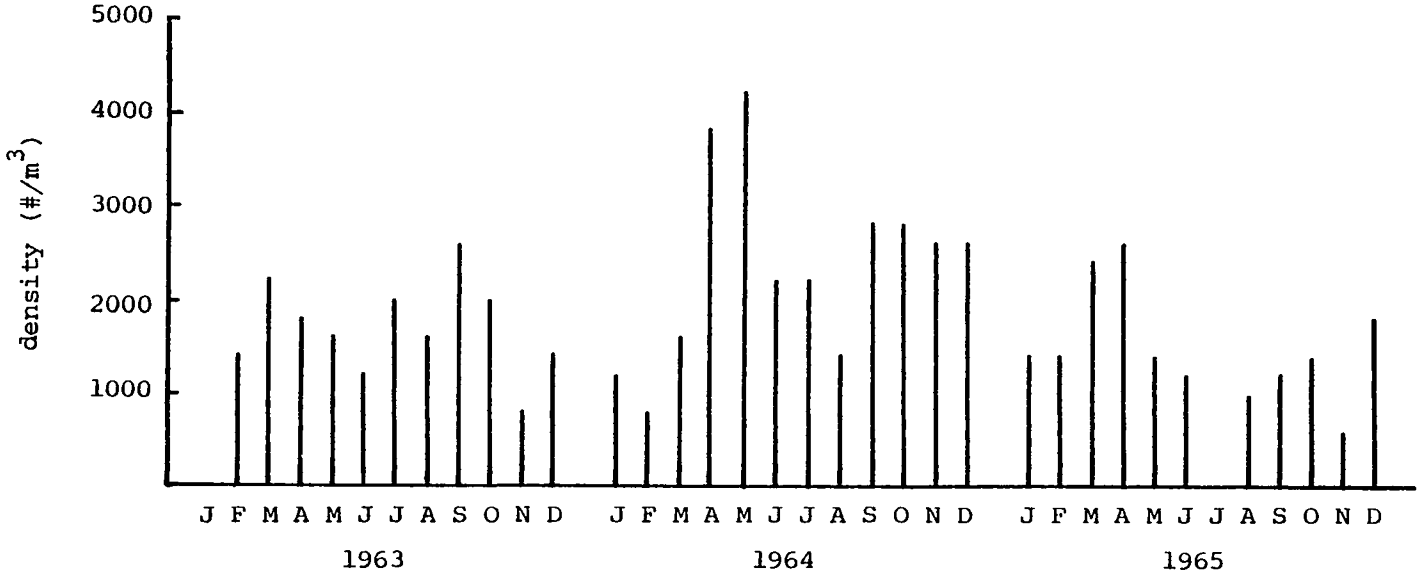


Figure 14. Mean monthly densities of zooplankton over the entire sampling area for the three years of the study. Values are averaged over transects and bottom depths.

Table 2. Analysis of variance and covariance for zooplankton groups. Probability values (percent) are listed from the analysis of variance for all groups. Results of the analysis of covariance with sampling time as the covariate are given below the horizontal line for some factors.

Group	Percent of zooplankton	Interactions						Main Effects			
		Depth Trans	Depth Month	Depth Year	Trans Month	Trans Year	Month Year	Depth	Trans	Month	Year
Zooplankton		9.4	ns	ns	ns	ns ns	1.6 *	0.9 0.4	ns ns	1.3 ns	0.2 4.5
Copepods	60.7	ns	ns	ns	ns	ns	* *	1.1 1.2	3.7 ns	ns ns	* 4.8
Larvacea	7.7	4.1	ns	2.6	ns	ns	0.6	4.9	ns	0.1	0.2
Bivalve larvae	5.5	2.9 3.1	1.4 0.1	ns ns	ns	ns	1.4 0.7	* *	ns	4.8 9.0	ns
Euconchoecia	4.7	ns	2.4 1.7	ns	0.4 0.4	ns	0.1 0.1	* *	8.9	9.0	ns
Chaetognaths	4.3	0.3 0.5	* *	7.3 6.0	5.1 5.7	5.0 3.0	0.5 0.4	0.6 0.8	ns ns	0.5 0.7	1.6 1.8
Gastropod larvae	3.6	* *	ns	ns ns	2.1 5.2	1.0 0.6	2.0 1.9	* *	ns ns	0.2 0.3	ns ns
Penilia	1.8	* *	ns	* *	1.6 0.8	ns ns	* *	ns ns	ns ns	ns 9.5	* *
Medusae	1.8	7.9	1.6	7.8	2.1	ns	ns	ns	1.2	3.5	0.2

* = less than 0.1%
ns = greater than 10%

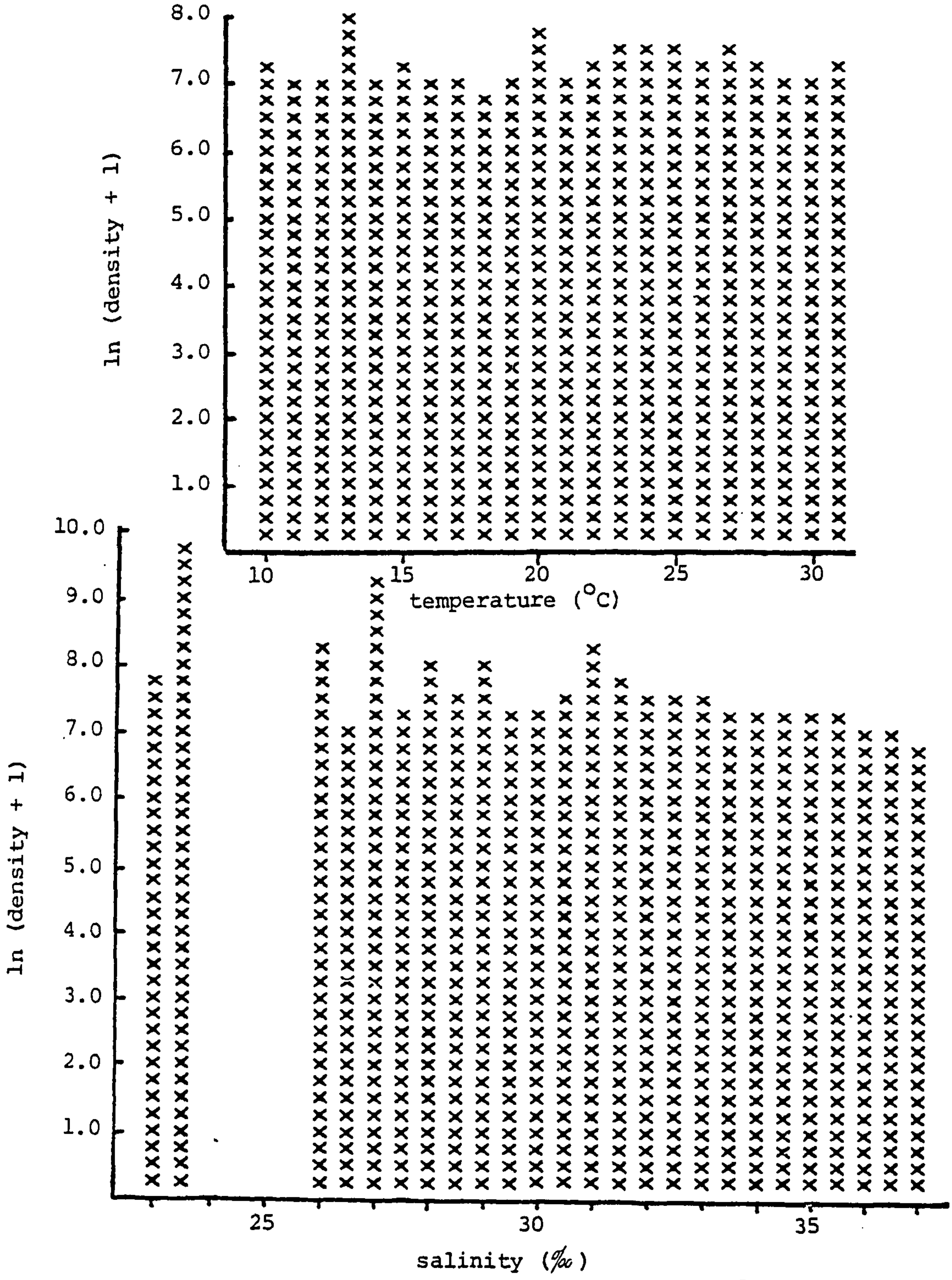


Figure 15. Zooplankton density relationships with surface temperature and surface salinity. Mean density values based on natural logs are plotted for 1°C temperature intervals and 0.5 °/oo salinity intervals. See Figure 7 (p. 29) for the frequency distributions of surface temperature and surface salinity in the samples analyzed.

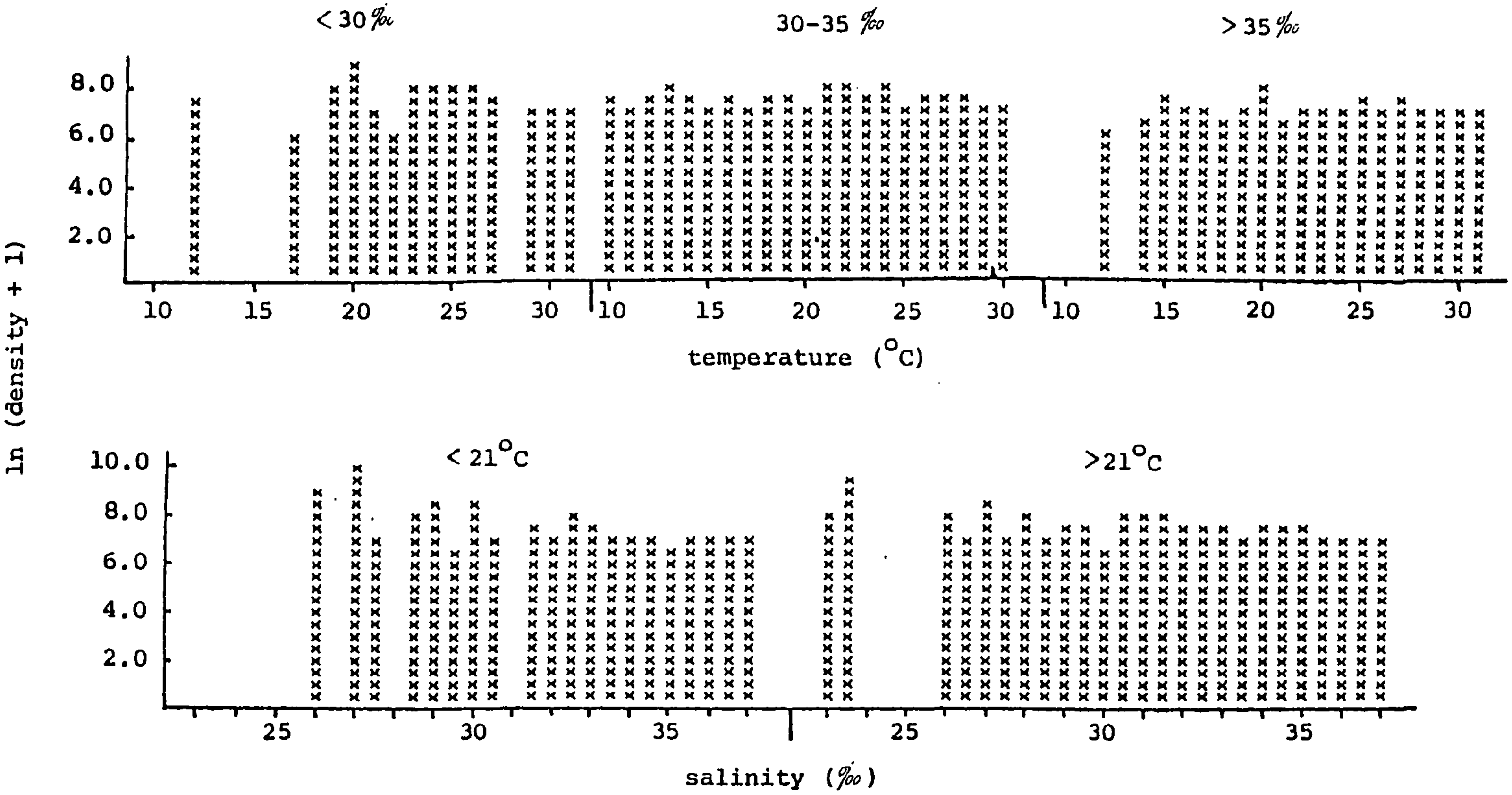


Figure 16. Densities of zooplankton at different surface temperature and surface salinity combinations. Mean density values based on natural logs are plotted for 1°C temperature intervals over three salinity ranges and for 0.5 °/oo salinity intervals over two temperature ranges. See Figure 8 (p. 30) for the frequency distribution of these temperature and salinity combinations in the samples analyzed.

Mean densities during the rest of the year ranged from approximately 500 to 4000 organisms/m^3. Decreasing densities with distance from shore were also reported by Park (1979). Although his stations were located slightly farther from shore than the GUS III stations, mean densities ranged from approximately 3000 organisms/m^3 at the inshore stations to approximately 1000/m^3 at the offshore stations.

Other studies reporting total zooplankton densities are not as comparable due to different sampling areas and techniques. In the neritic areas off the west coast of Florida, King (1950) found the greatest zooplankton densities at bottom depths of 9 m. Densities decreased at shallower and deeper stations. Caldwell and Maturo (1976) found a decrease in zooplankton density with increasing station depth. Their limited seasonal data indicated that the highest densities occurred during their winter sampling period. Off of the eastern coast of the United States Malone (1977) also reported a decrease in zooplankton densities with the distance from the shore.

Major Groups of Zooplankton

When monthly mean densities of all major groups of zooplankton were examined together (Fig. 17), the dominance of the copepods throughout the year was apparent. The only period when zooplankton densities were not tracked closely by copepod densities was during April. Spring density peaks of almost all of the other major groups occurred during this month. During the rest of the year, the chaetognaths and ostracods were found in relatively small numbers during the summer and these groups occurred in relatively large numbers during the late fall and early winter months. The larvacea maintained high densities throughout

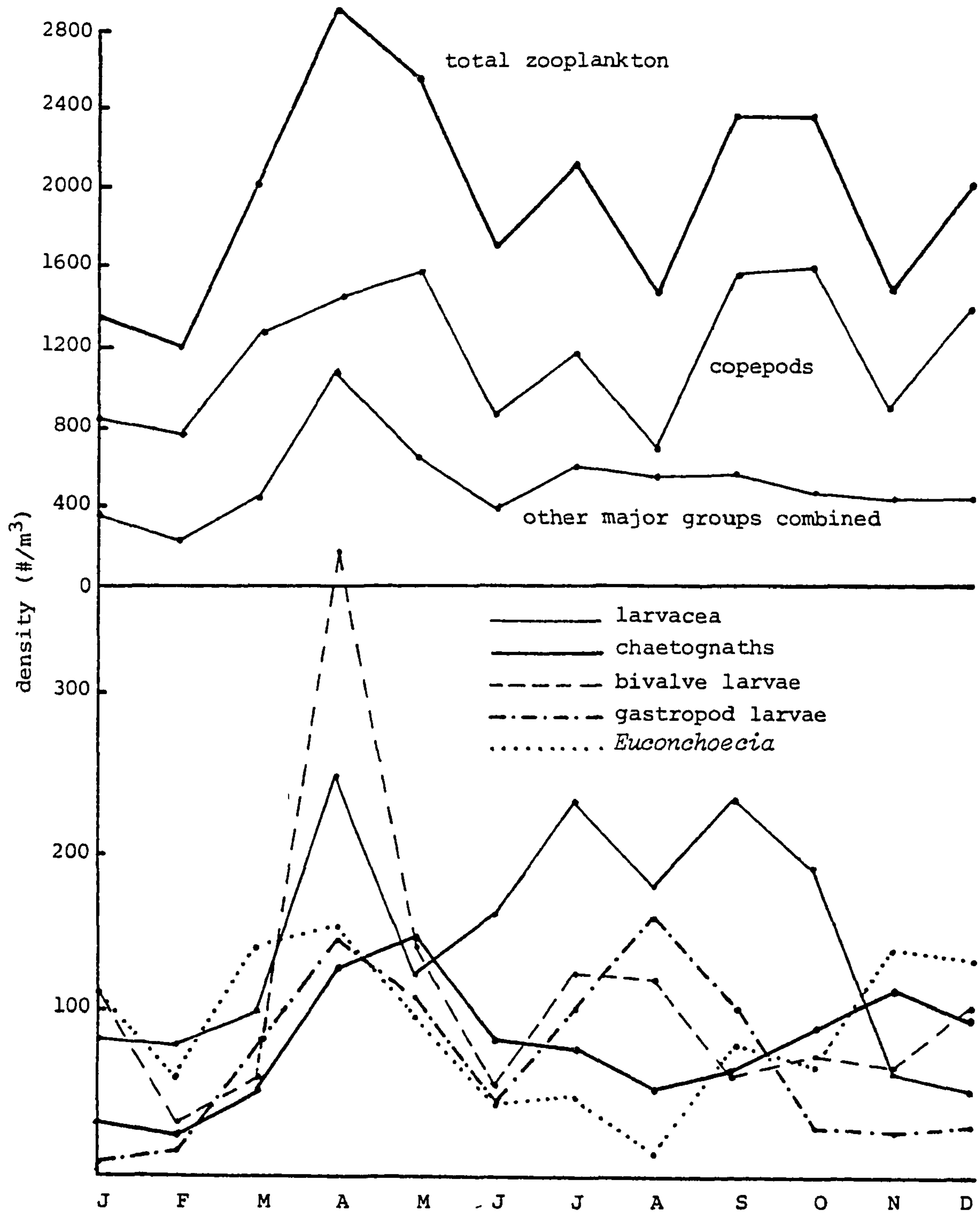


Figure 17. Monthly mean densities of major zooplankton groups averaged over the entire sampling area and the three years of the study.

the summer and early fall and were found in low densities during the winter. The meroplanktonic groups (gastropod and bivalve larvae) had density peaks in the summer months. Densities of these groups of mollusc larvae appeared to be highly correlated (r = 0.53) (Table 3).

The chaetognaths and the copepods were the only major zooplankton groups which had spring density peaks in May. Since the carnivorous chaetognaths prey mostly on copepods (Raymont, 1963; Barnes, 1974), this spring density distribution may indicate predator populations increasing with their food supply. The fall peak in chaetognath densities (November) lagged 1 month behind the fall copepod density peak which occurred in October. In comparison with the other major zooplankton groups, however, the seasonal density pattern of the chaetognaths was most similar to that of the copepods. The densities of these two groups were highly correlated (r = 0.42).

All of the major groups of zooplankton except the ostracods exhibited a general decrease in density with depth (Fig. 18). Ostracod densities were extremely low at the shallow stations and appeared to peak at the 46 m stations.

General abundance and distribution data for all of the zooplankton groups identified are listed in Table 4. Individual groups are discussed in detail in the following sections in the order of their abundance over the sampling area. The copepods, however, which were the most abundant organisms in the area, are examined last in much greater detail than the other groups.

Larvacea

Most of the organisms included in this category appeared to belong

Table 3. Correlation matrix for major groups of zooplankton. Correlation coefficients are based on log transformed densities. Probability value (percent) is indicated in parenthesis. vs = less than 0.1%, ns = greater than 10.0%.

	Copepods	Larvacea	Bivalve Larvae	*Euconchoecia*	*Chaetognaths*	Gastropod Larvae	*Penilia*
Copepods		0.33 (vs)	0.41 (vs)	0.03 (ns)	0.42 (vs)	0.37 (vs)	0.15 (vs)
Larvacea			0.25 (vs)	0.10 (2.0)	0.29 (vs)	0.40 (vs)	0.32 (vs)
Bivalve larvae				0.02 (ns)	0.41 (vs)	0.53 (vs)	0.15 (0.3)
Euconchoecia					0.22 (vs)	0.22 (vs)	0.07 (9.0)
Chaetognaths						0.48 (vs)	0.14 (0.1)
Gastropod larvae							0.31 (vs)
Penilia							

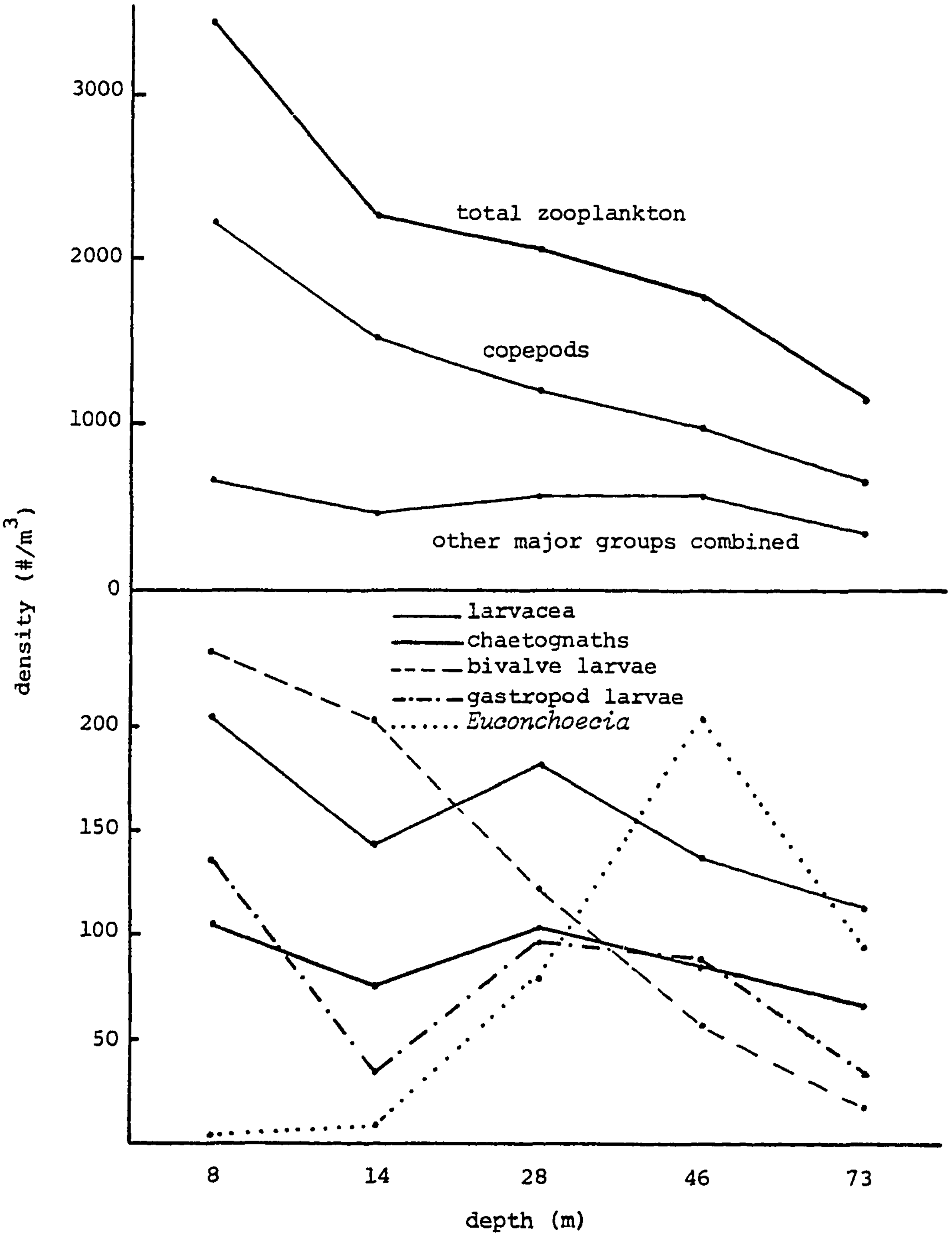


Figure 18. Mean densities of major zooplankton groups at each bottom depth sampled.

Table 4. List of zooplankton groups with general abundance and distribution data. Percent abundance (% Ab) was calculated from all samples (R = less than 0.5%). Freq = percent of occurrences out of 513 samples, Loc = location, i.e., I-inshore, O-offshore, B-both or between. Seasonality was determined by density (D) for the common species and by frequency of occurrence (x,i,o) for the rare species. Where seasonality differed with locality, i = inshore and o = offshore.

Phylum	% Ab	Freq	Loc	Season			
				Win	Spr	Sum	Fal
Cnidaria							
medusae	1.81	93.8	I	D	D	D	D
Annelida							
polychaete larvae	0.77	89.7	B	x	x	x	x
Mollusca*							
bivalve larvae	5.46	98.0	I		D		
gastropod larvae	3.64	98.0	B		D	D	
heteropods	R	22.4	B	x	x	x	x
pteropods	0.76	69.6	B	x	x	x	x
Arthropoda							
Crustacea							
Cladocera							
Evadne	R	28.3	B		D	D	
Penilia	1.82	62.0	I		D	D	
Podon	0.75	33.5	B		x	x	x
Ostracoda							
Conchoecia	R	13.5	O	x	x	x	x
Euconchoecia	4.72	77.0	O	D	D		D
Copepoda							
Planktonic	60.8	100					
Calanoida							
Cyclopoida							
Harpacticoida	1.46	71.9	I	D	D	D	D
Cirripedia							
barnacle nauplii	0.92	29.0	B	x	x	x	
barnacle cypris	R	40.5	B	x	x	x	
Malacostraca							
Amphipoda	R	82.3	B	x	x	x	x
Cumacea†	R	4.5	B		x		x
Euphausiacea	R	5.8	B	x	x	x	x
Isopoda†	R	3.5	I	x	x	x	x
Lucifer	R	55.2	B	x	x	x	x
Mysidacea	R	2.7	B	x	x	x	x
Stomatopod larvae	R	25.0	B		x	x	x

Table 4. (continued)

Phylum	% Ab	Freq	Loc	Season			
				Win	Spr	Sum	Fal
Chordata							
Urochordata							
Thaliacea							
Doliolida	0.90	67.4	B	D	D		
Salpida	R	23.2	O		x	x	x
Larvacea	7.70	97.9	B		D	D	D
Vertebrata†							
fish larvae	R	73.2	B	o	o	oi	oi
fish eggs	R	50.0	B	o	oi	oi	o
Chaetognatha	4.34	98.4	B		D		D

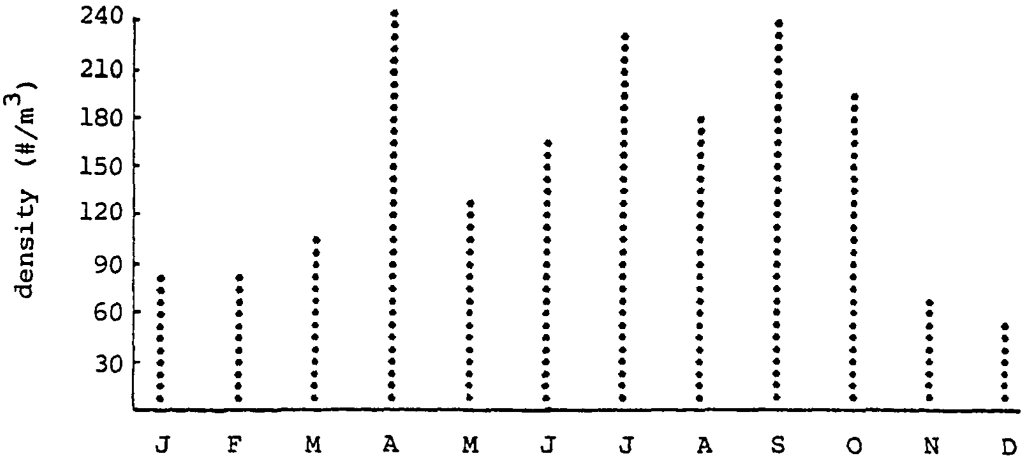
*Transect II not included (398 obs)
†Transects I, II and III not included (198 obs)

to the genus *Oikopleura*. This group was quite abundant, comprising 7.7% of the zooplankton over the entire sampling area. The only interaction that was significant at the 1% level in the AOV was the Month* Year interaction. The main effects of Month and Year were also highly significant and Depth was significant at the 5% level (P = 4.9%). The seasonal abundance of Larvacea averaged over the entire sampling area is shown in Figure 19. A spring density peak was indicated with a more prolonged peak in late summer and fall. Winter densities were generally low. The significance of the Month*Year interaction was probably due to the small spring density peak present in 1963 and the absence of a large fall peak in 1965. Although Depth was not extremely significant, there appeared to be a general decrease in density with depth (Fig. 19).

Regression models indicated that a significant positive relationship with temperature could explain 13.2% of the variability in the log density of this group (Fig. 20). The only other significant single factor was the cross shelf current explaining 4.1% of the variability. When these two factors were combined in a multiple regression model, however, they only explained 14.3% of the variability. Histograms indicated that the positive relationship between density and surface temperature appeared to be strongest in samples with salinities ranging between 30 and 35 ^{o}/oo (Fig. 21). Below and above this salinity range, no distinct relationship could be seen. There did not appear to be any relationship between density and salinity itself (Fig. 20).

Bivalve Larvae

Bivalve larvae appeared to be abundant in the zooplankton of this area (5.5% of overall zooplankton density), although subsampling



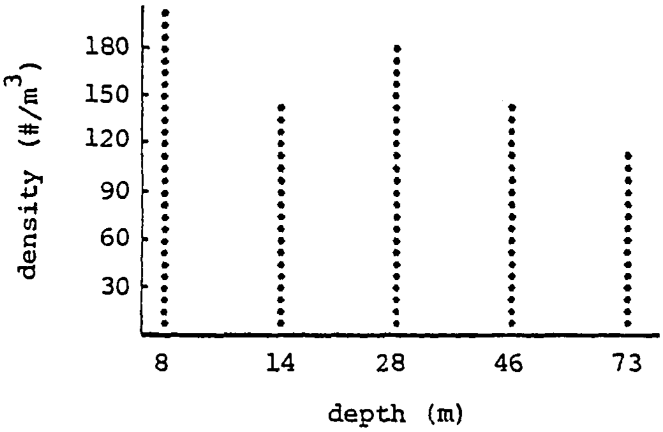


Figure 19. Mean density of larvacea for each month and bottom depth.

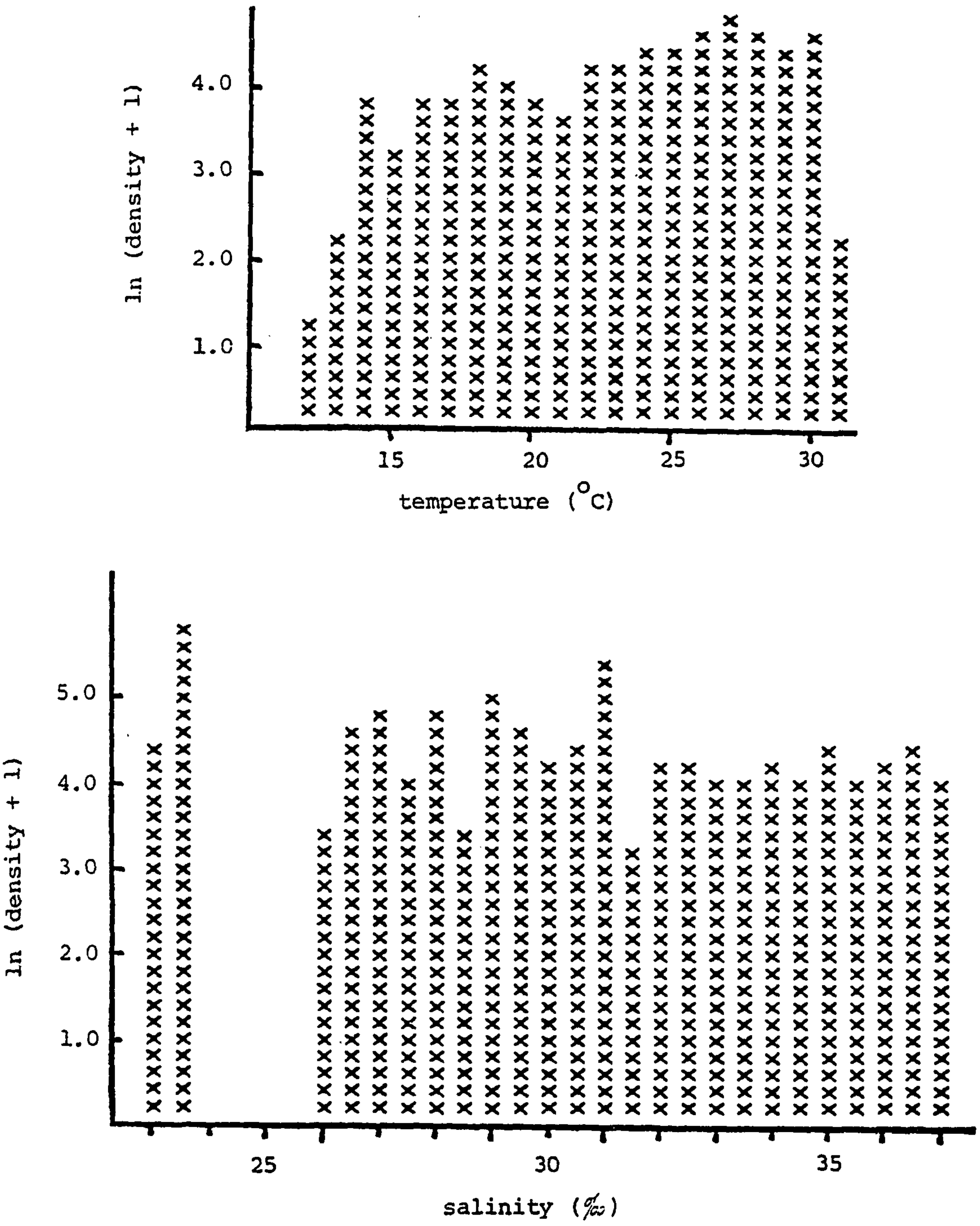


Figure 20. Density relationships with surface temperature and surface salinity for the larvacea. See legend of Figure 15 (p. 42).

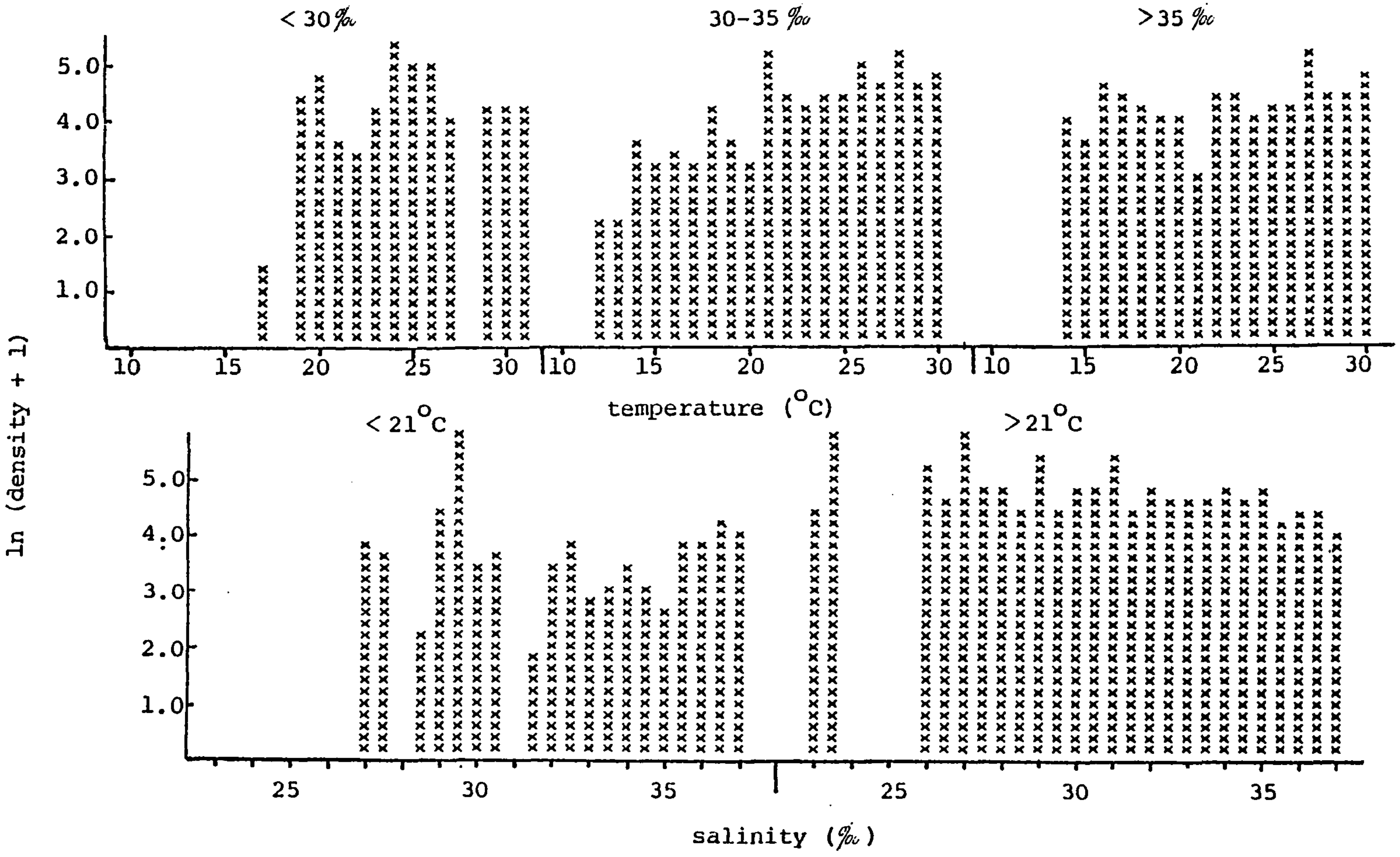


Figure 21. Densities of larvacea at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

problems with this group and other shelled organisms would indicate that no detailed analysis should be made from these data (Snider, 1975). No interactions were significant at the 1% level in the AOV results. Bottom depth was a highly significant factor (P = 0.1%) and Figure 22 shows the dramatic decrease in density with depth. The main effect of Month was significant at the 5% level (P = 4.8%) and a density peak during April was indicated (Fig. 22).

Regression results indicated that the density of this group could not be easily related to physical and chemical factors. Although a negative relationship with surface salinity appeared to be relatively important, no single factor in the analysis explained over 5% of the variability. All factors combined in a multiple regression model only explained slightly more than 10% of the variability in density. Histograms also showed no relationship between density and surface temperature and a negative relationship between density and surface salinity (Fig. 23). No obvious temperature salinity interactions were apparent.

Euconchoecia

The density of *Euconchoecia* (Ostracoda) generally appeared greatest from November to April or March. The lowest values occurred during the summer although this period of low density was not as apparent on Transect III and it occurred earlier in the year on Transects IV and V (Fig. 24). The very significant Month*Year interaction (P = 0.1%) could probably be attributed to the extremely low densities found during the summers of 1963 and 1965 (Fig. 25). Also, the large spring density peak which occurred in March in 1963 did not appear until April in 1964 and 1965. Significant density differences were also related to bottom

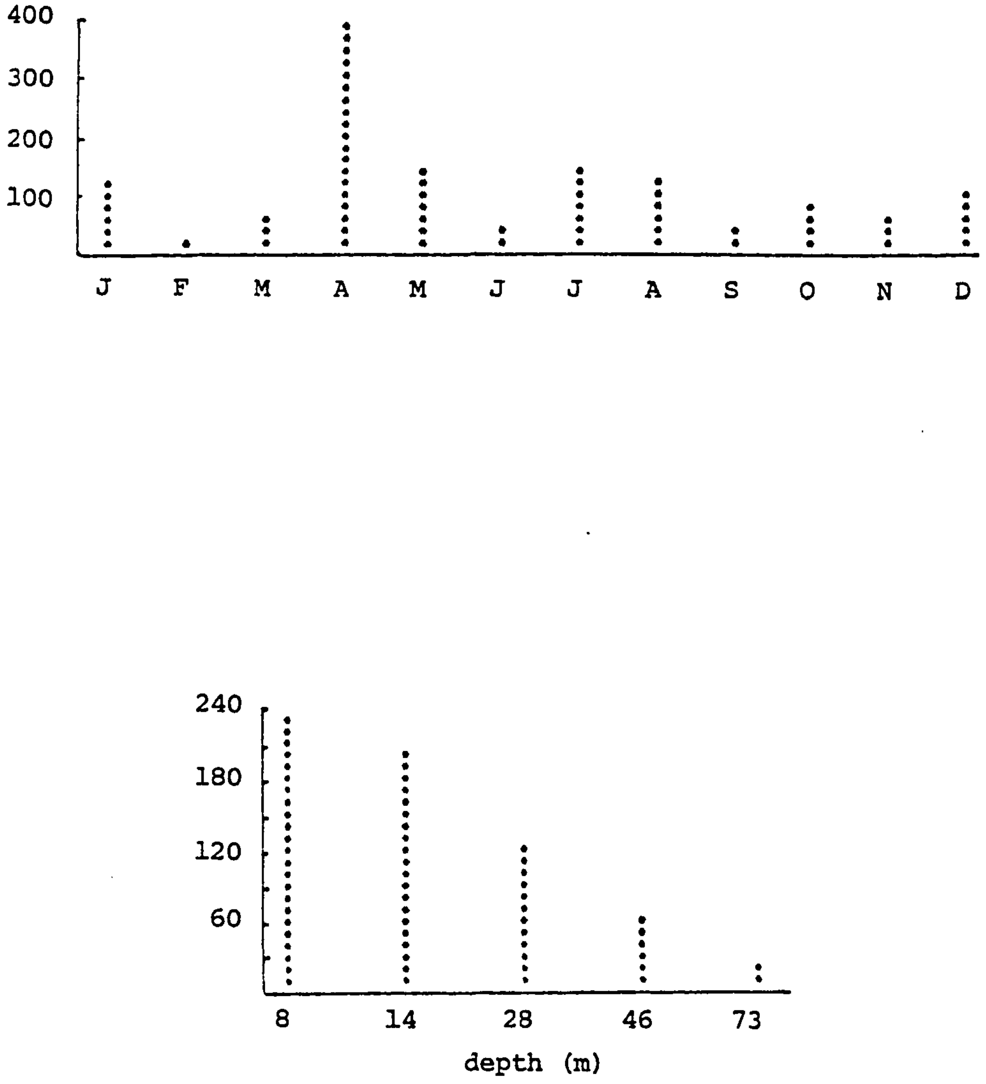


Figure 22. Mean density of bivalve larvae for each month and bottom depth.

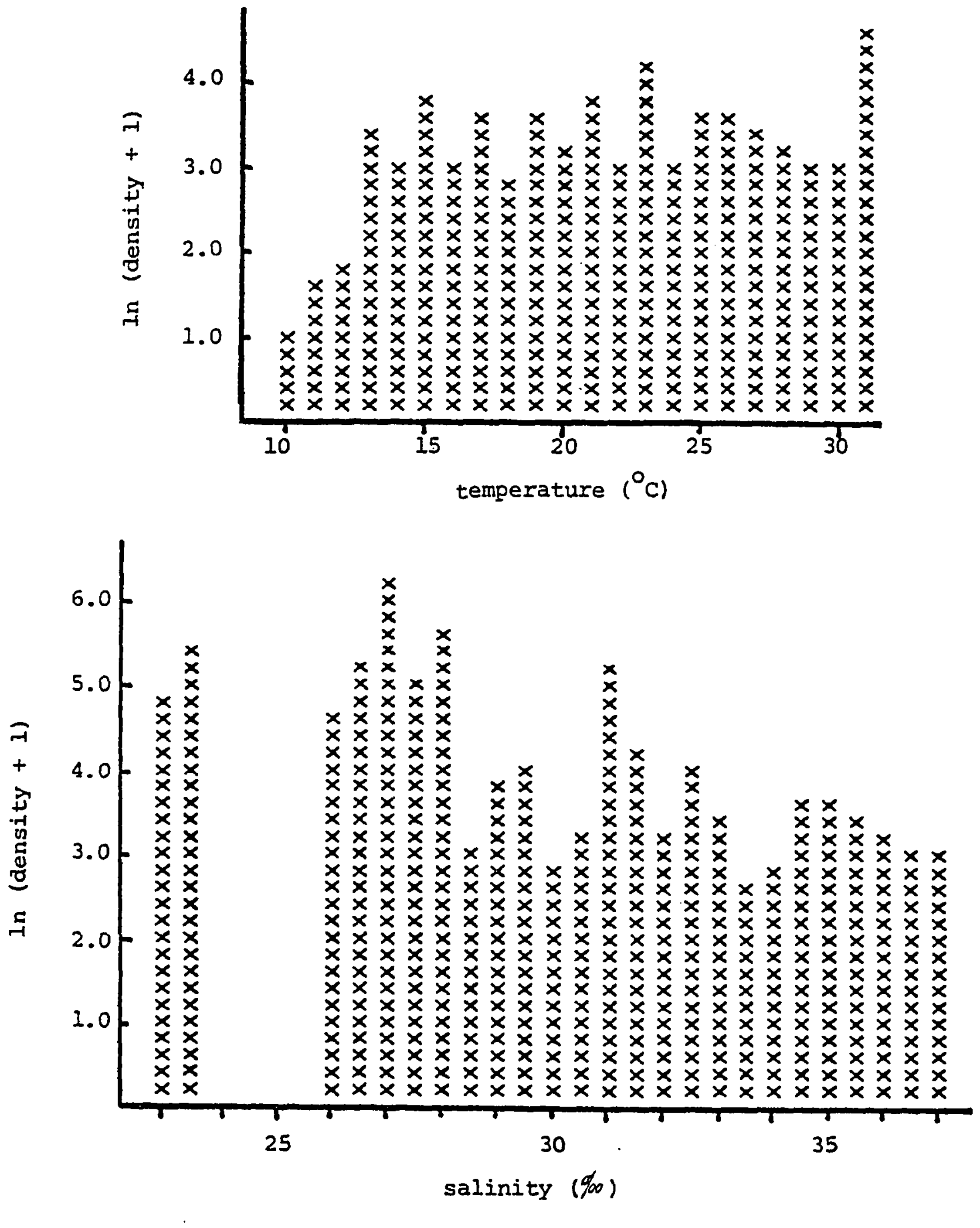


Figure 23. Density relationships with surface temperature and surface salinity for bivalve larvae. See legend of Figure 15 (p. 42).

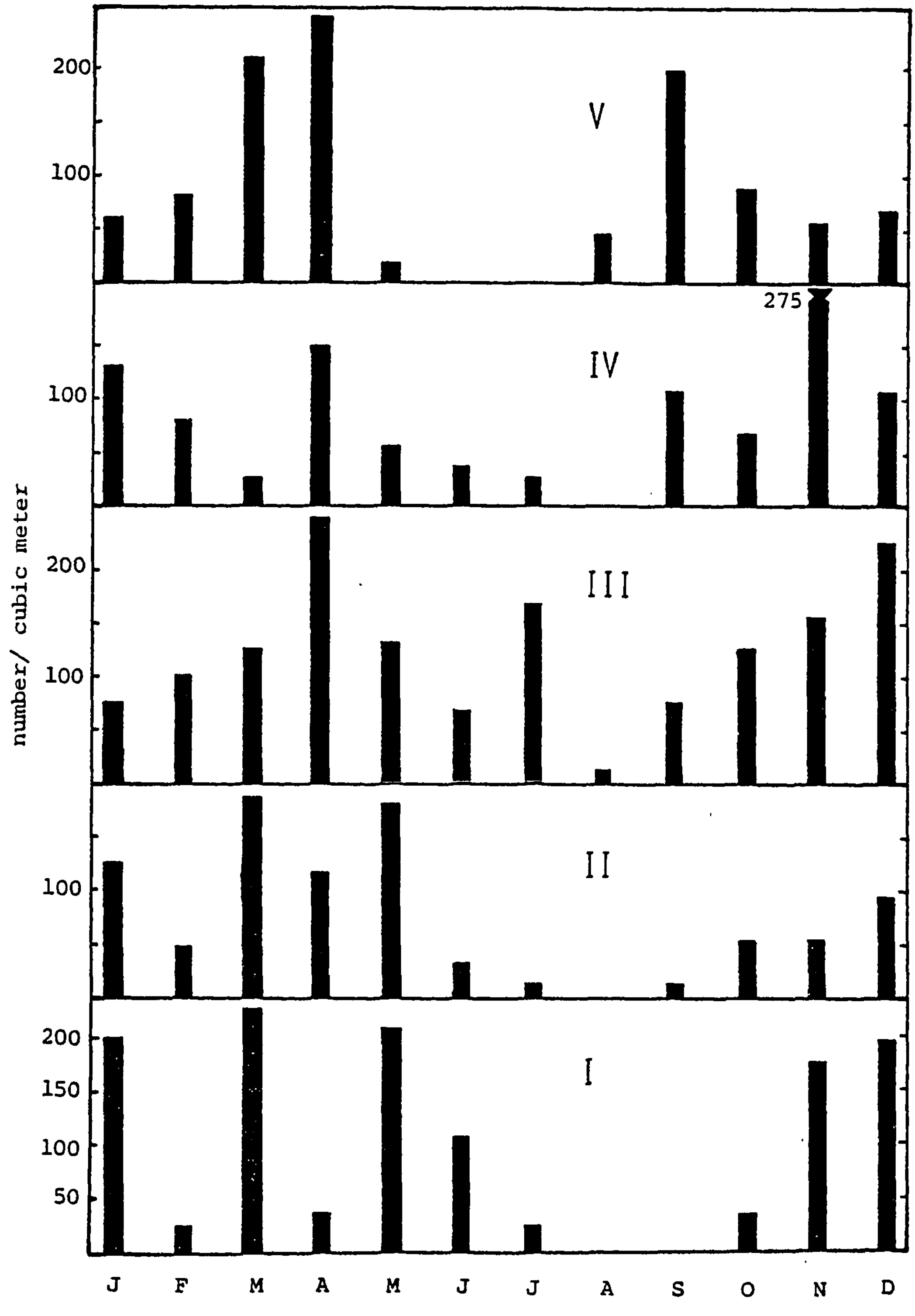


Figure 24. Mean monthly densities of *Euconchoecia* on each transect. Values are averaged over bottom depths and years.

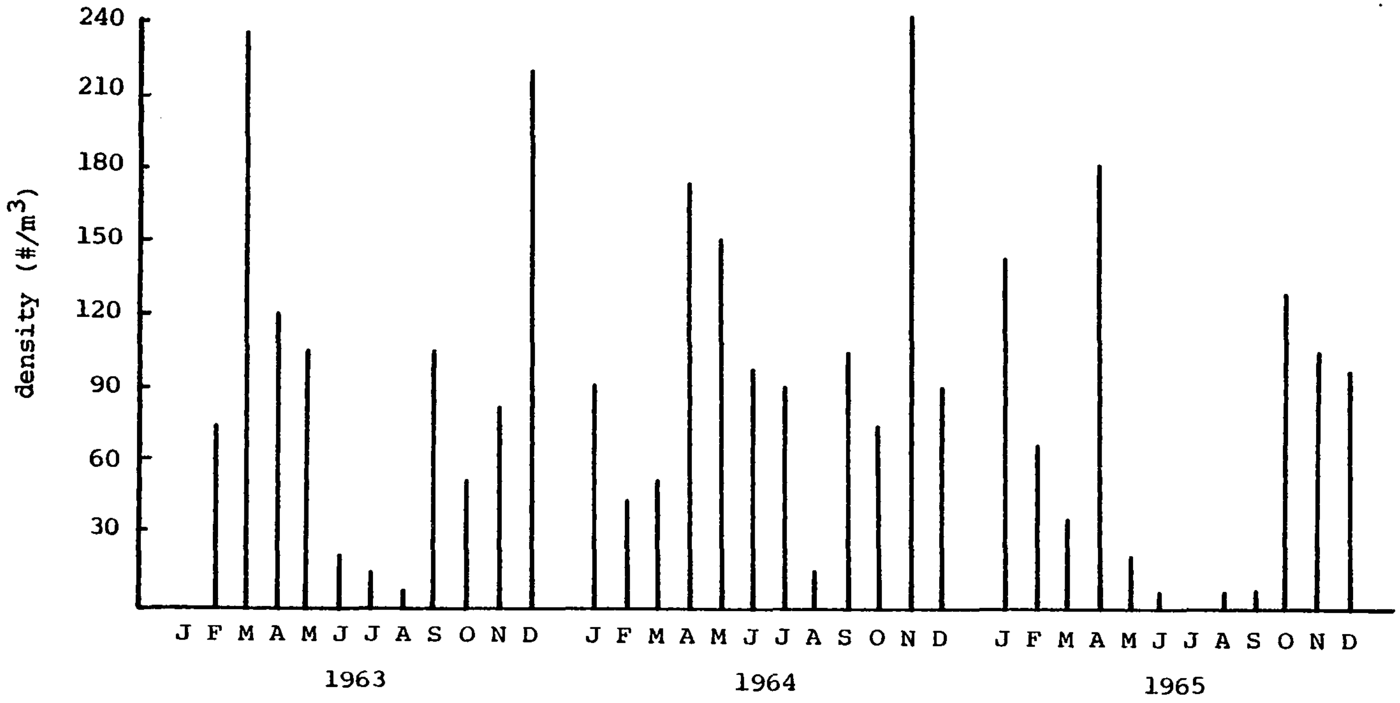


Figure 25. Mean monthly densities of *Euconchoecia* over the entire sampling area for the three years of the study. Values are averaged over transects and bottom depths.

depth. Very low values were found at the 8 and 14 m stations and the greatest density was found at stations with a depth of 46 m (Fig. 26). The AOCOV used to remove the effect of sampling time did not alter these results.

Regression models indicated a positive relationship with salinity which accounted for 11.5% of the variability in the density of *Euconchoecia*. Salinity, combined with surface temperature and the previous month's Mississippi runoff in a multiple regression model, accounted for approximately 15% of the variability. The relationship between the density of this genus and surface salinity and temperature is shown in Figure 27. The optimum temperature appeared to be around 22 or 23°C with densities decreasing at higher and lower temperatures. This probably accounts for the poor linear fit with temperature in the regression models. This type of relationship with surface temperature was common for organisms examined in this study. When temperature salinity interactions were examined (Fig. 28), the positive relationship between density and salinity appeared most pronounced at temperatures below 21°C.

Chaetognaths

A spring density peak in April and May appeared consistently over depth although this peak was not large at the 14 m stations (Fig. 29). Elevated densities in the fall and early winter were also present at all depths although more pronounced at the shallower stations. January and February were low density months at all depths. This general seasonal distribution appeared in 1964 and 1965. The 1963 samples indicated no large seasonal peaks of density. Overall densities were highest in 1964 (Fig. 30). The mean density response at different

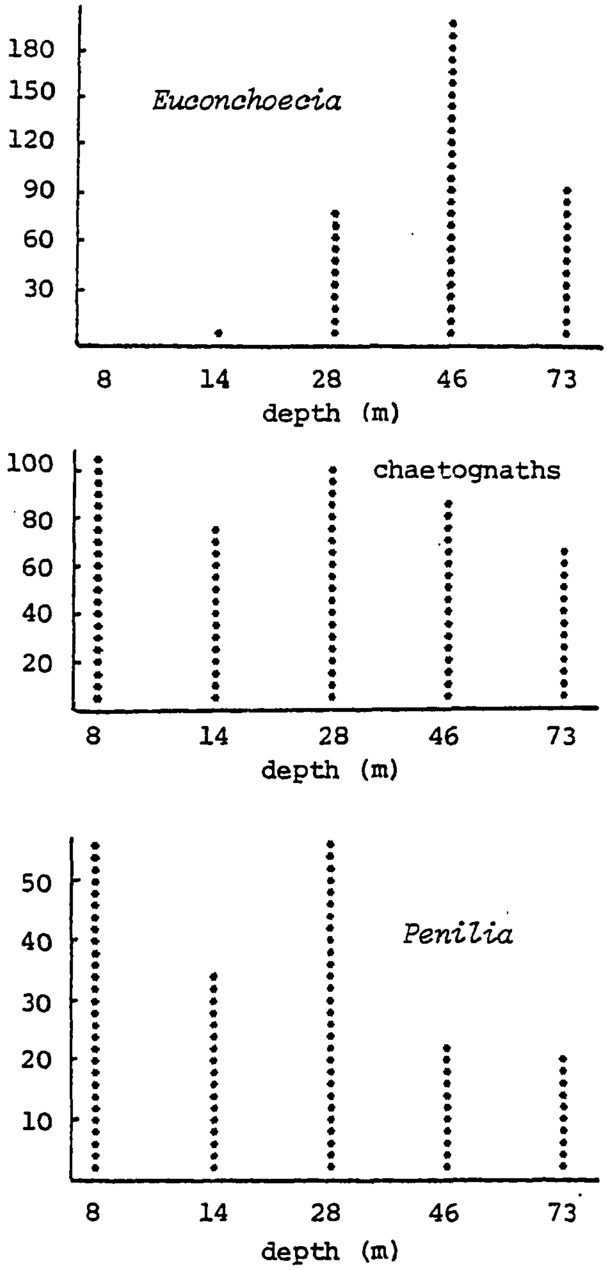


Figure 26. Mean densities of *Euconchoecia*, chaetognaths, and *Penilia* at each bottom depth.

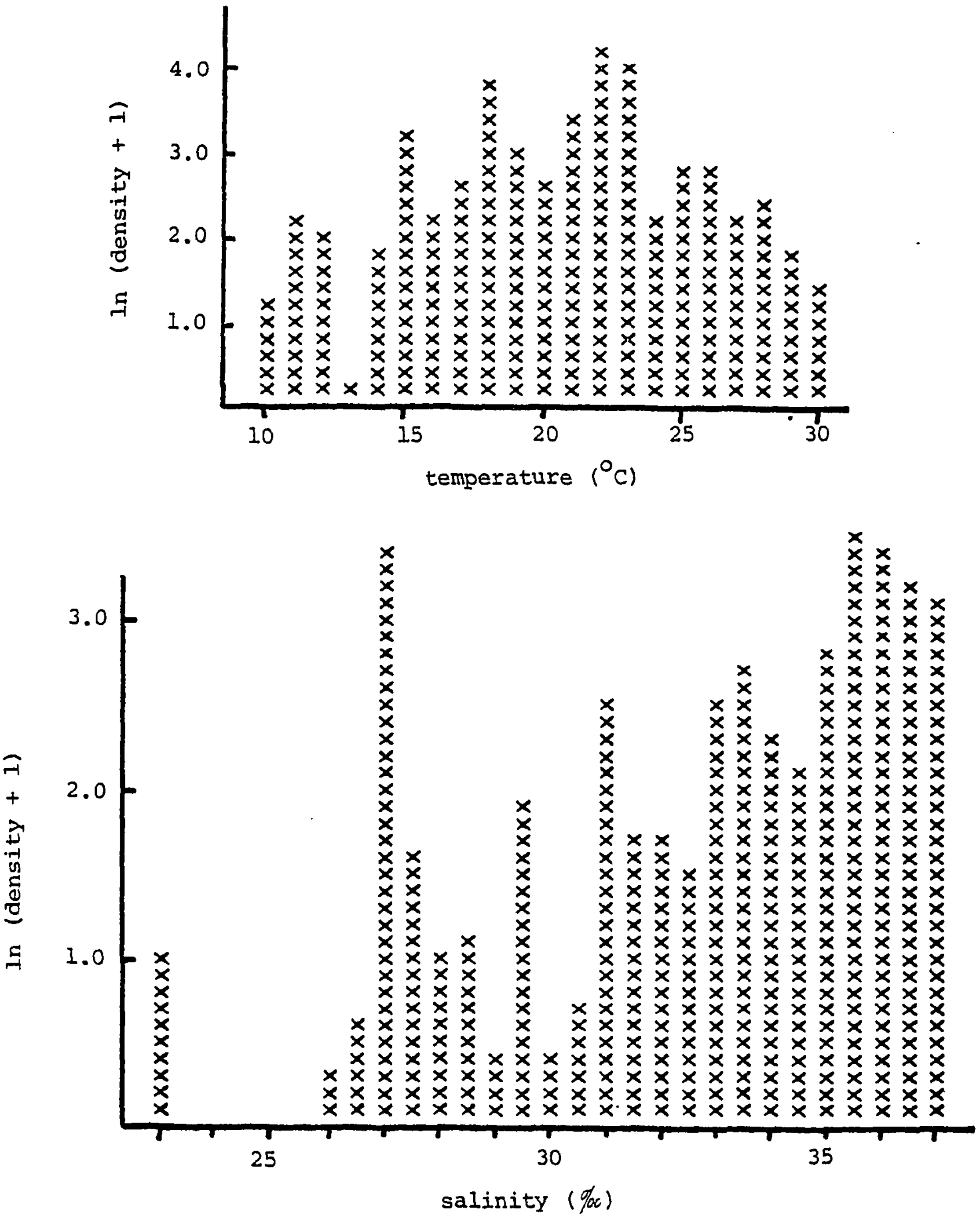


Figure 27. Density relationships with surface temperature and surface salinity for *Euconchoecia*. See legend of Figure 15 (p. 42).

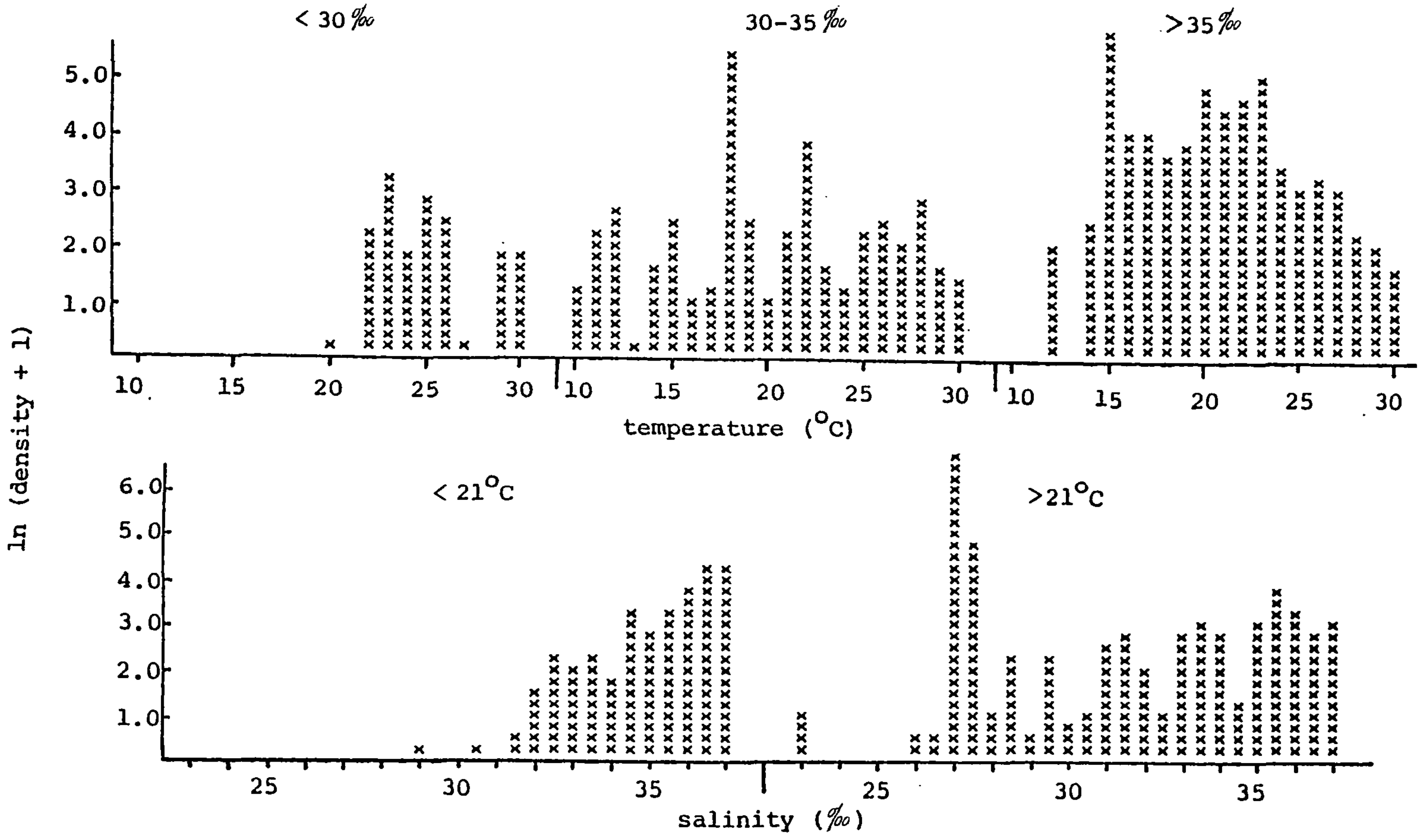


Figure 28. Densities of *Euconchoecia* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

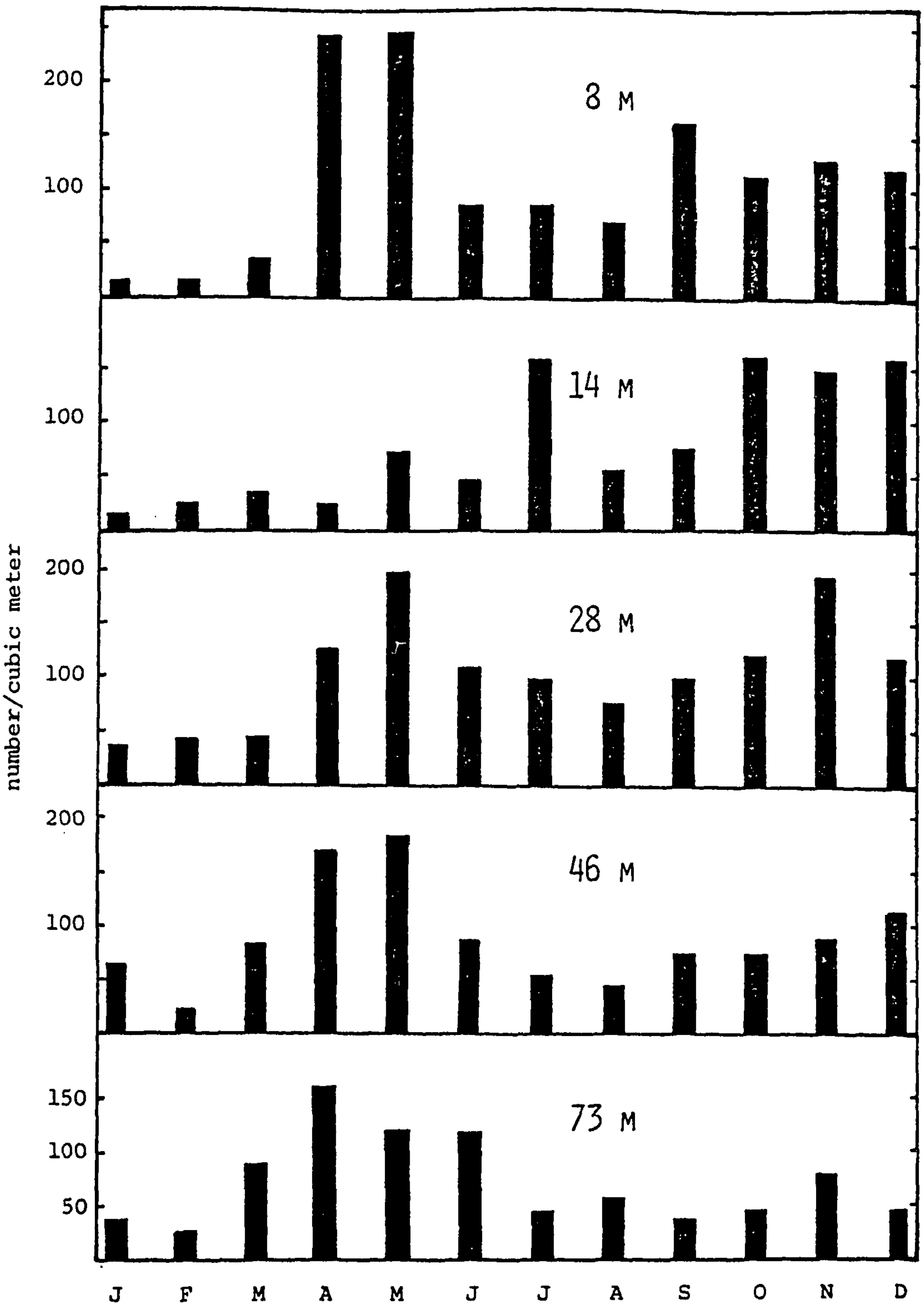


Figure 29. Mean monthly densities of chaetognaths at each bottom depth sampled. Values are averaged over transects and years.

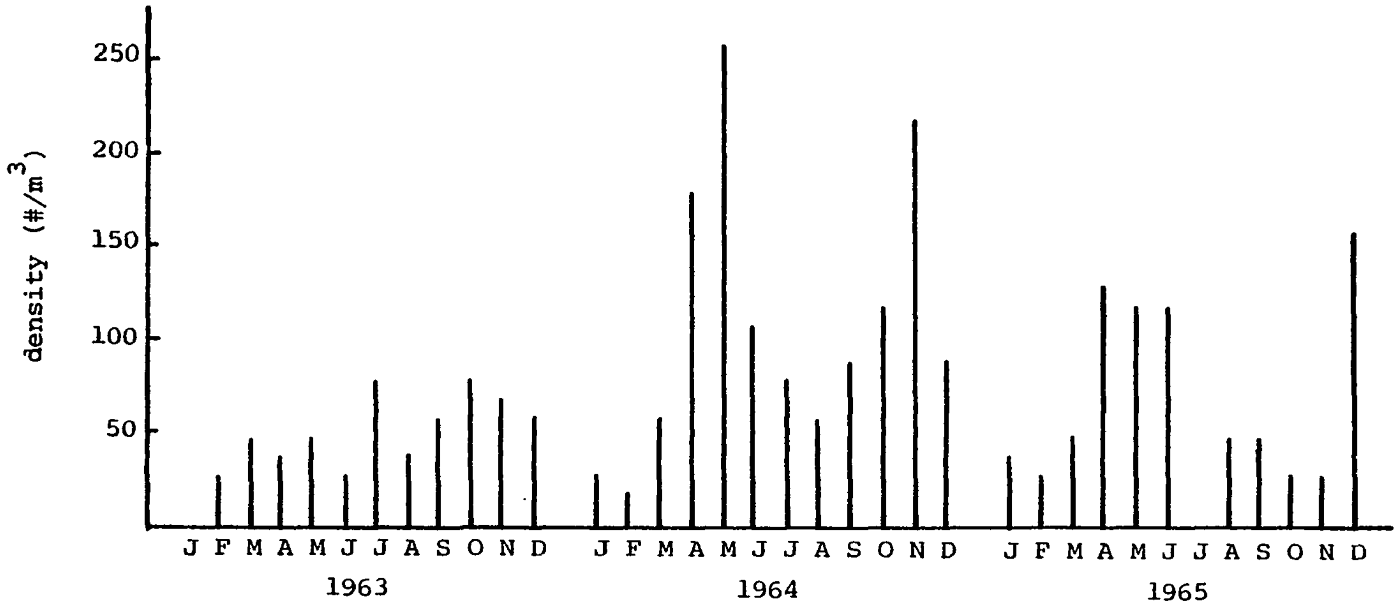


Figure 30. Mean monthly densities of chaetognaths over the entire sampling area for the three years of the study. Values are averaged over transects and bottom depths.

transects was similar at the 14 and 46 m stations, showing generally high values on Transect III (Fig. 31). This differed from the profiles at the 28 and 73 m stations where the greatest densities occurred on Transects I and IV. The high densities on Transect IV could be related to the time of sampling. The stations with the highest densities (Stations 2, 3, and 54) had large percentages of night and twilight samples. The analysis of covariance however indicated that overall, sampling time was not a significant factor affecting this Depth*Transect interaction.

The regression models indicated that no physical or chemical factors explained any great portion of the variability in the density of the chaetognaths. All of the factors combined in a multiple regression model only explained approximately 6% of the variability. Although no apparent relationship between density and surface salinity could be seen in the histograms, there did appear to be a positive relationship between density and surface temperature up to about 20-23°C (Fig. 32). Temperature salinity interactions did not appear significant.

Gastropod Larvae

Seasonally, gastropod larvae appeared to be most abundant during the spring and late summer with density peaks occurring in April and August. The intermediate depth stations of 28 and 46 m were higher in density than the 14 and 73 m stations (Fig. 33). Extremely high mean densities were present at the 8 m station on Transect I and the 46 m station on Transect V. The Depth*Transect interaction was highly significant in the AOV.

Simple regressions with physical and chemical factors indicated that 14.5% of the variability in the density of this group could be

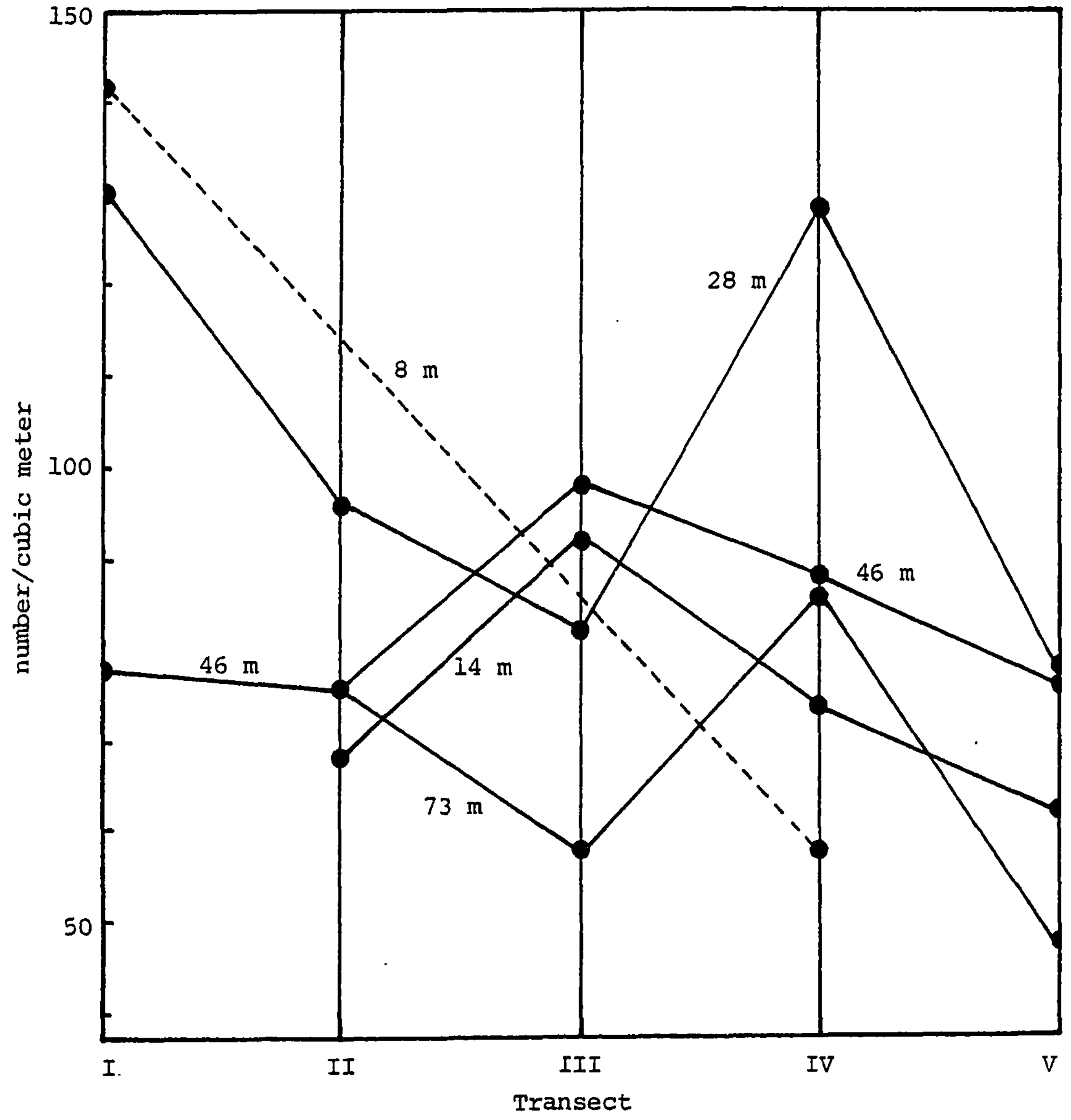


Figure 31. Mean density of chaetognaths at each sampling station. Values are averaged over months and years. Graphed as in Figure 6 (p. 28).

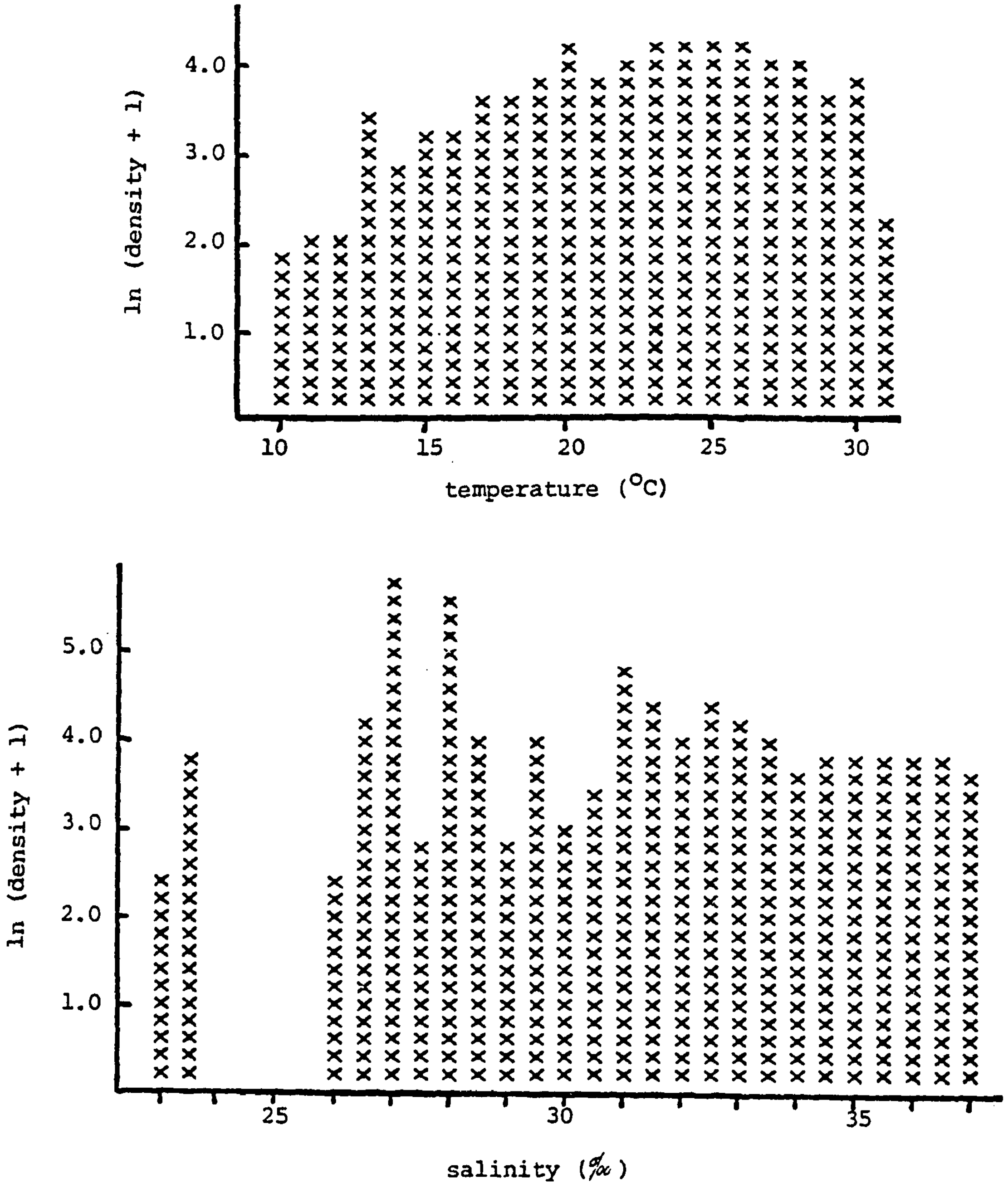


Figure 32. Density relationships with surface temperature and surface salinity for chaetognaths. See legend of Figure 15 (p. 42).

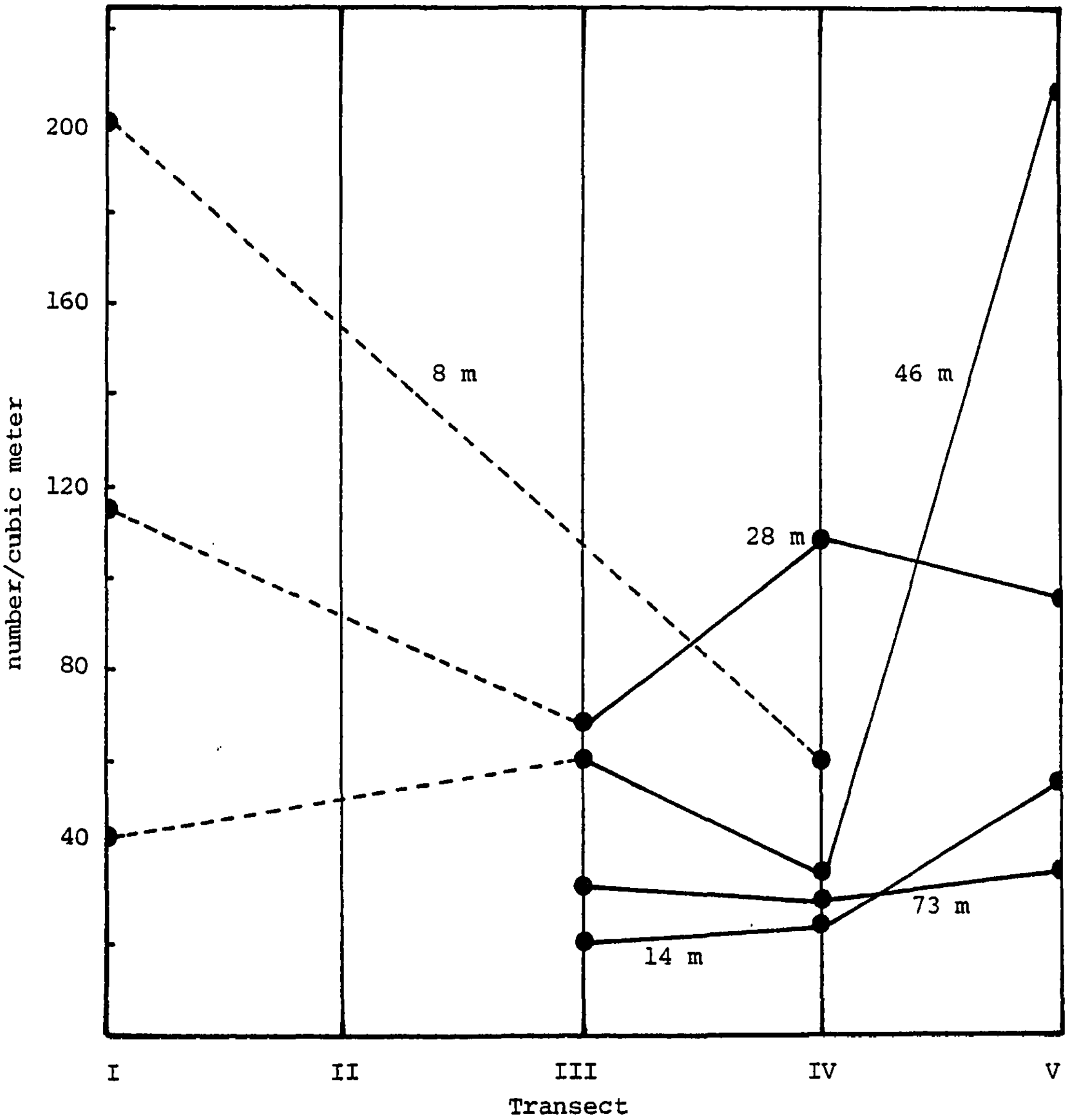


Figure 33. Mean density of gastropod larvae at each sampling station. Values are averaged over months and years. No counts were made on samples from Transect II. Graphed as in Figure 6 (p. 28).

explained by a positive relationship with surface temperature. Mississippi runoff and the cross shelf current also appeared to be significant factors. These three factors along with the local runoff variable explained approximately 21% of the variability in a multiple regression model. The relationship between density and surface temperature is shown in Figure 34. The positive trend was not as apparent when only samples with salinities lower than 30 $^{o}/oo$ were examined. Salinity itself, however, did not appear to be strongly related to density.

Penilia

The cladoceran *Penilia* generally appeared in the sampling area between April and August. It was found only in very small numbers during other parts of the year. The overall density was very low in 1965 and the month of peak abundance also varied depending upon the year (Fig. 35). In 1963 density peaks occurred in April, May, and August. In 1964 only one large density peak occurred in June. Spatially, densities were greatest at the 8 m stations although very high density values were recorded at the 28 m stations on Transects I and IV (Fig. 36). The 46 m station on Transect IV also had a high mean density value. The absence of samples from 1965 (a very low density year for *Penilia*) on Transect IV along with the preponderance of night samples at the 28 and 46 m stations on this transect probably contributed to these high density values. The analysis of covariance, however, did not appear to change the basic results of the AOV.

Surface temperature and the cross shelf current appeared to be the most significant single factors in the simple regression analysis, explaining 15.2 and 11.6% of the variability, respectively. Combined

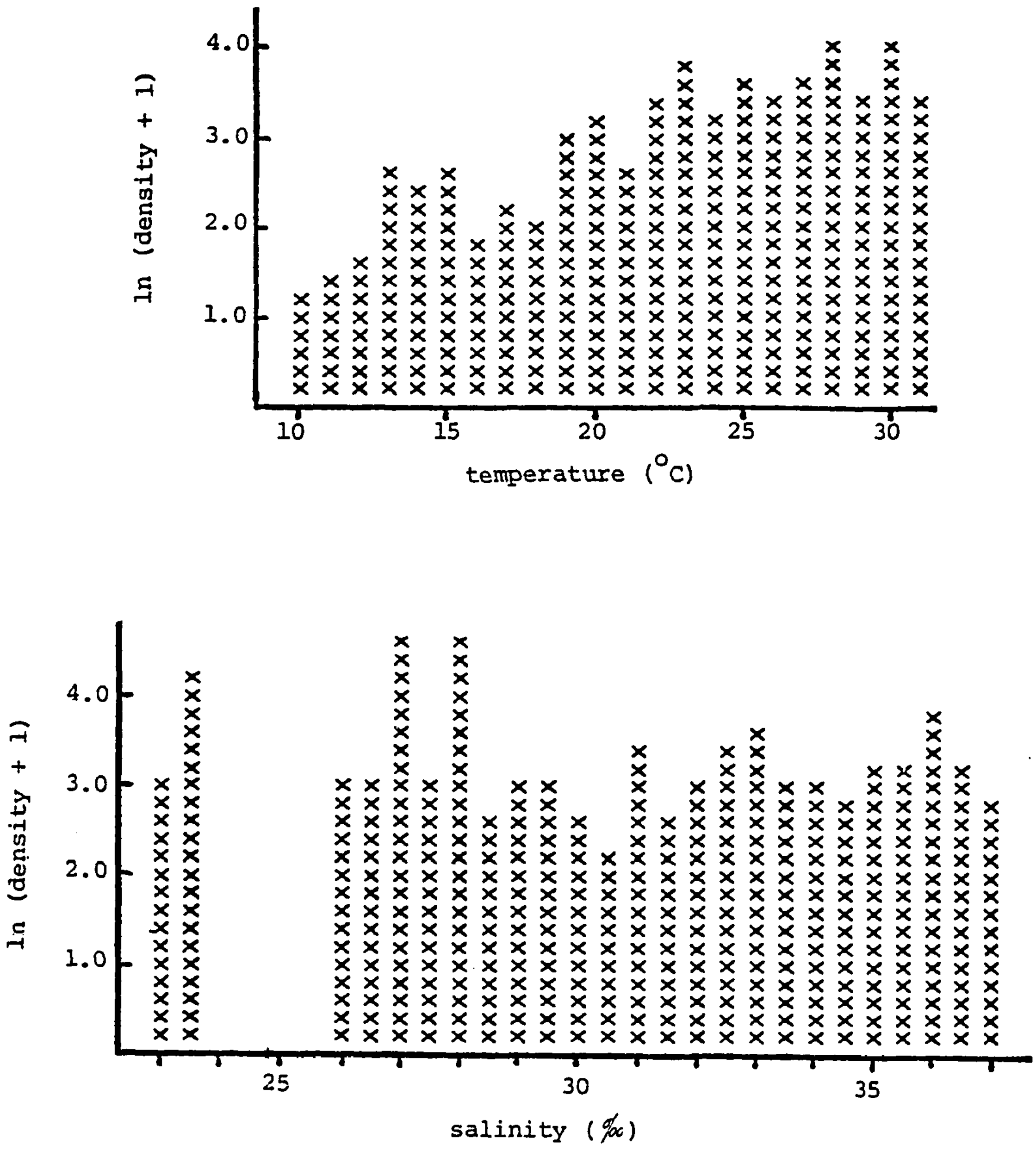


Figure 34. Density relationships with surface temperature and surface salinity for gastropod larvae. See legend of Figure 15 (p.42).

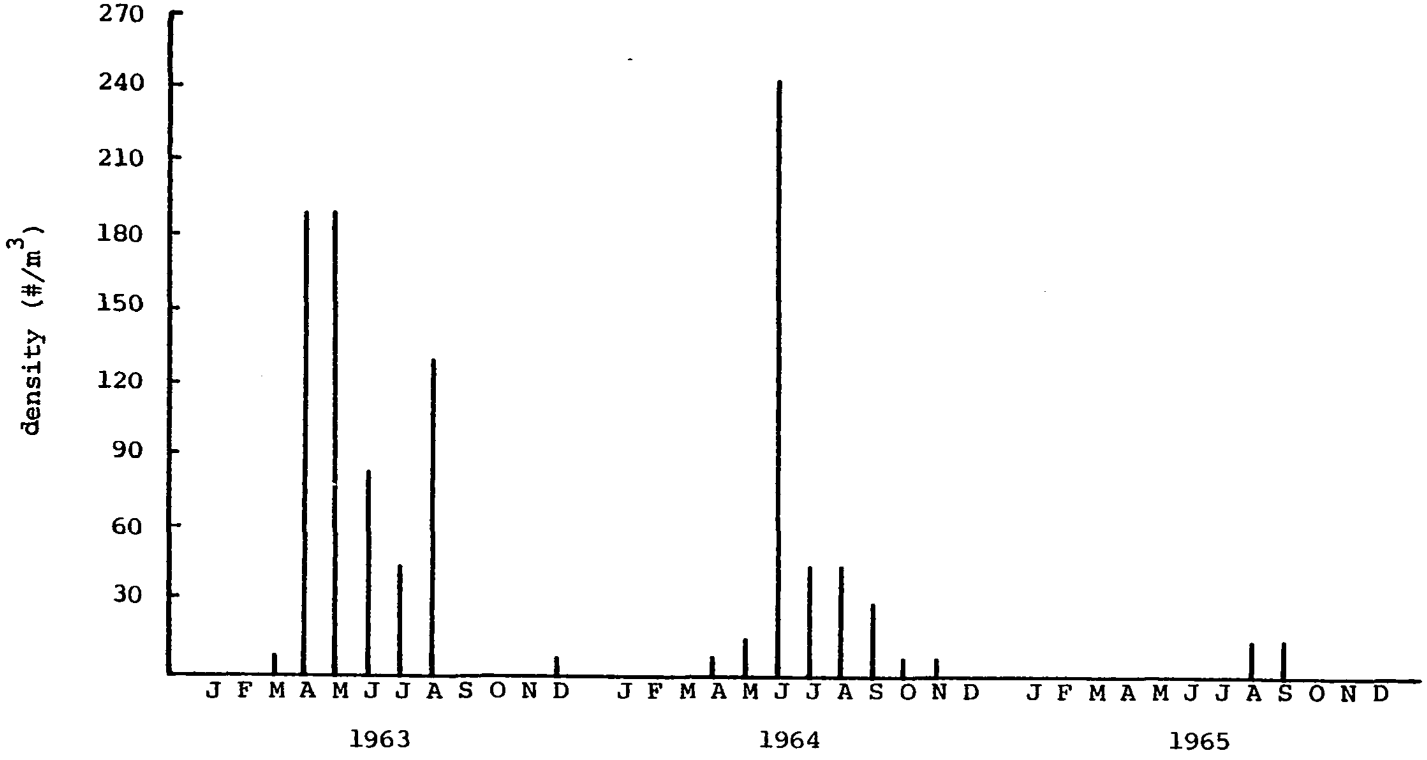


Figure 35. Mean monthly densities of *Penilia* over the entire sampling area for the three years of the study. Values are averaged over transects and bottom depths.

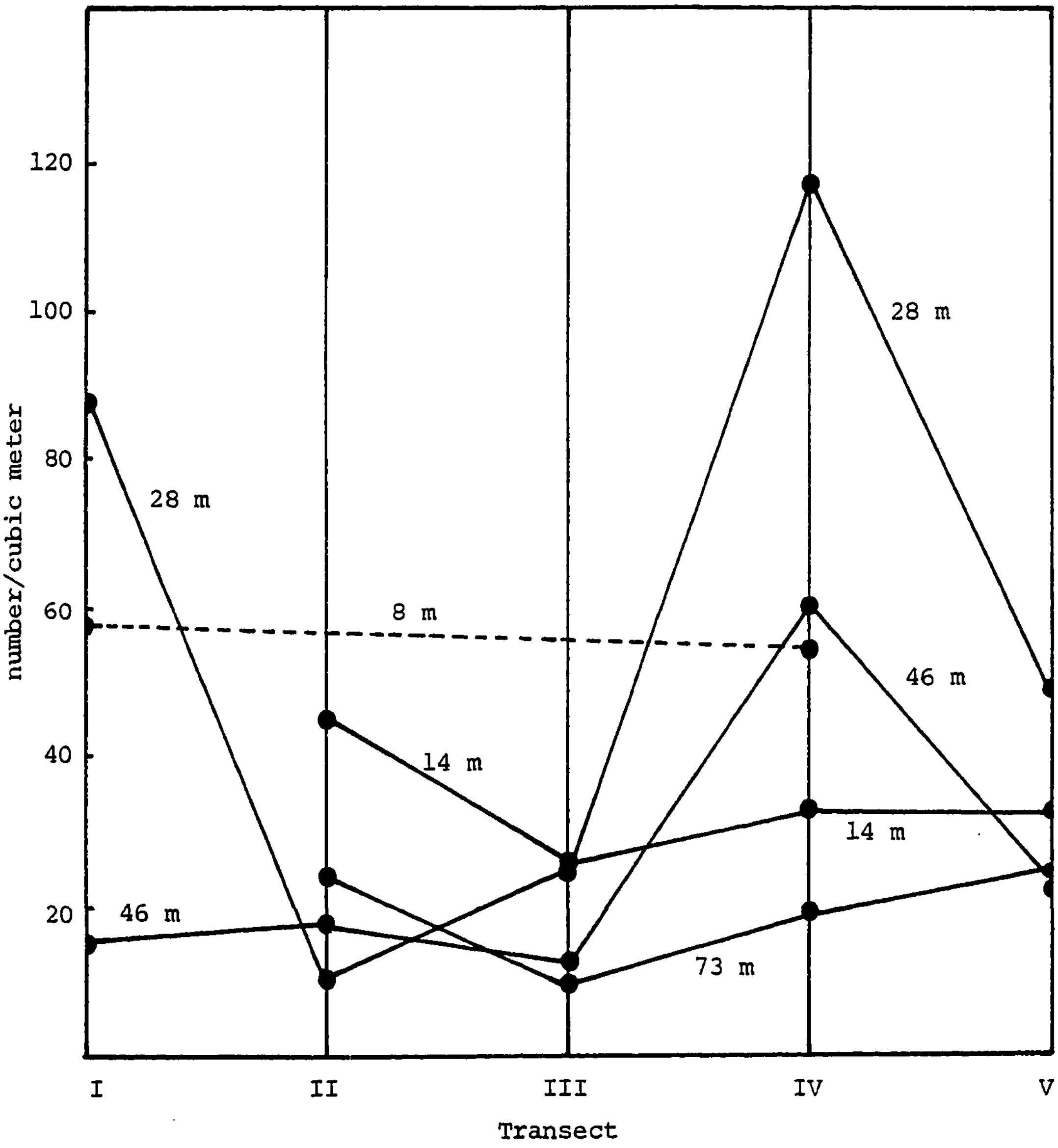


Figure 36. Mean density of *Penilia* at each sampling station. Values are averaged over months and years. Graphed as in Figure 6 (p. 28).

in a multiple regression model these two factors explained 21% of the variability. None of the other factors that were examined appeared to be important. Up to 28°C the relationship between density and temperature seemed to be positive (Fig. 37) and this was exhibited by the overall positive slope in the regression analysis. Above 28°C however there appeared to be a negative relationship with temperature. There appeared to be little relationship between density and salinity (Fig. 37).

Medusae

This group included a wide variety of different organisms and often included unidentifiable jelly-like structures. The AOV revealed few highly significant spatial or temporal effects for the group. The only effect that was significant at the 1% level was the main effect of Years. This appeared to be due to low density values in the year 1965.

The most significant single factor in the regression analysis, surface salinity, only explained 3.2% of the variability in the density of the medusae. All of the physical factors combined in a multiple regression model only explained 7.6% of the variability. The relationships between density and surface temperature and salinity are shown in Figure 38.

Copepods

The variability in copepod densities (Fig. 39) appeared similar to that of the zooplankton as a whole. The effect of Month, however, was not significant in the analysis of variance due to the highly significant Month*Year interaction, the term used to test for monthly

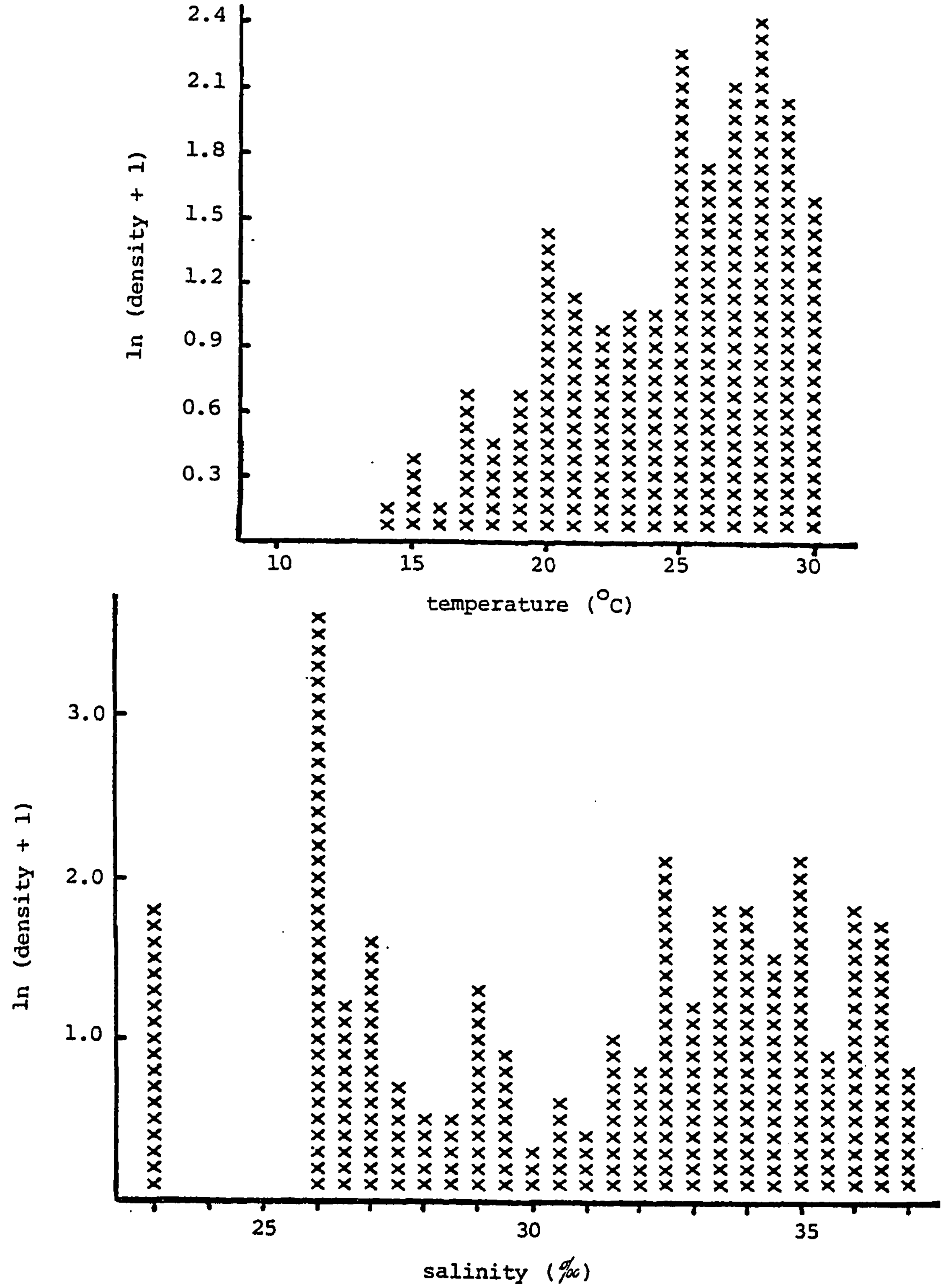


Figure 37. Density relationships with surface temperature and surface salinity for *Penilia*. See legend of Figure 15 (p. 42).

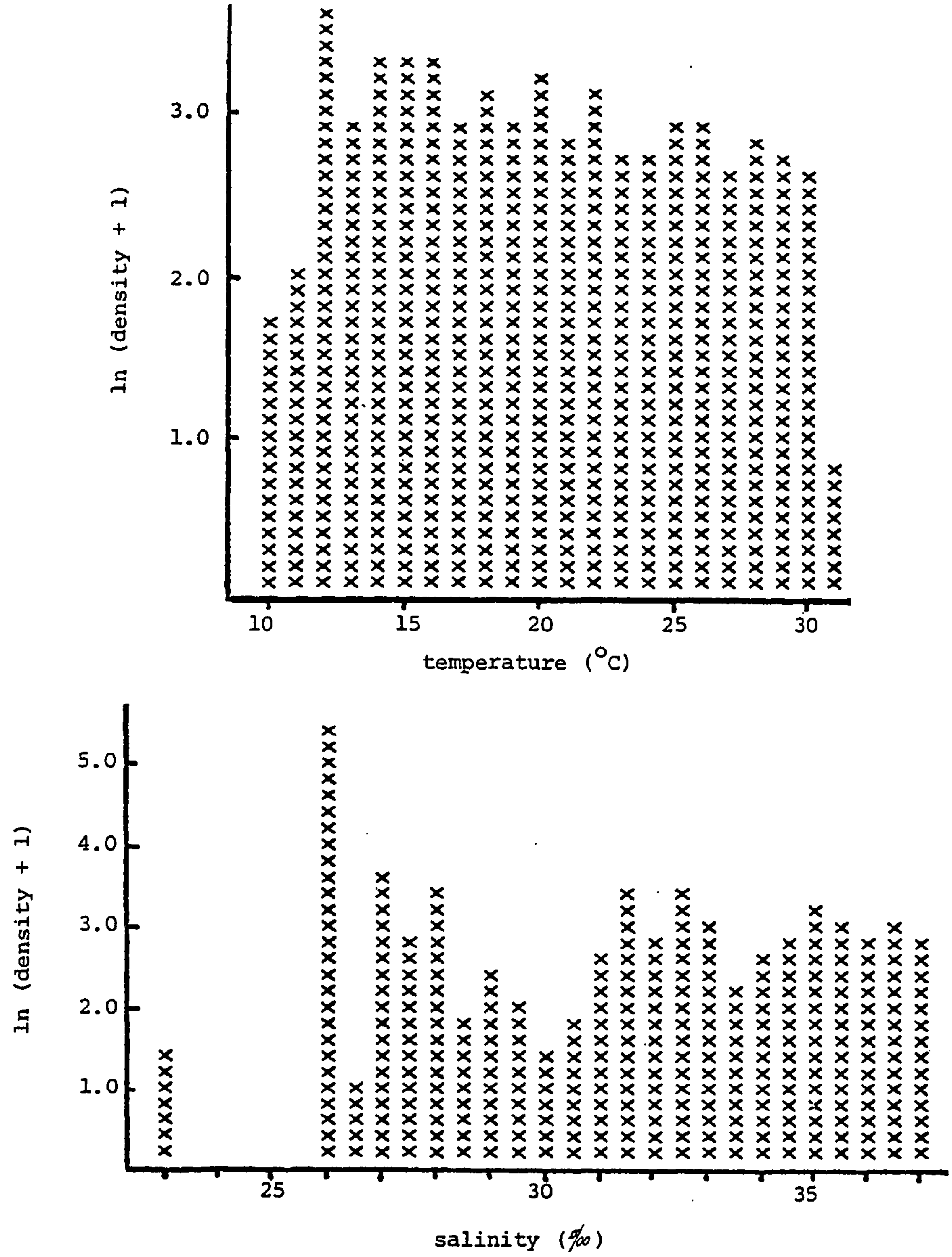


Figure 38. Density relationships with surface temperature and surface salinity for medusae. See legend of Figure 15 (p. 42).

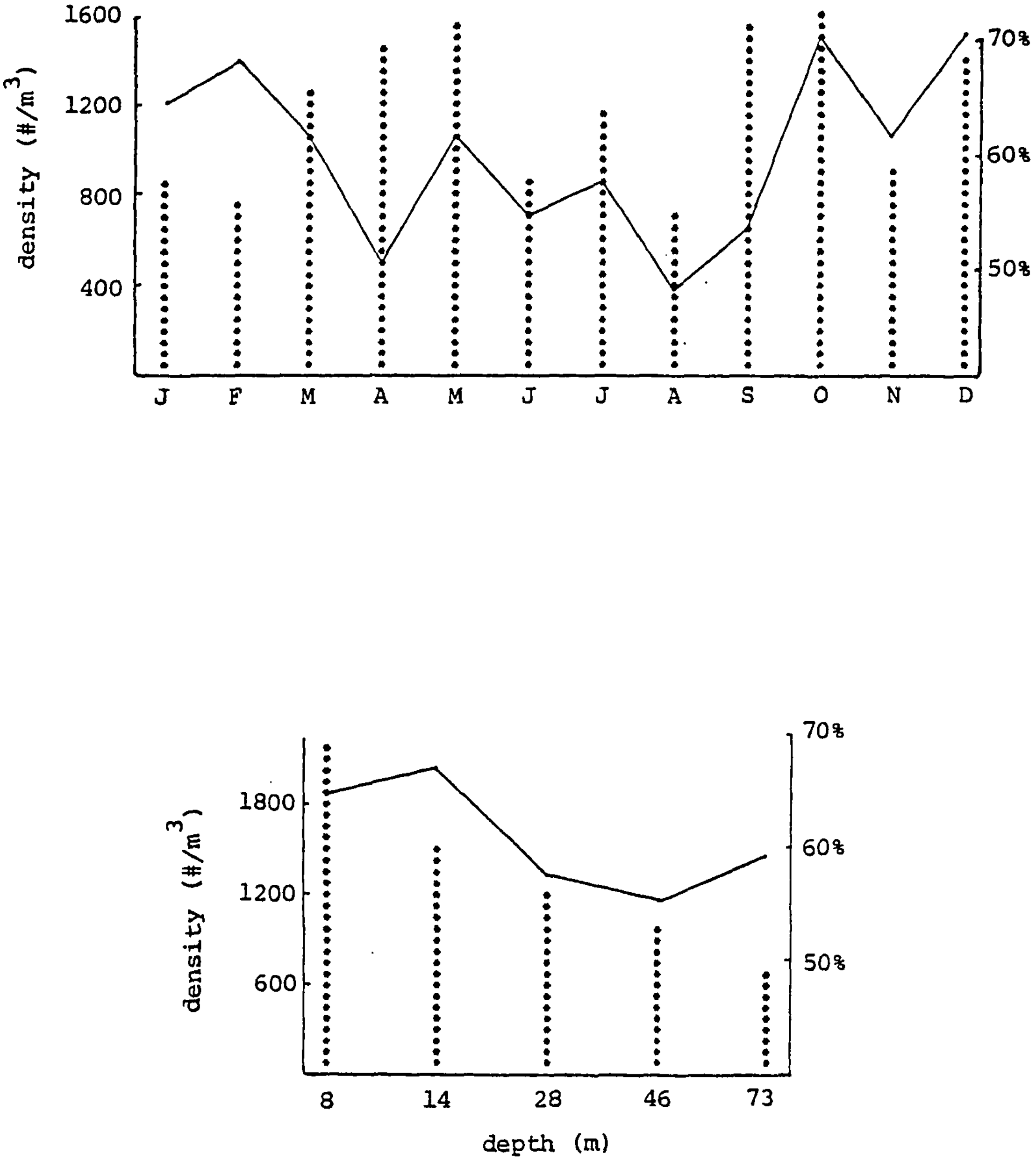


Figure 39. Mean density of copepods (vertical bars) and their percentage of the zooplankton (solid line) for each month and bottom depth.

variability. Although monthly variability generally appeared similar over the 3 years, overall density peaks in 1964 were relatively large in relation to the other years (Fig. 40). The effect of depth was significant and the decrease in density with depth is also shown in Figure 39. The Transect effect was significant in the AOV until the effect of sampling time was removed through the analysis of covariance.

The percentage of the zooplankton made up by the copepods (calculated from mean densities) was generally greatest in the winter with maximums in October (70.7%) and December (70.8%) and lowest in the spring and summer with a minimum during August (48.0%) (Fig. 39). This percentage also appeared to change with the depth of the station. The shallowest stations had the highest values (64.7 and 64.2%) and the values at the deeper stations ranged between 55.8 and 59.3%. No relationship between the percent of copepods and transect was apparent.

The percentage of the copepods that were mature females, mature males, and copepodids is shown over months, depths, and transects in Figure 41. Copepodids generally made up around 50% of the copepods while adult females were slightly less abundant. Males contributed a relatively small percentage. The seasonal variability did not appear high in these figures although the percentage of copepodids was generally great before and during overall copepod density peaks, indicating their relationship with increasing population densities. Changes in these percentages with depth indicated that copepodids were relatively abundant inshore. Their percentage decreased and the percent of adult females increased at the deeper stations. At the 73 m stations their percentages were similar with copepodids and females making up 42.9 and

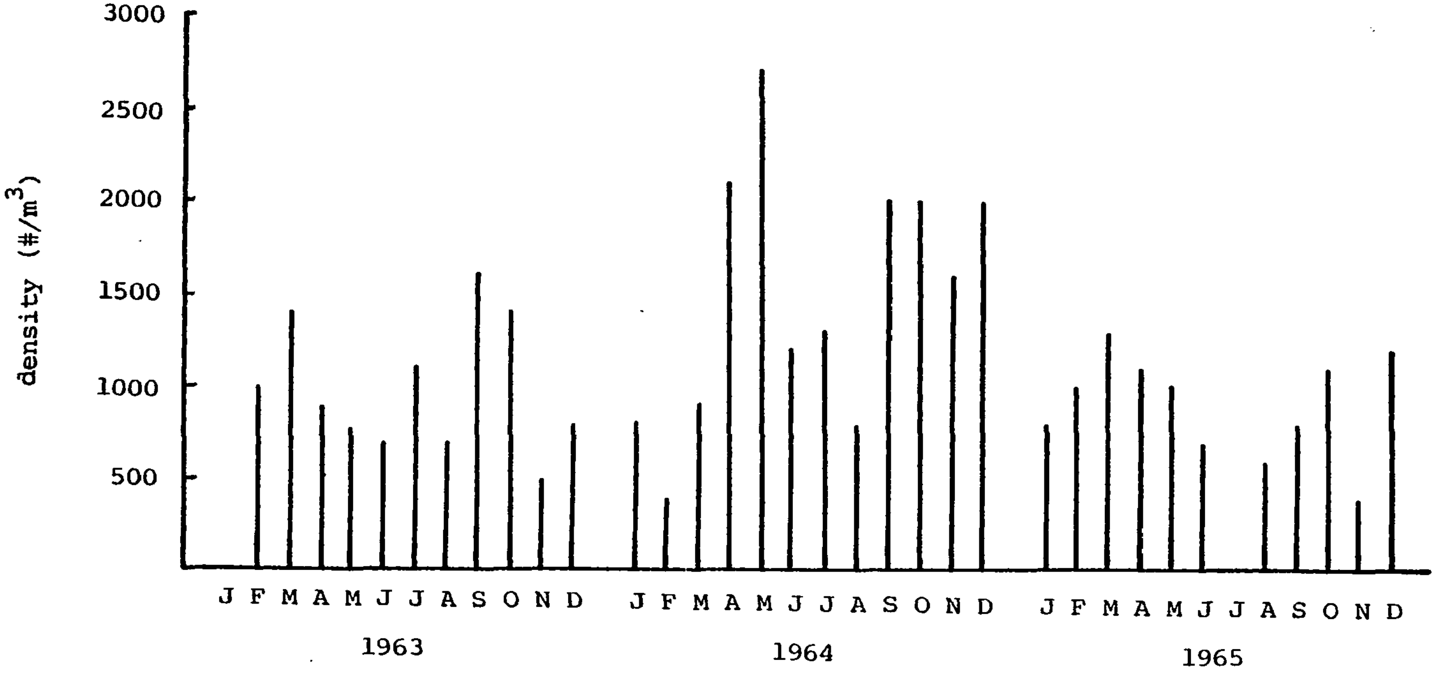


Figure 40. Mean monthly densities of copepods over the entire sampling area for the three years of the study. Values are averaged over transects and bottom depths.

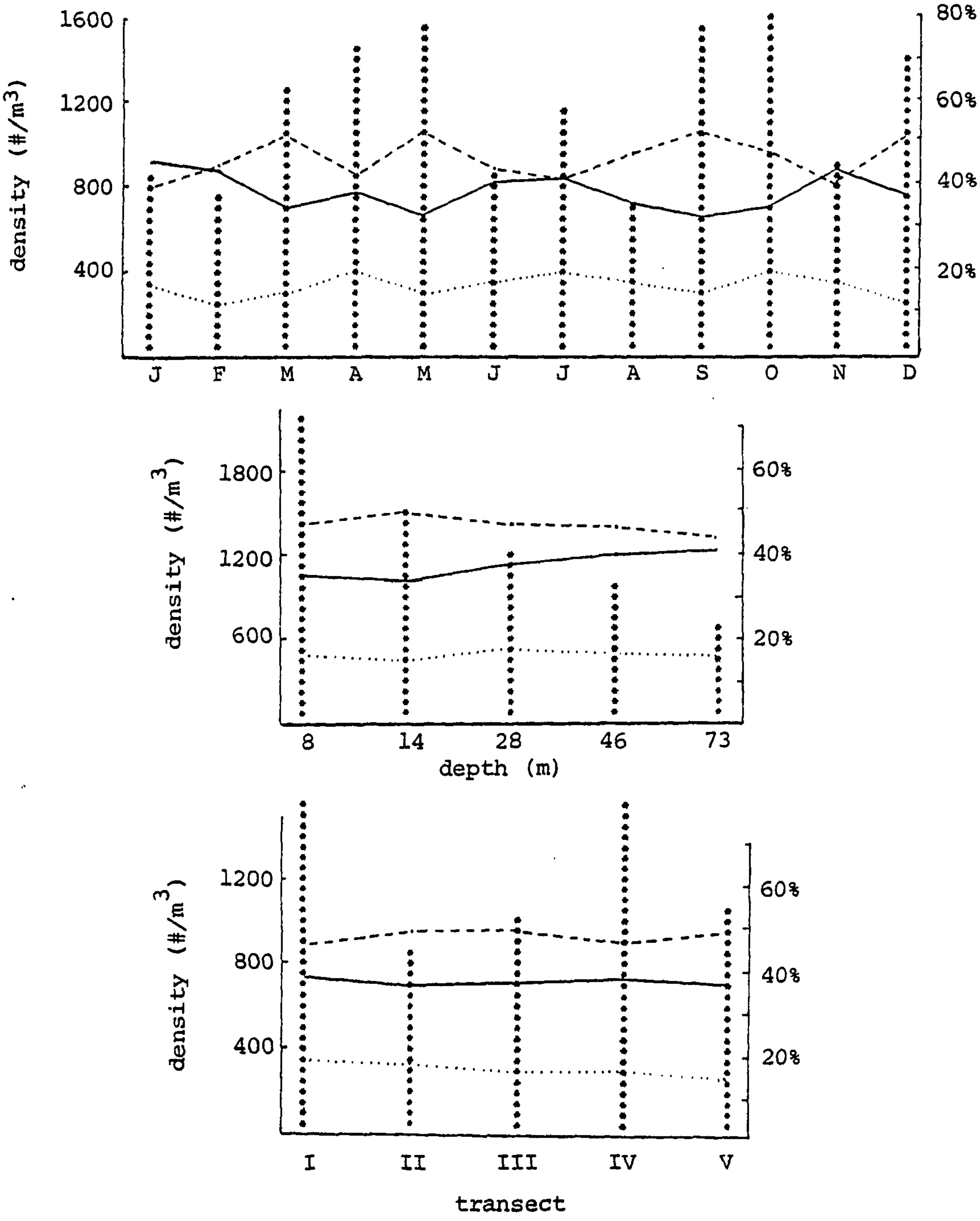


Figure 41. Percentage of adult female, adult male, and immature copepods for each month, bottom depth, and transect. Females are represented by the solid line, males by the dotted line, and immature forms by the dashed line. Bars represent mean copepod densities.

40.5% of the copepods, respectively. The percentage of males did not appear to vary over depth. Percentages over transects for all categories were remarkably stable.

A similar graphical method was used to examine the percentages of calanoids, cyclopoids and harpacticoids in the copepods (Fig. 42). Sexes and developmental stages were combined for these figures. Overall monthly variability in these percentages did not appear high. Calanoids were by far the dominant group with the highest values in the winter and spring reaching 83.1% of the copepods in May. The lowest percentage of calanoids occurred during July (65.4%). The cyclopoid percentages were generally the inverse of the calanoids with a low value of 14.4% in May and a high value of 31.7% in August. Harpacticoids made up only a small percentage of the copepods.

The percent of calanoids and cyclopoids showed a distinct trend with depth. The percent of calanoids decreased with depth from 85% at 8 m to 61.6% at 73 m, while the percent of cyclopoids increased with depth from 11.4% at 8 m to 36.4% at 73 m. The percentage of harpacticoids, although small, also appeared to change with depth decreasing from 3.7% inshore to 2.1% offshore. Again, the variability over transects did not appear to be large.

The simple regression models indicated that a significant negative relationship with salinity (Fig. 43) could explain 7.3% of the variability in the log of copepod densities. The stability of the water column and the cross shelf current also appeared to be marginally significant factors, each explaining approximately 2% of the variability as single regression factors. These three factors in a multiple

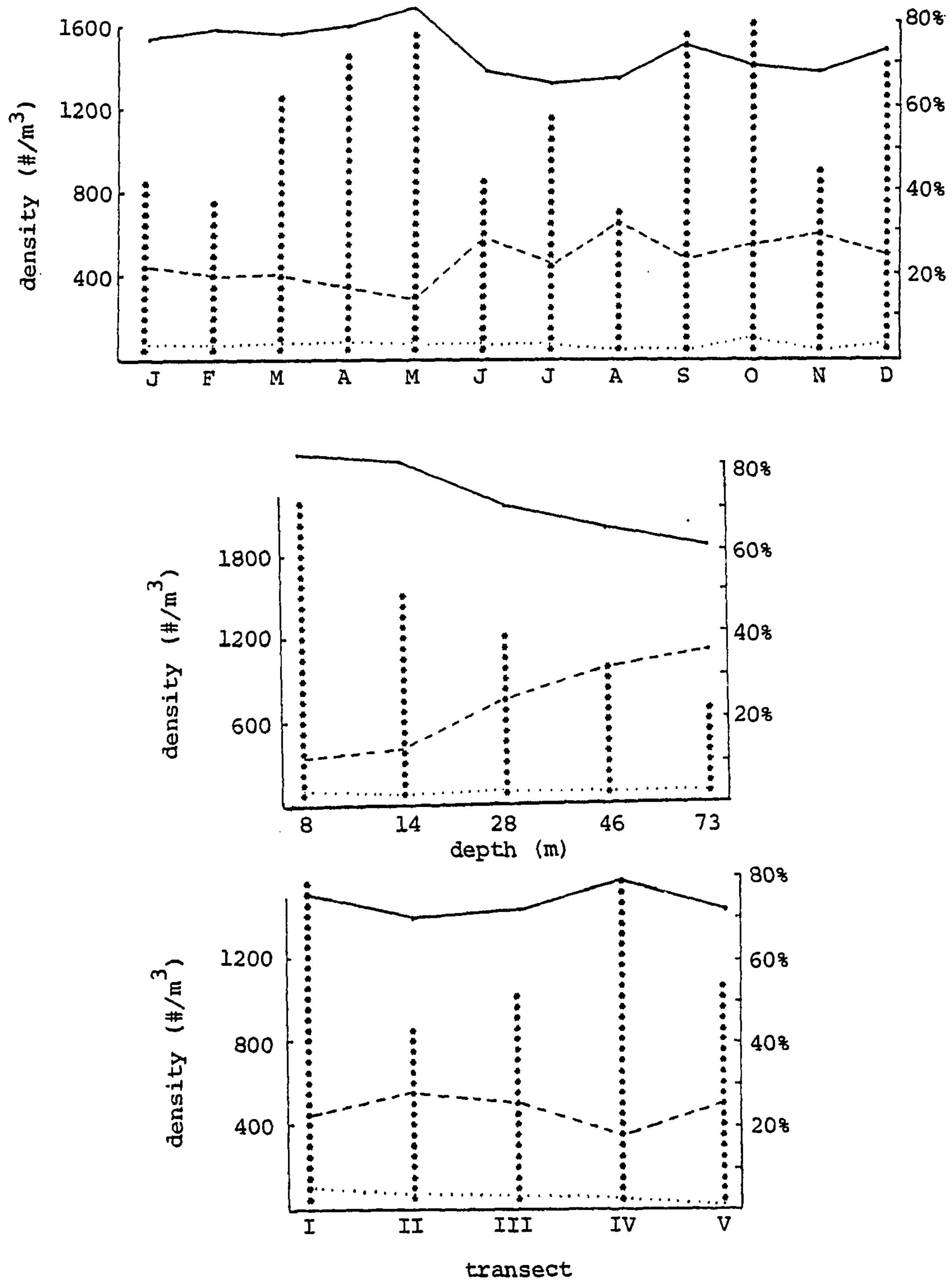


Figure 42. Percentage of calanoid (solid line), cyclopoid (dashed line), and harpacticoid (dotted line) copepods for each month, bottom depth, and transect. Bars represent mean copepod densities.

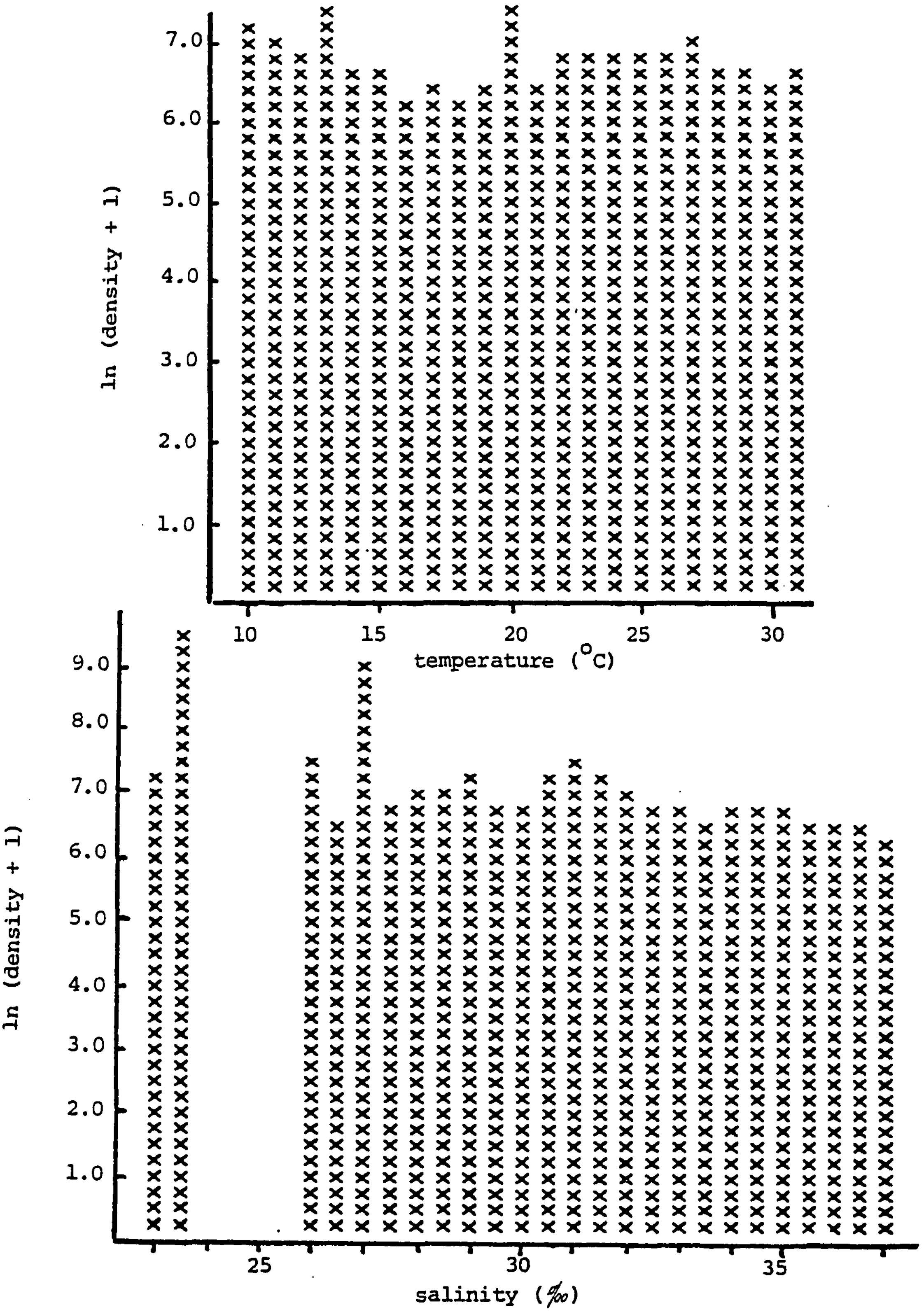


Figure 43. Copepod density relationships with surface temperature and surface salinity. See legend of Figure 15 (p. 42).

regression model explained 11.9% of the variability. The relationships between density and surface temperature and salinity indicated by the histograms were similar to those found for total zooplankton. Mean densities at different temperature and salinity combinations are shown in Figure 44.

Grice (1957) reported densities of copepods from inshore waters off of West Florida to range from $2000/m^3$ at Knights Key to $45,000/m^3$ off of Cedar Key. The largest densities occurred in the spring and the summer. The mesh size of his finest nets, however, was 150 μm which was considerably smaller than the nets used on the GUS III cruises. In offshore waters Grice reported densities ranging from 2100 to 19,900 organisms/m^3.

Park (1979) reported distributions for copepods off of South Texas which were similar to those found in the GUS III samples. He found a general decrease in density with bottom depth. From monthly data averaged over the entire sampling area, the highest mean densities occurred in the spring (approximately 2300 organisms/m^3) and in the fall. Averaged over the years and months, the percentage of adult females did not appear to change with depth remaining around 50 to 55%. This percentage was greatest in the summer however when it reached 67 to 70% in July and August. The percentage of copepodids varied inversely with the percentage of adult females. Adult males were not well represented.

Density trends for copepods from a number of studies conducted off of the coast of New York have been summarized by Malone (1977). In this more northern neritic area the copepods made up a much larger percentage of the zooplankton reaching 99% in some samples from offshore stations.

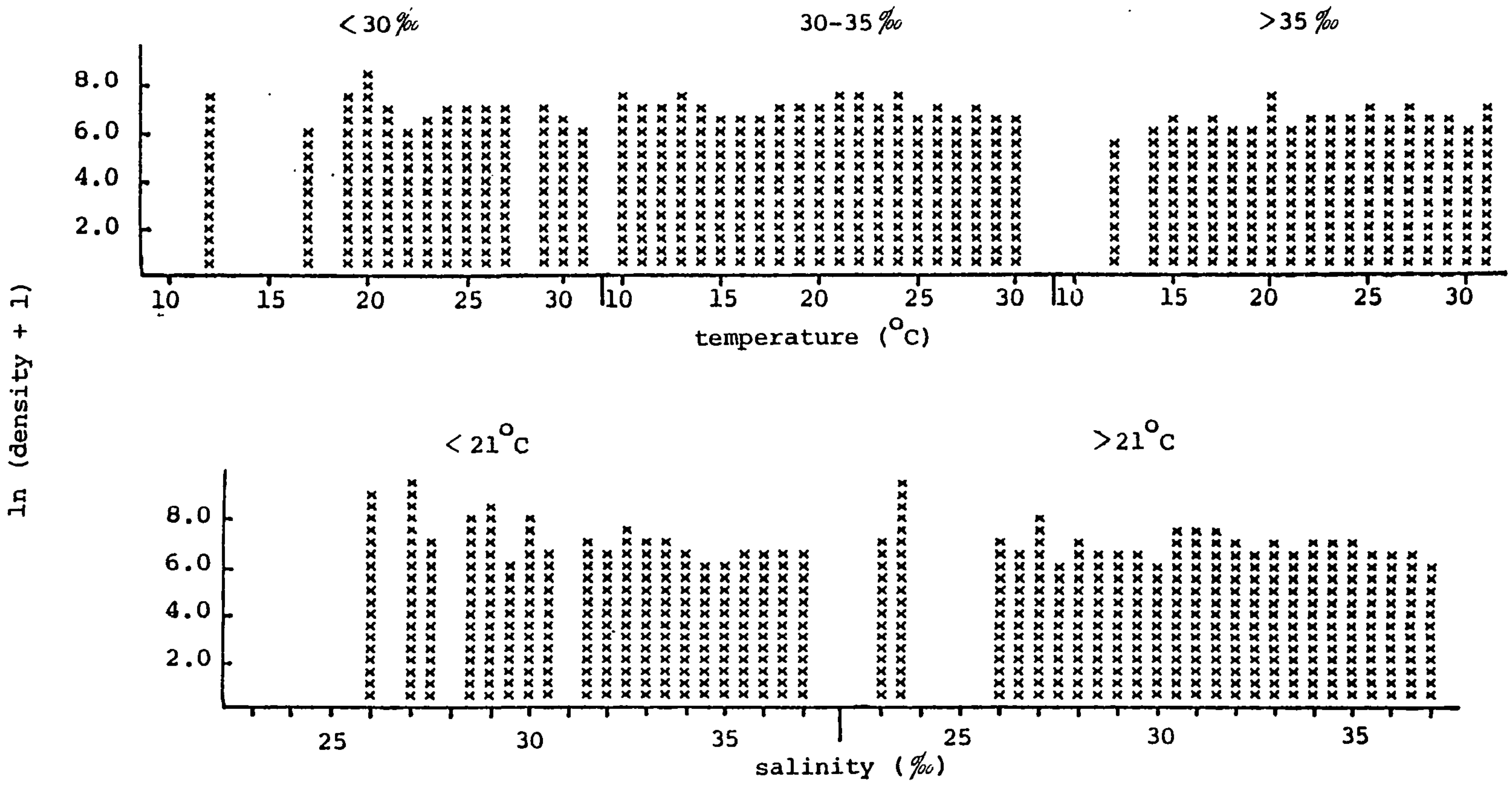


Figure 44. Densities of copepods at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

Copepod densities ranged between 200 to 8000 organisms/m^3.

Distributions of Common Species

General abundance and distribution data for all of the copepod species identified in the samples are listed in Table 5. The analysis of variance results for the 18 most abundant species in the sampling area are listed in Table 6. Temporal and spatial distributions along with possible relationships with physical and chemical variables are examined for each of these common species in the following discussion.

Paracalanus indicus. This species was the most abundant copepod in the study area, making up 16% of all female copepods examined. The mean monthly variability, averaged over depths, transects, and years, indicated peaks in density in the late spring to early summer and the late fall to early winter. When this monthly variability was examined at each depth, a similar seasonal pattern could be seen although the spring-summer density peaks appeared to occur mostly in the summer (Fig. 45). Densities were low at the 73 m stations and the seasonal variability at these stations was reduced. When the AOCOV was calculated, the effect of Transect became highly significant (P = 0.6%). This appeared to be due to a relatively high mean density on Transect I, a transect without a 73 m station (Fig. 46).

The regression results indicated that physical and chemical factors did not appear to explain the variability in the density of this species to any great extent. The simple regression models showed moderately high R^2 values for stability (2.1%), PMMSROFF (1.9%), and upwelling (1.5%). When these were combined in a multiple regression model, they

Table 5. List of copepod species with general abundance and distribution data. Percent abundance (% Ab) was calculated from all samples (R = less than 0.5%). Freq = percent of occurrences out of 513 samples, Loc = location, i.e., I-inshore, 0-offshore, B-both or between. Seasonality was determined by density (D) for the common species and by frequency of occurrence (x,i,o) for the rare species. Where seasonality differed with locality, i = inshore and o = offshore.

Species	% Ab	Freq	Loc	Season			
				Win	Spr	Sum	Fal
CALANOIDA							
Calanidae							
Calanus tenuicornis Dana, 1849	R	3.7	0	x	x	x	
Nannocalanus minor (Claus, 1863)	R	31.6	0	x	x	x	x
Neocalanus gracilis (Dana, 1849)	R	1.6	0	x	x		
Undinula vulgaris (Dana, 1849)	R	11.5	B			x	x
Eucalanidae							
Eucalanus hyalinus (Claus, 1866)	R	2.7	0	x	x		
E. monachus Giesbrecht, 1888	R	1.8	0	x	x		
E. pileatus Giesbrecht, 1888	0.89	65.3	B	x	x	x	x
E. sewelli Fleminger, 1973	R	2.5	0	x	x		
Rhincalanus cornutus (Dana, 1849)	R	7.0	0	x	x		
Mecynocera clausii I.C. Thompson, 1888	R	22.8	0	x	x	x	x
Paracalanidae							
Acrocalanus andersoni Bowman, 1958	R	10.3	0	x		x	x
A. longicornis Giesbrecht, 1888	R	30.4	0	x		x	x
Paracalanus aculeatus Giesbrecht, 1888	3.00	73.9	B	D			D
P. crassirostris F. Dahl, 1894	9.68	58.7	I	D	D		
P. denudatus Sewell, 1929	R	13.5	0	x	x	x	x
P. indicus (Wolfenden, 1905)	16.0	96.9	B	D	D	D	
P. nudus Sewell, 1929	R	6.0	0	x	x	x	

Table 5. (continued)

Species	% Ab	Freq	Loc	Season			
				Win	Spr	Sum	Fal
P. quasimodo Bowman, 1971	10.7	94.5	B		D		D
Calocalanus contractus Farran, 1926	R	8.4	0	x	x	x	x
C. elegans Shmeleva, 1965	R	1.4	0		x	x	
C. gracilis Tanaka, 1956	R	19.9	0	x	x	x	x
C. neptunus Shmeleva, 1965	R	4.1	0	x	x	x	
C. pavo Dana, 1849	0.49	37.4	0		x	x	x
C. pavoninus Farran, 1936	0.50	43.7	0	x	x	x	x
C. styliremis Giesbrecht, 1888	R	48.1	0	x	x	x	x
Calocalanus sp. 2	R	6.4	0	x			
Ischnocalanus plumulosus (Claus, 1863)	R	18.5	0	x	x	x	x
Pseudocalanidae							
Clausocalanus arcuicornis (Dana, 1849)	R	5.7	0	x	x		x
C. furcatus (Brady, 1883)	6.81	75.4	0	D		D	D
C. jobei Frost and Fleminger, 1968	1.09	43.3	0	D	D	D	
C. mastigophorus (Claus, 1863)	R	4.5	0	x	x		
C. parapergens Frost and Fleminger, 1968	R	6.6	0	x	x		
C. paululus Farran, 1926	R	6.4	0	x	x		
C. pergens Farran, 1926	R	7.0	0	x	x		
Ctenocalanus vanus Giesbrecht, 1888	R	19.7	0	x	x	x	
Aetideidae							
Aetideus acutus Farran, 1929	R	2.7	0	x			
Bradyidius sp.	R	0.2	0	x			
Euchirella amoena Giesbrecht, 1888	R	0.2	0	x			

Table 5. (continued)

Species	% Ab	Freq	Loc	Season			
				Win	Spr	Sum	Fal
Aetideidae (cont.)							
E. rostrata (Claus, 1866)	R	0.4	0	x	x		
Paivella inaciae Vervoort, 1965	R	0.2	0	x			
Euchaetidae							
Euchaeta marina (Prestandrea, 1833)	R	9.6	0	x	x	x	
E. media Giesbrecht, 1888	R	0.2	I		x		
E. paraconcinna Fleminger, 1957	R	6.4	0	x	x	x	x
Phaennidae							
Phaenna spinifera Claus, 1863	R	0.2	0	x			
Scolecithricidae							
Scaphocalanus subcurtus Park, 1970	R	1.2	0	x			
Scolecithricella ctenopus (Giesbrecht, 1888)	R	0.2	0		x		
S. dentata (Giesbrecht, 1888)	R	0.4	0	x	x		
S. tenuiserrata (Giesbrecht, 1892)		R	1.2	0	x	x	
Scolecithrix bradyi Giesbrecht, 1888	R	0.8	0	x	x		
S. danae (Lubbock, 1856)	R	6.6	0	x	x	x	x
Tharybidae							
Parundinella spinodenticulata Fleminger, 1957	R	2.9	0	x			
Stephidae							
Stephos deichmannae Fleminger, 1957	R	8.4	0	x	x		x

Table 5. (continued)

Species	% Ab	Freq	Loc	Season			
				Win	Spr	Sum	Fal
Temoridae							
Temora stylifera (Dana, 1849)	R	43.9	B	x	x	x	x
T. turbinata (Dana, 1849)	3.60	83.6	I			x	x
Temoropia mayumbaensis T. Scott, 1894	R	0.2	0	x			
Metridiidae							
Pleuromamma abdominalis (Lubbock, 1856)	R	0.4	0	x			
P. gracilis (Claus, 1863)	R	1.0	0	x	x		
P. piseki Farran, 1929	R	1.4	0	x	x		
Centropagidae							
Centropages caribbeanensis Park, 1970	R	1.6	0		x	x	
C. hamatus (Lilljeborgi, 1853)	0.73	12.5	I	D	D		
C. velificatus De Oliveira, 1947	1.24	61.0	I			D	D
Pseudodiaptomidae							
Pseudodiaptomus sp.	R	1.8	I	x	x	x	x
Lucicutiidae							
Lucicutia flavicornis (Claus, 1863)	R	17.2	0	x	x	x	x
L. guassae Grice, 1963	R	6.2	0	x	x	x	x
L. paraclausi Park, 1970	R	7.0	0	x	x	x	x
Heterorhabdidae							
Heterorhabdus papilliger (Claus, 1863)	R	1.0	0	x			
H. spinifer Park, 1970	R	0.8	0	x			

Table 5. (continued)

Species	% Ab	Freq	Loc	Season			
				Win	Spr	Sum	Fal
Augaptilidae							
Haloptilus longicornis (Claus, 1863)	R	1.6	0	x	x	x	
Candaciidae							
Candacia curta (Dana, 1849)	R	7.4	0	x	x	x	x
C. pachydactyla (Dana, 1849)	R	2.0	0	x	x		x
Paracandacia bispinosa (Claus, 1863)	R	0.6	B	x			
P. simplex (Giesbrecht, 1889)	R	5.1	0	x	x		
Pontellidae							
Anomalocera ornata Sutcliffe, 1949	R	0.6	0	x			
Calanopia americana F. Dahl, 1894	R	34.1	B	o	o	oi	oi
Labidocera acutifrons (Dana, 1852)	R	0.2	0				x
L. aestiva Wheeler, 1901	R	14.4	I	x	x	x	x
L. scotti Giesbrecht, 1897	R	5.5	I			x	x
Pontella meadii Wheeler, 1900	R	0.4	B		x	x	
P. securifer Brady, 1883	R	0.4	0			x	
Pontellina plumata (Dana, 1849)	R	0.6	0	x			
Pontellopsis villosa Brady, 1883	R	0.6	B	x		x	x
Acartiidae							
Acartia danae Giesbrecht, 1889	R	23.4	0		D	D	
A. lilljeborgii Giesbrecht, 1889	2.15	13.6	I				D
A. tonsa Dana, 1849	11.9	49.1	I		D		

Table 5. (continued)

Species	% Ab	Freq	Loc	Season			
				Win	Spr	Sum	Fal
CYCLOPOIDA							
Oithonidae							
Oithona colcarva Bowman, 1975	R	10.5	I	x	x		x
O. decipiens Farran, 1913*	R	4.3	0	x	x	x	
O. hamata Rosendorn, 1917*	R	4.8	0	x	x		
O. hebes Giesbrecht, 1891*	R	12.6	B	x	x	x	x
O. nana Giesbrecht, 1892	5.62	75.4	I			D	D
O. plumifera W. Baird, 1843	3.86	76.2	0			D	D
O. robusta Giesbrecht, 1892*	R	0.7	0	x	x		
O. setigera Dana, 1849*	R	15.7	0	x	x	x	x
O. similis Claus, 1866*	R	13.1	0	x	x		
O. simplex Farran, 1913*	R	12.9	I	x		x	x
O. tenuis Rosendorn, 1917	R	7.6	0		x	x	
O. vivida Farran, 1913*	R	4.5	0	x	x		
Oithona sp. 1	R	13.1	0	x	x		
Paroithona pulla Farran, 1913	R	1.6	B		x	x	
Paroithona sp.	R	1.2	0	x	x	x	x
Oncaeidae							
Oncaea conifera Giesbrecht, 1891	R	17.9	0	x	x	x	x
O. dentipes Giesbrecht, 1891	R	1.8	0	x	x		
O. media Giesbrecht, 1891	6.10	82.3	B		D	D	
O. mediterranea Claus, 1863	1.03	51.5	0	D	D	D	
O. similis Sars, 1918	R	0.8	B	x	x		
O. venusta Philippi, 1843	3.14	69.8	0	D		D	D
Lubbockia squillimana Claus, 1863	R	9.0	0	x	x	x	

Table 5. (continued)

Species	% Ab	Freq	Loc	Season			
				Win	Spr	Sum	Fal
Sapphirinidae							
Sapphirina angusta Dana, 1852	R	0.4	0			x	
S. auronitens Claus, 1863	R	1.2	0	x		x	x
S. intestinata Giesbrecht, 1891	R	0.2	B		x		
S. lactens Giesbrecht, 1892	R	0.2	B				x
S. metallina Dana, 1852	R	1.2	0	x	x		x
S. nigromaculata Claus, 1863	R	15.2	B	x	x	x	x
S. ovatolanceolata Dana, 1852	R	0.4	B			x	
Corissa parva Farran, 1936	R	0.4	0	x	x		
Copilia lata Giesbrecht, 1892	R	1.0	0		x	x	
C. mirabilis Dana, 1852	R	8.0	0		x	x	x
C. quadrata Dana, 1852	R	0.4	0	x	x		
Corycaeidae							
Corycaeus amazonicus F. Dahl, 1894	1.81	79.3	B		D		D
C. americanus M. Wilson, 1949	1.55	70.2	I	D	D		D
C. clausi F. Dahl, 1894	R	5.1	0	x	x		
C. flaccus Giesbrecht, 1891	R	2.7	0	x			x
C. furcifer Claus, 1863	R	0.2	0	x			
C. giesbrechti F. Dahl, 1894	0.88	64.7	B			D	D
C. latus (Dana, 1849)	R	21.8	0	x		x	x
C. lautus Dana, 1849	R	1.9	0	x			x
C. limbatus Brady, 1888	R	2.1	0	x			
C. minimus indicus M. Dahl, 1894	R	0.6	0	x		x	
C. speciosus Dana, 1849	R	17.3	0		x	x	x

Table 5. (continued)

Species	% Ab	Freq	Loc	Season Win	Season Spr	Season Sum	Season Fal
Corycaeidae (cont.)							
C. typicus (Kroyer, 1849)	R	1.8	O	x			
Farranula gracilis (Dana, 1853)	1.80	46.4	O			D	D
F. rostrata (Claus, 1863)	R	10.9	O	x	x	x	
Sabelliphelidae							
Hermanella sp.†	R	3.0	I	x	x		x
Kelleria sp.†	R	16.2	B		x	x	x
Sabelliphelidae spp.‡	R	25.7	B	x	x	x	x

*Transect V not included (420 obs)

†Transects I, II and III not included (198 obs)

‡Transects IV and V not included (315 obs)

Table 6. Analysis of variance and covariance results for copepod species. See legend for Table 2 (p. 41).

Species	Percent of Copepods	Interactions						Main Effects			
		Depth Trans	Depth Month	Depth Year	Trans Month	Trans Year	Month Year	Depth	Trans	Month	Year
Paracalanus indicus	16.0	ns	$\frac{*}{*}$	ns	7.4	ns	$\frac{7.6}{2.9}$	$\frac{0.2}{*}$	$\frac{2.8}{0.6}$	$\frac{2.7}{\text{ns}}$	$\frac{0.3}{0.8}$
Acartia tonsa	11.9	$\frac{*}{*}$	$\frac{0.6}{0.2}$	ns	7.6	ns	$\frac{*}{0.1}$	$\frac{*}{*}$	$\frac{4.9}{8.0}$	$\frac{1.1}{1.0}$	5.5
Paracalanus quasimodo	10.7	$\frac{*}{0.5}$	ns	$\frac{\text{ns}}{\text{ns}}$	$\frac{0.2}{*}$	ns	$\frac{3.5}{8.8}$	$\frac{*}{0.3}$	ns	$\frac{0.3}{0.2}$	ns
Paracalanus crassirostris	9.7	2.1	0.1	ns	0.3	ns	0.3	*	*	0.7	ns
Clausocalanus furcatus	6.8	$\frac{4.7}{3.8}$	$\frac{*}{*}$	$\frac{\text{ns}}{\text{ns}}$	$\frac{2.9}{3.9}$	$\frac{\text{ns}}{\text{ns}}$	$\frac{*}{*}$	$\frac{*}{*}$	$\frac{2.4}{1.6}$	ns	$\frac{0.5}{0.2}$
Oncaea media	6.1	ns	$\frac{*}{*}$	$\frac{1.4}{0.3}$	$\frac{*}{*}$	$\frac{2.5}{3.5}$	$\frac{\text{ns}}{\text{ns}}$	$\frac{*}{0.1}$	ns	$\frac{0.2}{*}$	ns
Oithona nana	5.6	ns	*	ns	1.2	ns	*	*	*	ns	ns
Oithona plumifera	3.9	ns	$\frac{*}{*}$	ns	$\frac{2.4}{0.8}$	ns	$\frac{*}{*}$	$\frac{*}{*}$	$\frac{0.8}{1.1}$	$\frac{\text{ns}}{\text{ns}}$	$\frac{\text{ns}}{\text{ns}}$
Temora turbinata	3.6	ns	ns	ns	0.4	ns	*	0.2	1.6	ns	ns

Table 6. (continued)

Species	Percent of Copepods	Interactions						Main Effects			
		Depth Trans	Depth Month	Depth Year	Trans Month	Trans Year	Month Year	Depth	Trans	Month	Year
Oncaea venusta	3.1	ns	2.9	ns	1.6	ns	0.6	*	1.0	ns	1.1
Paracalanus aculeatus	3.0	ns	* *	ns	1.0 2.6	ns	0.6 0.4	* *	3.7 0.5	1.0 1.0	ns ns
Acartia lilljeborgii	2.2	4.5	*	ns	*	ns	ns	*	0.2	*	ns
Corycaeus amazonicus	1.8	ns	* *	ns	0.6 0.3	ns	ns ns	* *	ns	* 0.1	ns
Farranula gracilis	1.8	7.4	*	ns	ns	ns	*	*	ns	0.2	ns
Corycaeus americanus	1.6	ns	*	ns	ns	ns	7.9	*	ns	0.2	4.5
Centropages velificatus	1.2	ns	*	ns	ns	ns	*	0.1	0.7	0.8	*
Clausocalanus jobei	1.1	ns	1.9	ns	0.6	ns	*	0.1	ns	ns	ns
Oncaea mediterranea	1.0	ns	ns	ns	ns	ns	ns	*	ns	ns	ns

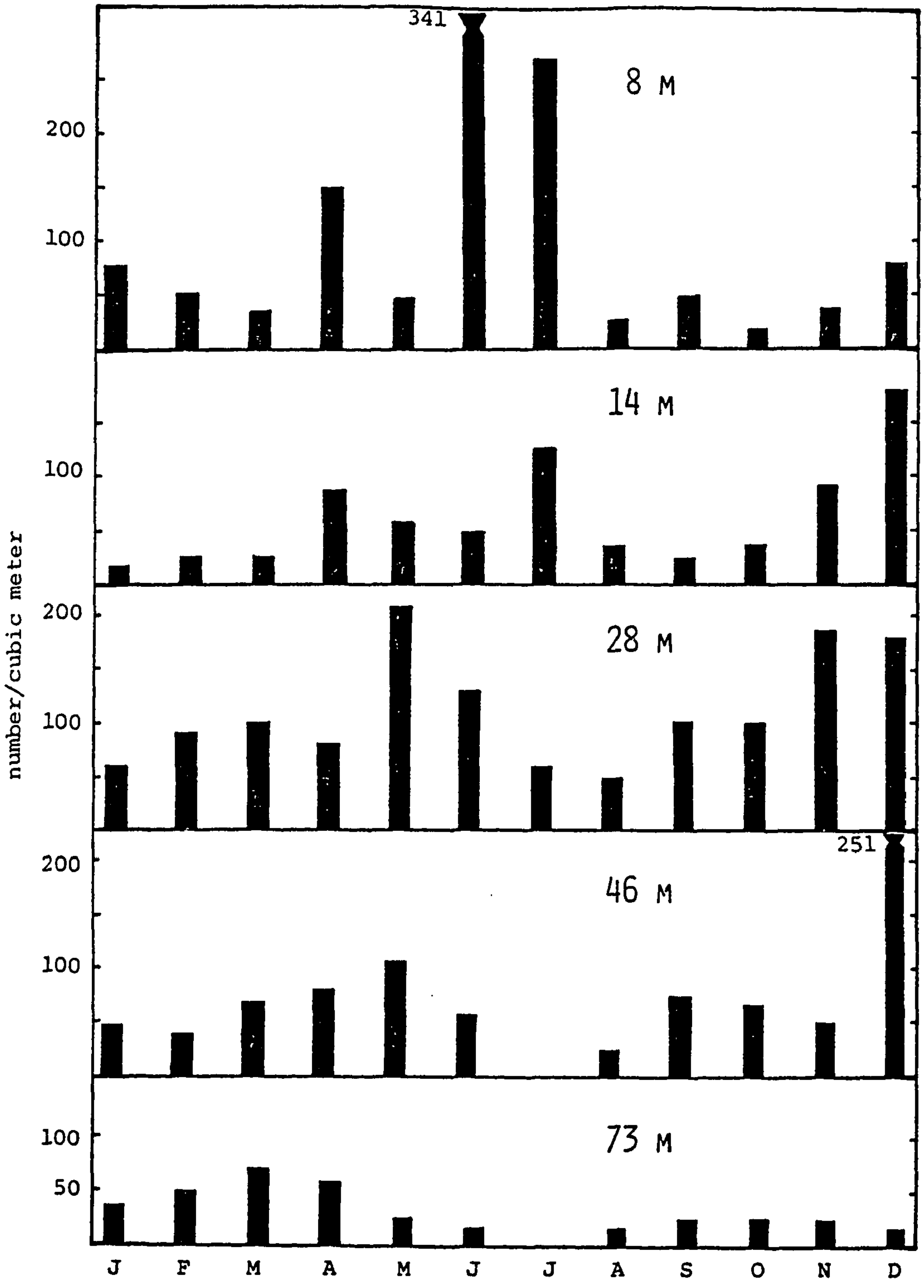


Figure 45. Mean monthly densities of *Paracalanus indicus* at each bottom depth sampled. Values are averaged over transects and years.

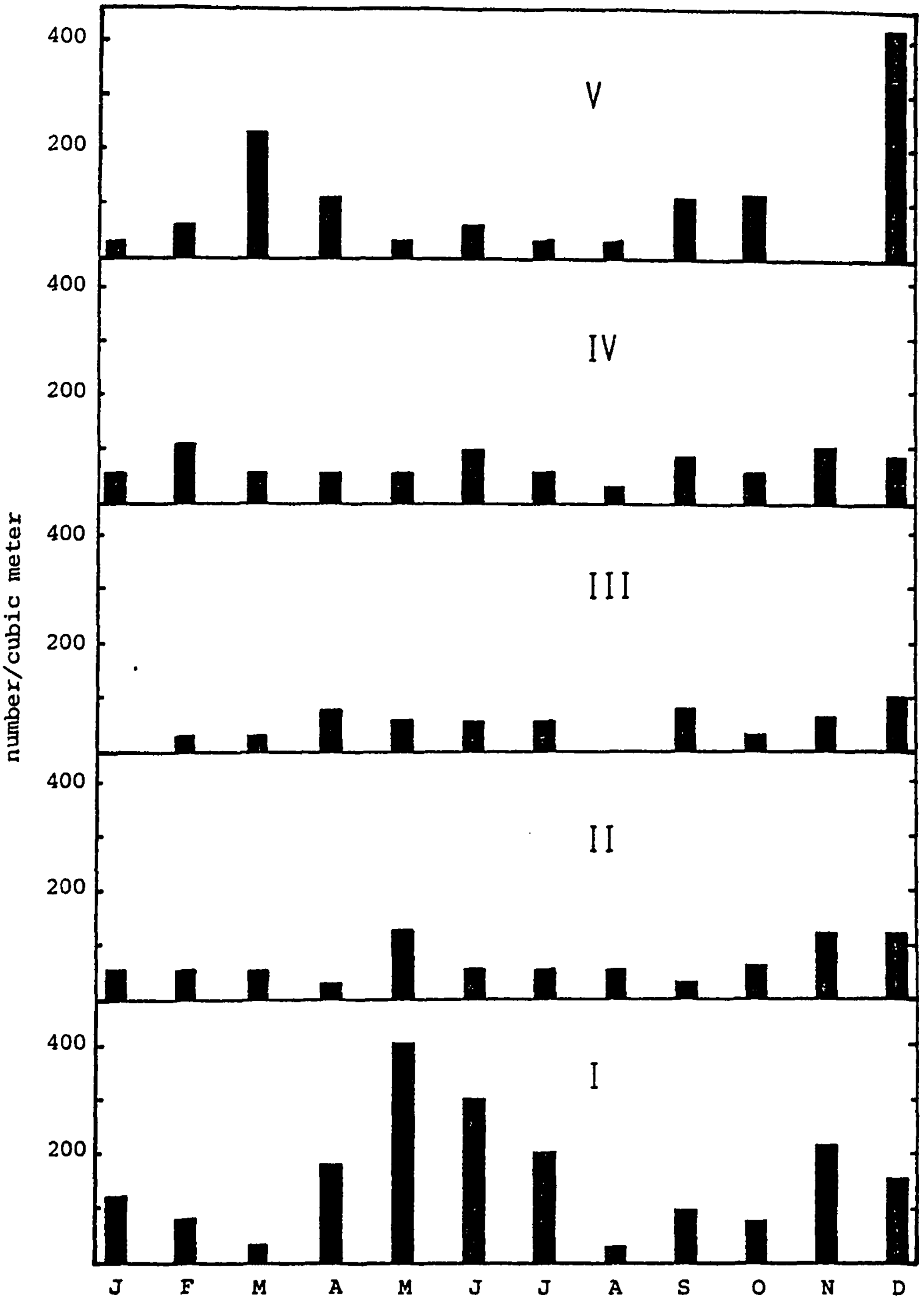


Figure 46. Mean monthly densities of *Paracalanus indicus* on each transect. Values are averaged over bottom depths and years.

explained 8.9% of the variability in the density of this species. Temperature and salinity did not appear to be significant factors. The graph of density versus surface salinity also showed no obvious relationship (Fig. 47). There did appear to be an optimum surface temperature, however, of approximately 20°C. Mean densities decreased in both directions from this temperature. No apparent temperature salinity interactions could be seen (Fig. 48).

Regression results for surface temperature and salinity were also examined for each month and each depth (Fig. 49). Density was positively related to surface temperature during March and negatively related during October. The relationship between density and salinity also appeared to change from negative to positive during the year. When regressions were calculated at each depth, no apparent relationship with either temperature or salinity was exhibited at the shallow stations. Densities appeared to be negatively related however to both temperature and salinity at the deeper stations.

Acartia tonsa. Although *Acartia tonsa* had a limited seasonal and spatial distribution, it was a very abundant copepod in the sampling area making up approximately 12% of the females examined. This species occurred in significant numbers only at the 8 and 14 m stations (Fig. 50). At both of these depths a distinct spring density peak was present during April and May. The largest spring densities occurred in 1964. At the 8 m station on Transect IV a density peak also occurred in October of 1963. When mean values at each station averaged over time (Fig. 51) were examined, it was apparent that large numbers of *Acartia*

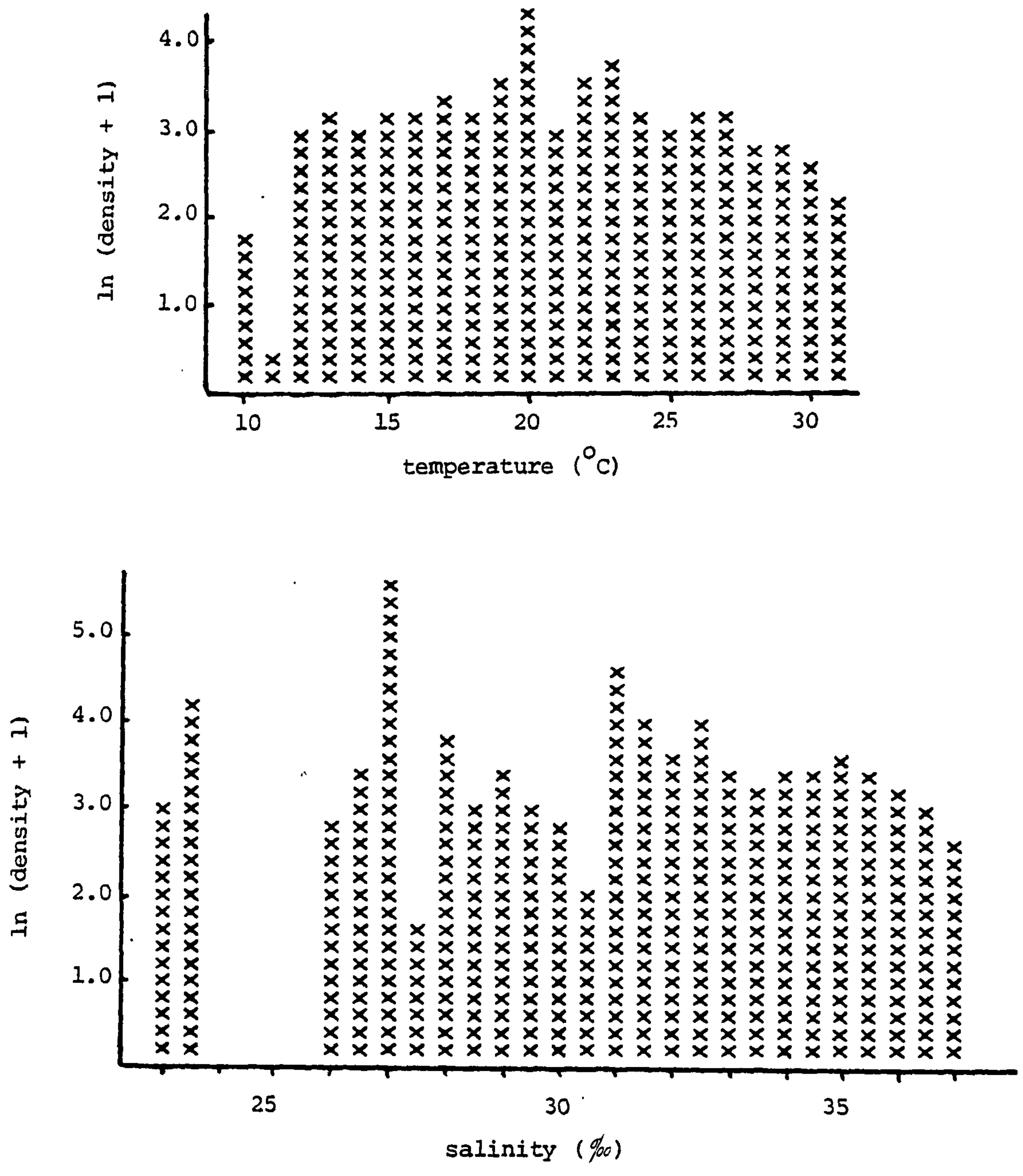


Figure 47. Density relationships with surface temperature and surface salinity for *Paracalanus indicus*. See legend of Figure 15 (p. 42).

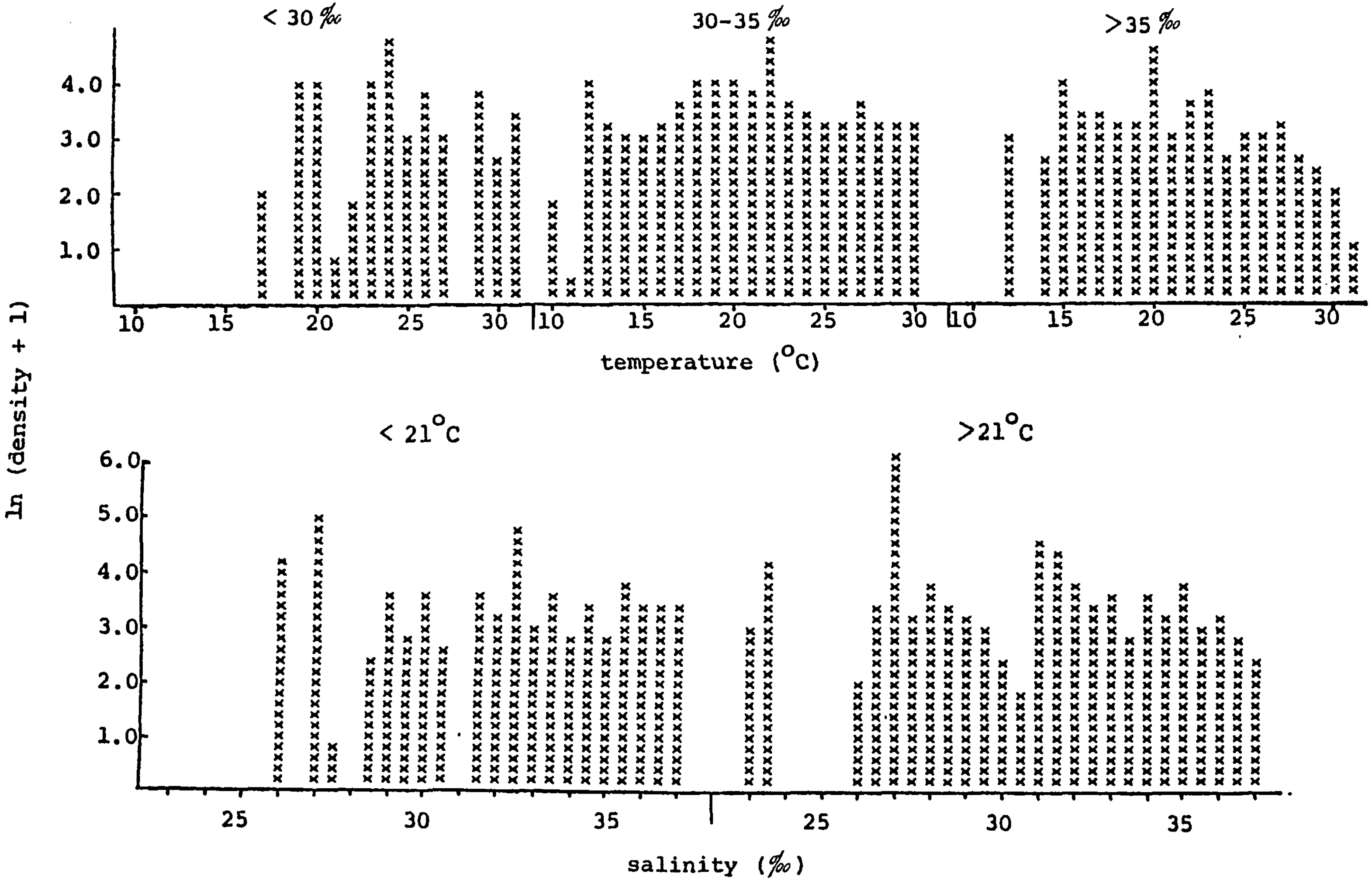


Figure 48. Densities of *Paracalanus indicus* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

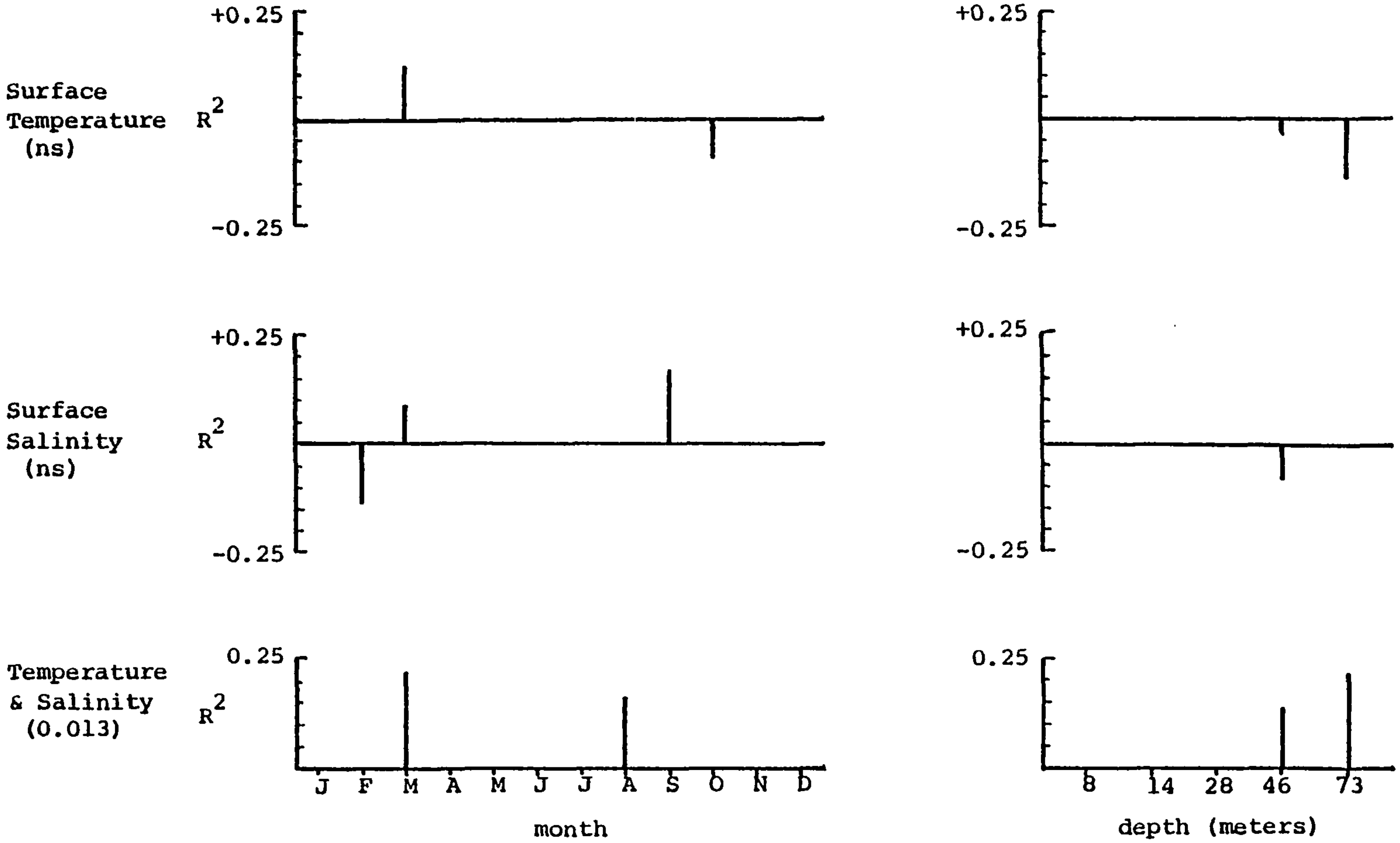


Figure 49. Regression results with surface temperature and surface salinity for *Paracalanus indicus*. Linear regressions were calculated on log transformed densities for each month and each bottom depth. Vertical bars indicate the R^2 values (if significant at the 5% level). For the simple regressions, the bars also indicate the sign of the slope. The overall R^2 value is in parenthesis below each factor (ns = not significant).

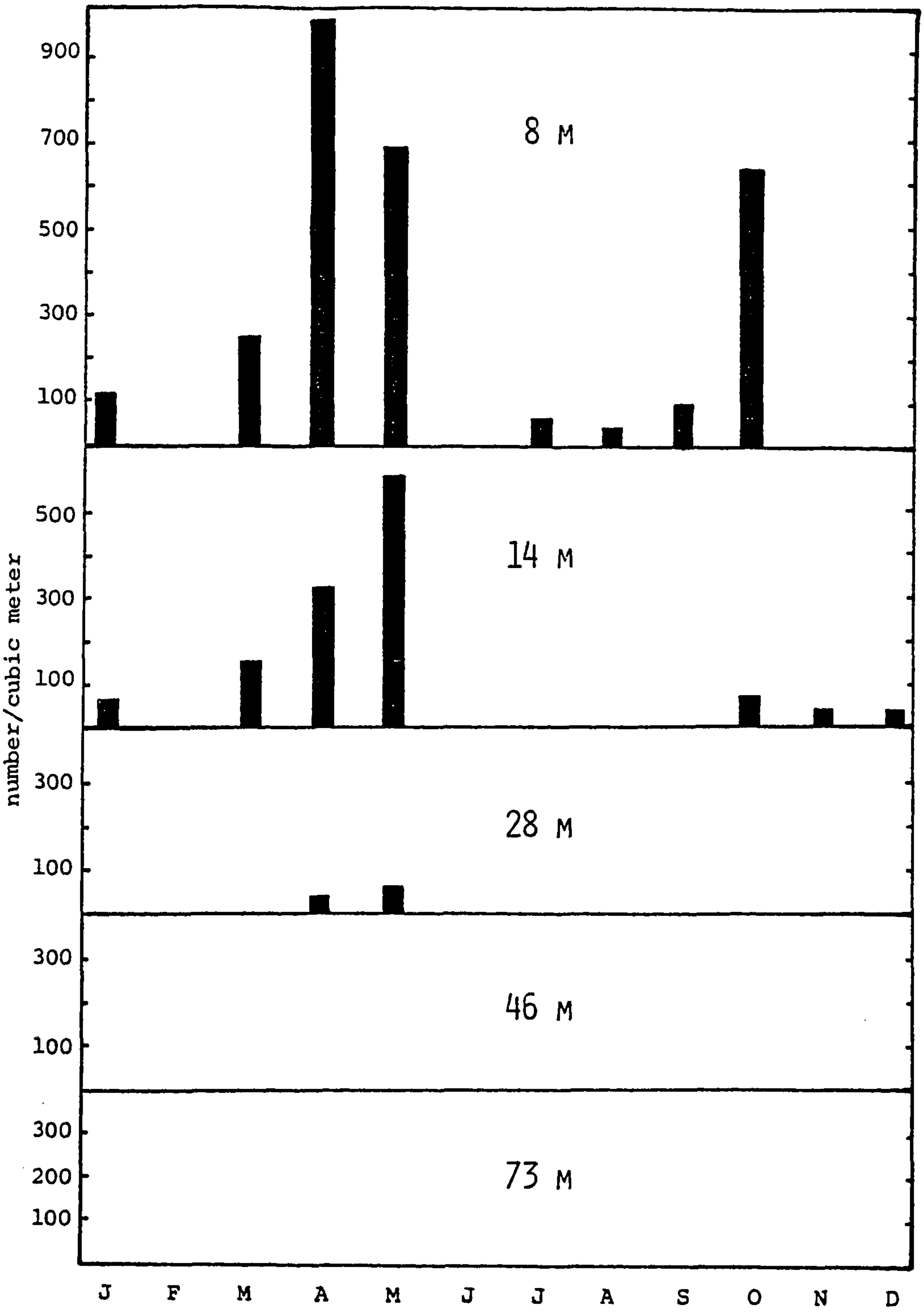


Figure 50. Mean monthly densities of *Acartia tonsa* at each bottom depth sampled. Values are averaged over transects and years.

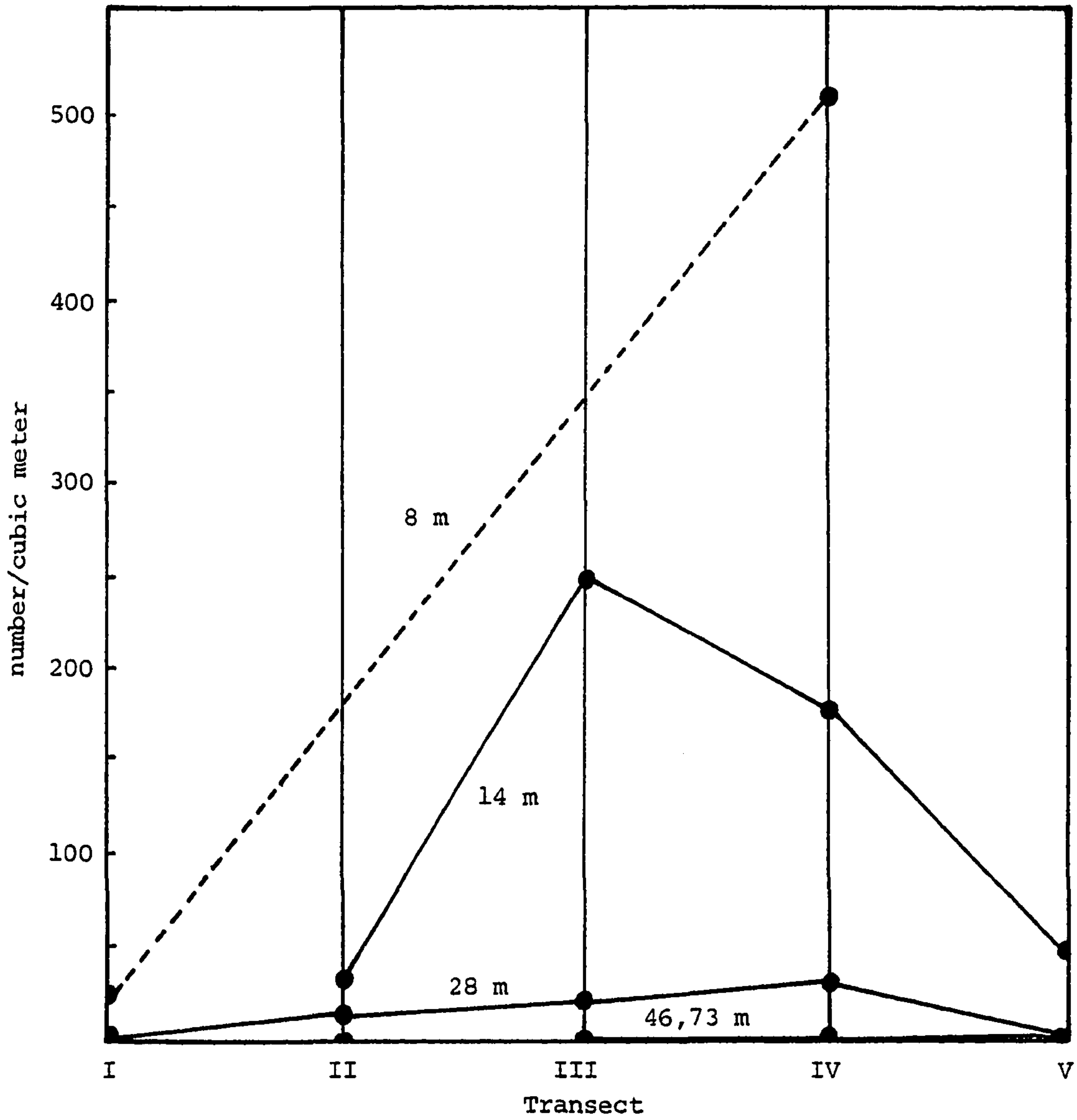


Figure 51. Mean density of *Acartia tonsa* at each sampling station. Values are averaged over months and years. Graphed as in Figure 6 (p. 28).

were frequently found only at the shallow stations on Transects III and IV. The analysis of covariance calculated to examine the effect of sampling time on these data did not appear to alter the results of the AOV.

Simple linear regression models indicated that the density of *Acartia tonsa* appeared to be closely related to surface salinity. This negative relationship with salinity explained 43.5% of the variability. When added to surface temperature in a two variable multiple regression model the R^2 was 46.1%. Density did not appear to be related to the other physical factors examined. The negative relationship between density and surface salinity can be seen graphically in Figure 52. A negative relationship with temperature also appeared to be present up to approximately 18°C. At higher temperatures no distinct trend was evident. The combination of high salinity and high temperature generally resulted in very low densities of this species (Fig. 53). The relatively large mean density at 31°C for salinities over 35°/oo came from one anomalous sample.

Figure 54 shows the regression results for salinity and temperature for each month and also for each depth. Highly significant relationships were frequently found in regressions with temperature and salinity for each month. Since this species was almost exclusively found at inshore stations, the seasonal distribution of temperature and salinity at each depth (Fig. 3, p. 24 and Fig. 9, p. 31) appeared to be responsible for these high R^2 values. There seemed to be little relationship between temperature and density at any depth but salinity regressions were negative at all depths and the R^2 values were high at all depths

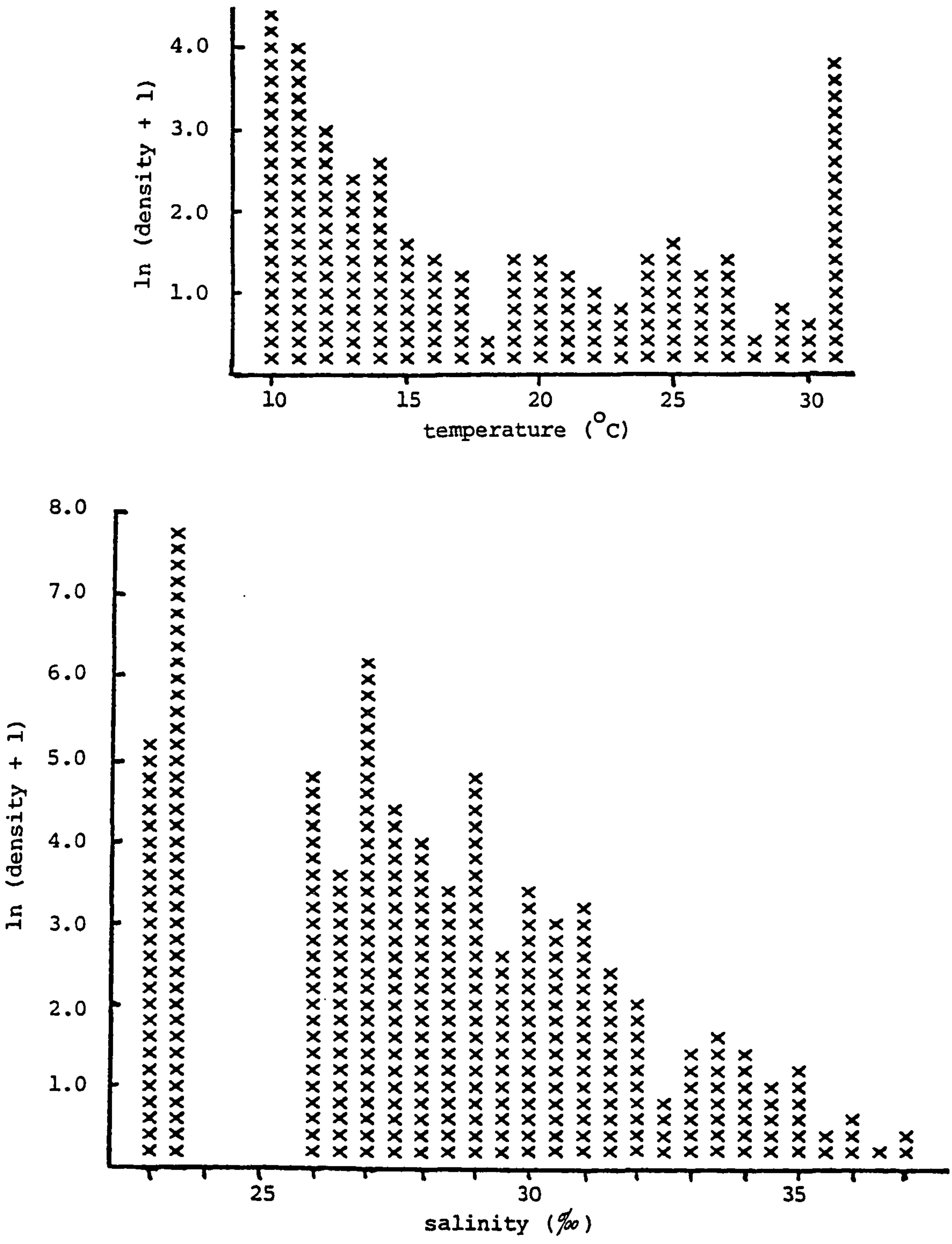


Figure 52. Density relationships with surface temperature and surface salinity for *Acartia tonsa*. See legend of Figure 15 (p. 42).

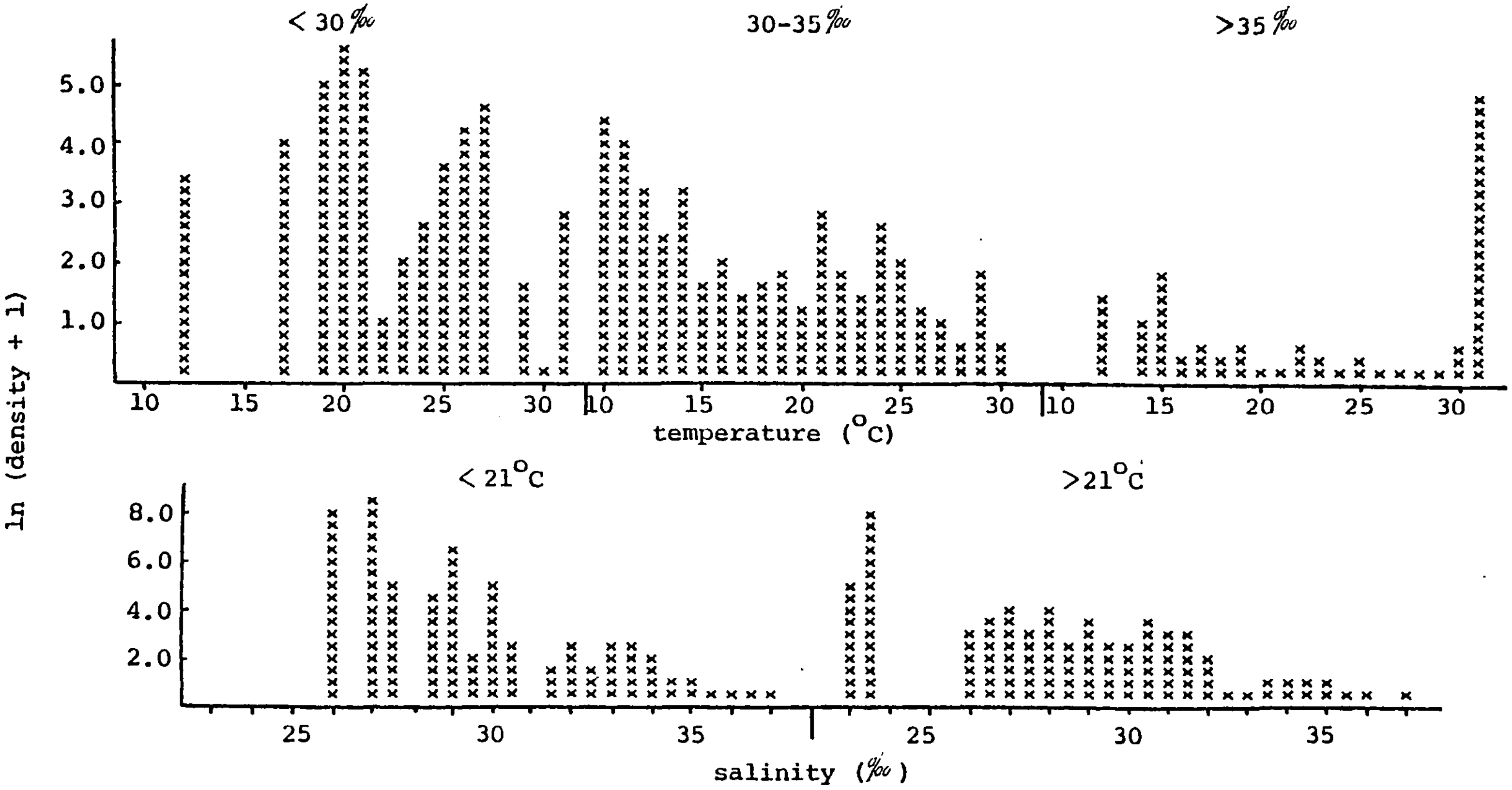


Figure 53. Densities of *Acartia tonsa* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

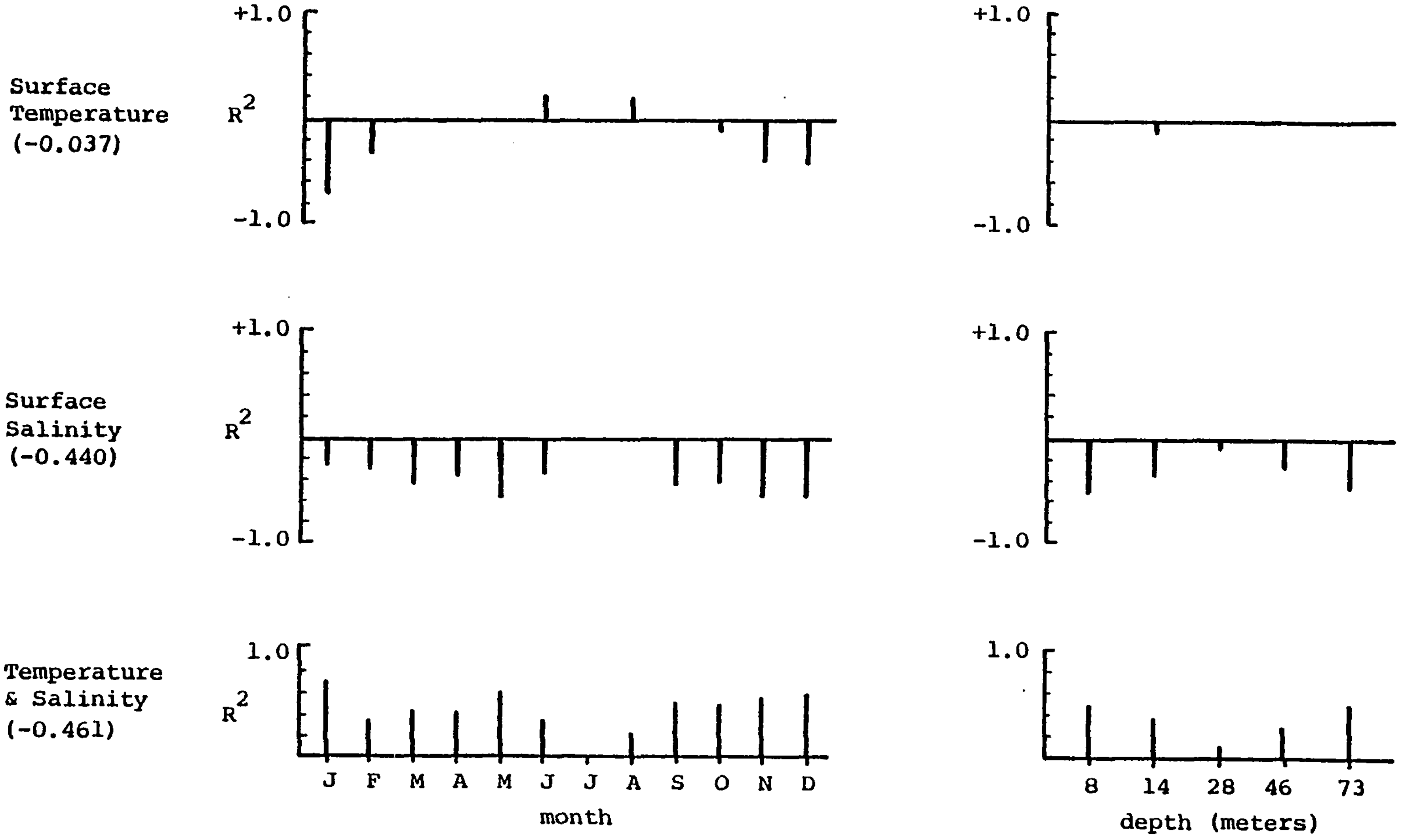


Figure 54. Regression results with surface temperature and surface salinity for *Acartia tonsa*. See legend of Figure 49 (p. 102).

except 46 m. In general, these results indicated that the seasonal and spatial abundance of *Acartia tonsa* appeared to be closely related to changes in surface salinity.

Paracalanus quasimodo. The mean monthly densities of this species appeared to be different from those of *P. indicus*. *Paracalanus quasimodo* had density peaks in April and September. Although more pronounced at the inshore stations, this seasonal distribution appeared to be consistent over depth (Fig. 55). Upon examining the monthly variability at each transect however (a significant interaction, P = 0.2%) it could be seen that much of the seasonal variability in Figure 55 came from Transect I, and that densities on Transects IV and V showed little seasonal variability (Fig. 56). The plot of density versus transect for each depth (Fig. 57) indicated that the stations at 73 m generally had the lowest densities. The 28 m stations had the highest densities on all but one of the transects. The AOCOV with sampling time as the covariate did not appear to affect these results significantly.

The density of this species did not appear to be strongly related to any of the physical or chemical factors examined. The highest R^2 values in the simple regression models were for PMMSROFF (2.7%), surface salinity (2.7%, negative), and the cross shelf current (1.7%). All of the variables combined in a multiple regression model however only had an R^2 value of 6.7%. The negative relationship between density and surface salinity is shown in Figure 58. When temperature salinity interactions were examined (Fig. 59), the negative trend between density and salinities above $31^{o}/oo$ was more apparent at

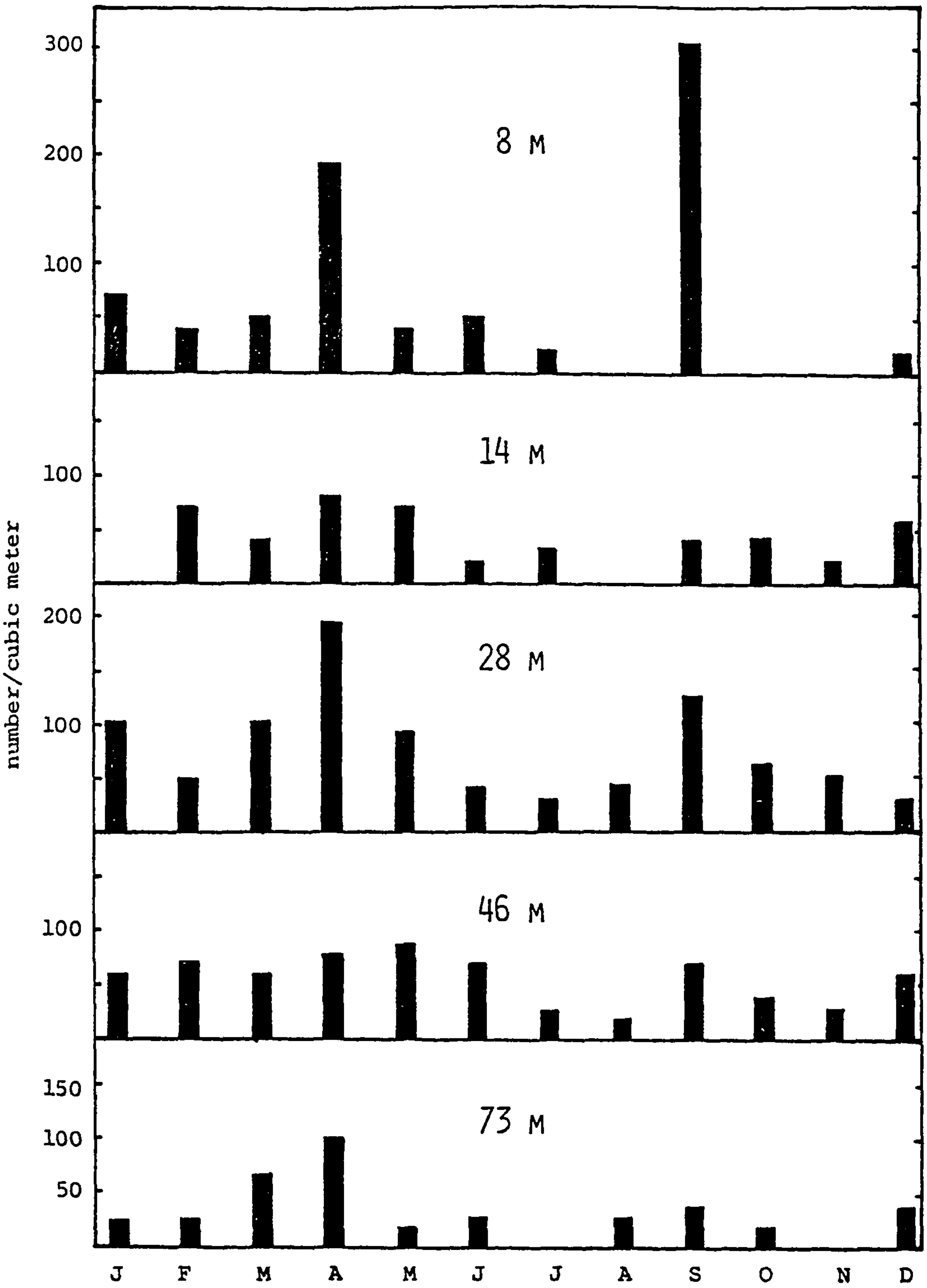


Figure 55. Mean monthly densities of *Paracalanus quasimodo* at each bottom depth sampled. Values are averaged over transects and years.

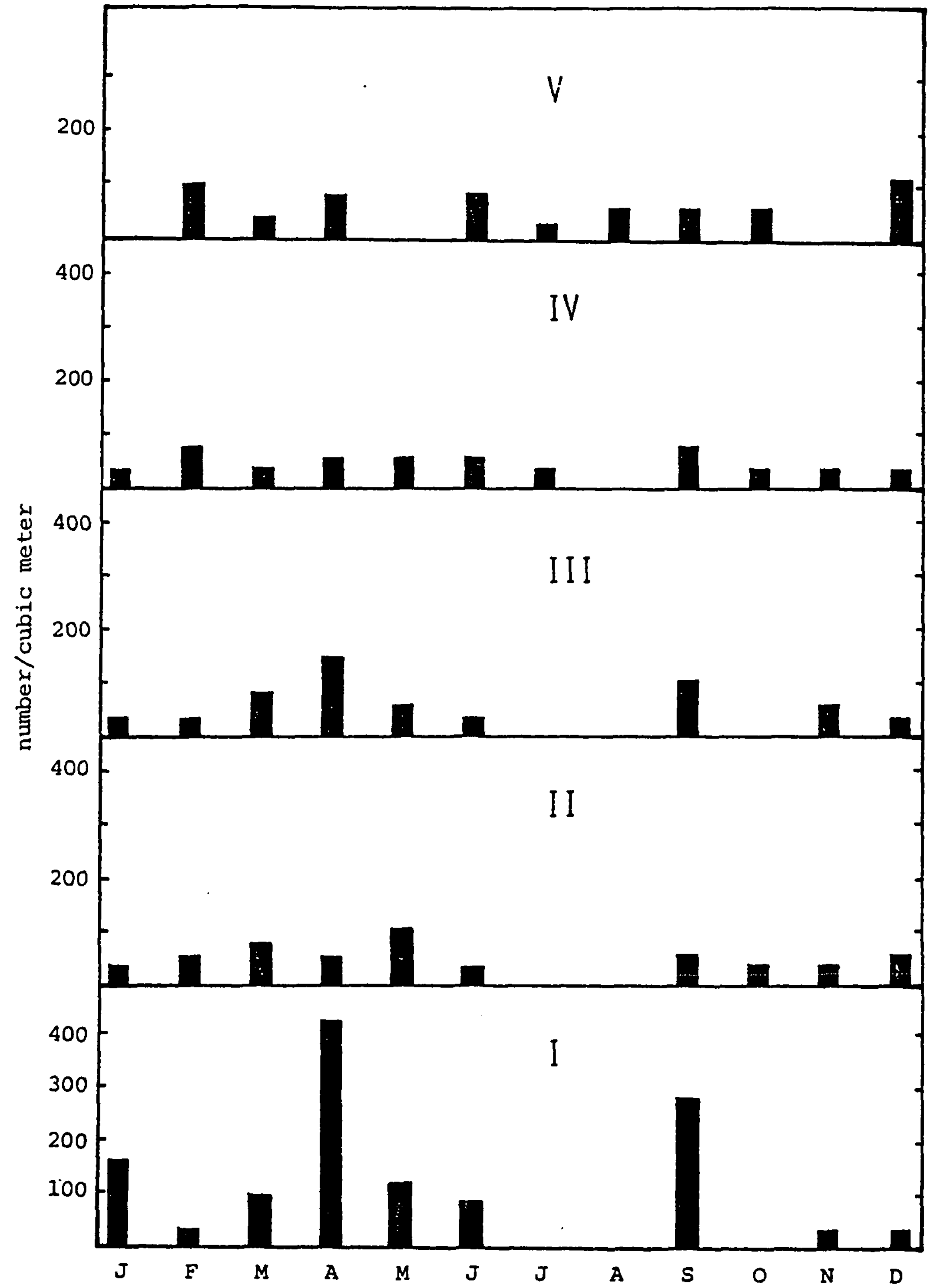


Figure 56. Mean monthly densities of *Paracalanus quasimodo* on each transect. Values are averaged over bottom depths and years.

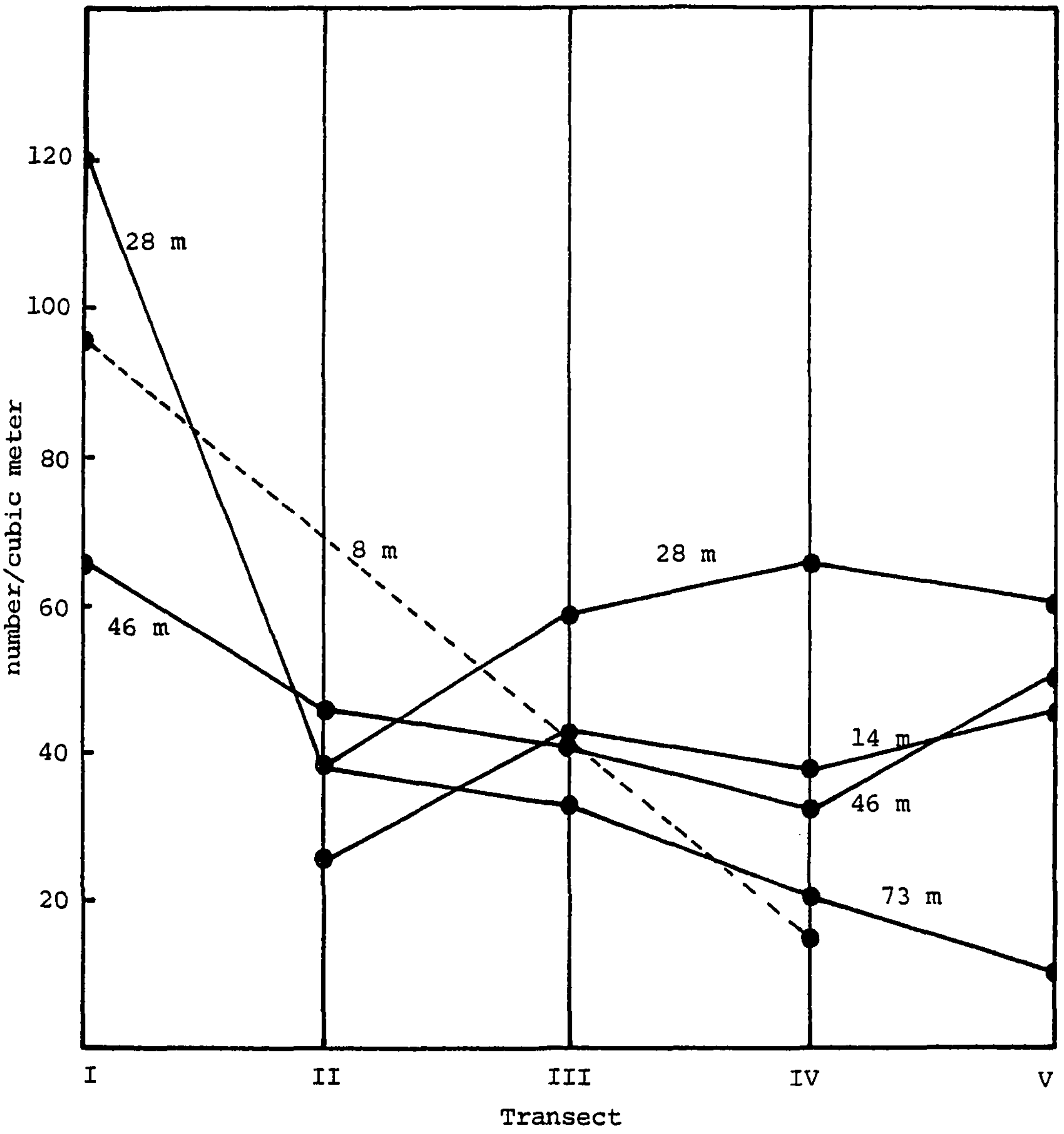


Figure 57. Mean density of *Paracalanus quasimodo* at each sampling station. Values are averaged over months and years. Graphed as in Figure 6 (p. 28).

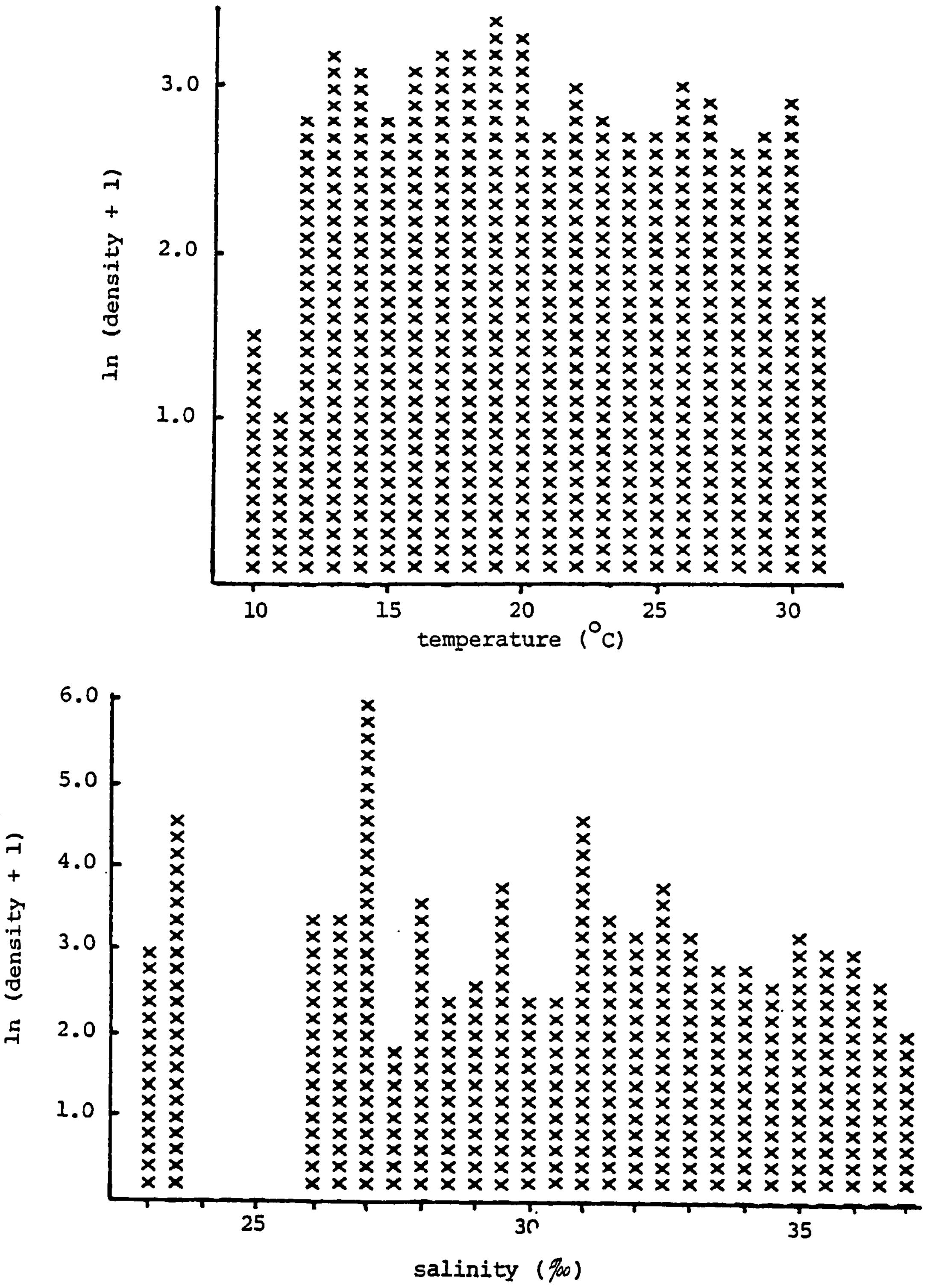


Figure 58. Density relationships with surface temperature and surface salinity for *Paracalanus quasimodo*. See legend of Figure 15 (p. 42).

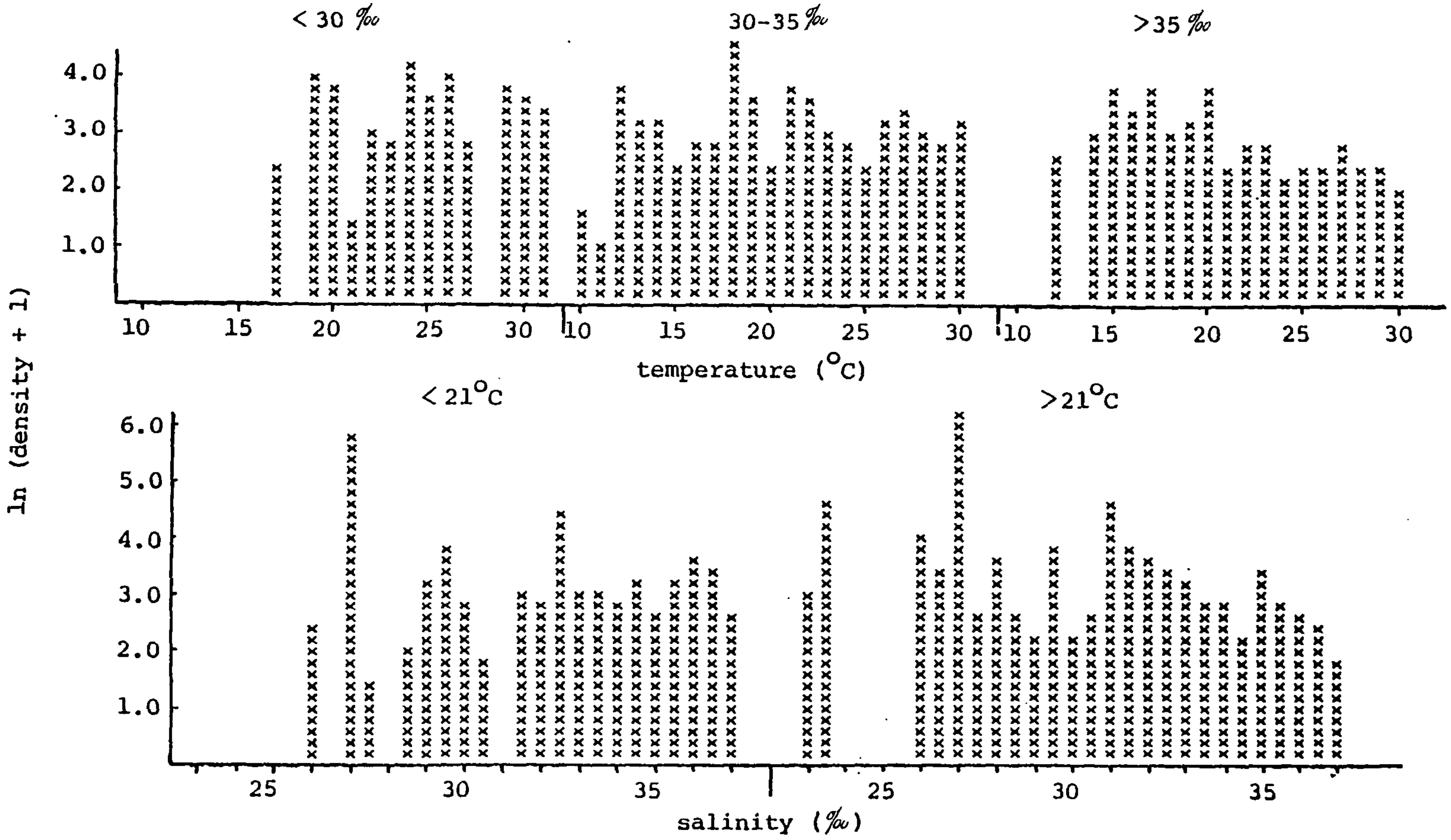


Figure 59. Densities of *Paracalanus quasimodo* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

temperatures above 21°C than in the histogram including all temperatures. The relationship between density and surface temperature itself showed no distinct pattern.

Temperature and salinity regressions for each month separately are shown in Figure 60. A positive relationship with temperature was present during the month of March. A negative relationship with salinity occurred during the summer months of July and August. When regressions between density and temperature were examined at each depth, no significant relationships were found. The negative relationship between density and salinity was present at four out of the five depths. The 46 and 73 m stations had the highest R^2 values. These results indicated that the density of *Paracalanus quasimodo* was affected only by seasonal changes in salinity. Densities were probably not related to changes in salinity with depth. The only negative seasonal regressions occurred in July and August when there appeared to be little change in surface salinity over depth (Fig. 9, p. 31).

Paracalanus crassirostris. *Paracalanus crassirostris* was abundant at the 8 and 14 m stations and rarely found at the deeper stations (Fig. 61). Seasonally, peaks of abundance occurred in the winter and early spring. Densities appeared to be greatest on Transects IV and V (Fig. 62).

The regression models indicated that a negative relationship with salinity could explain 22.4% of the variability of this species. A negative relationship with temperature explained 15.1% of the variability. The stability of the water column also appeared to be important in a simple linear regression model, explaining 8.6% of the

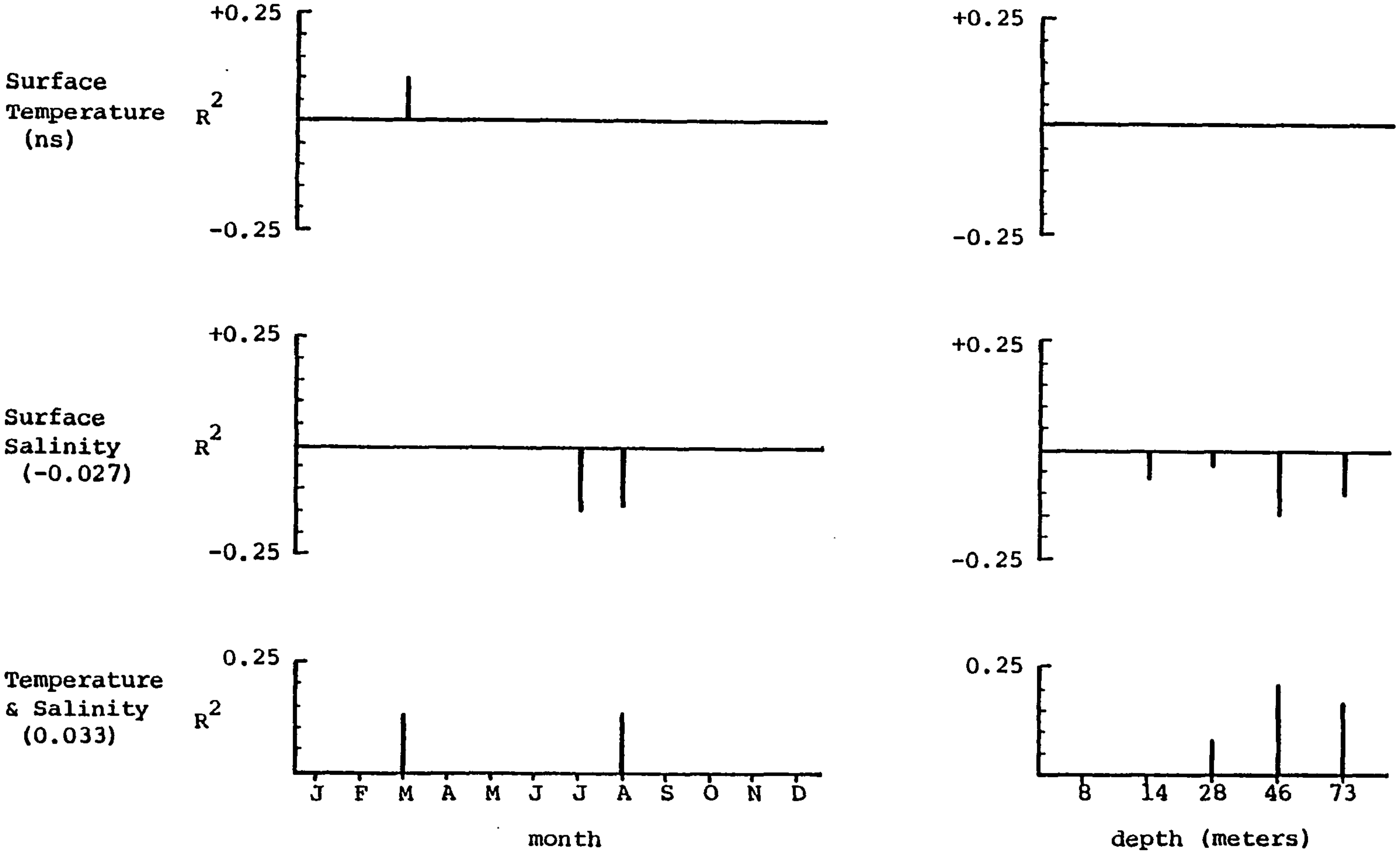


Figure 60. Regression results with surface temperature and surface salinity for *Paracalanus quasimodo*. See legend of Figure 49 (p. 102).

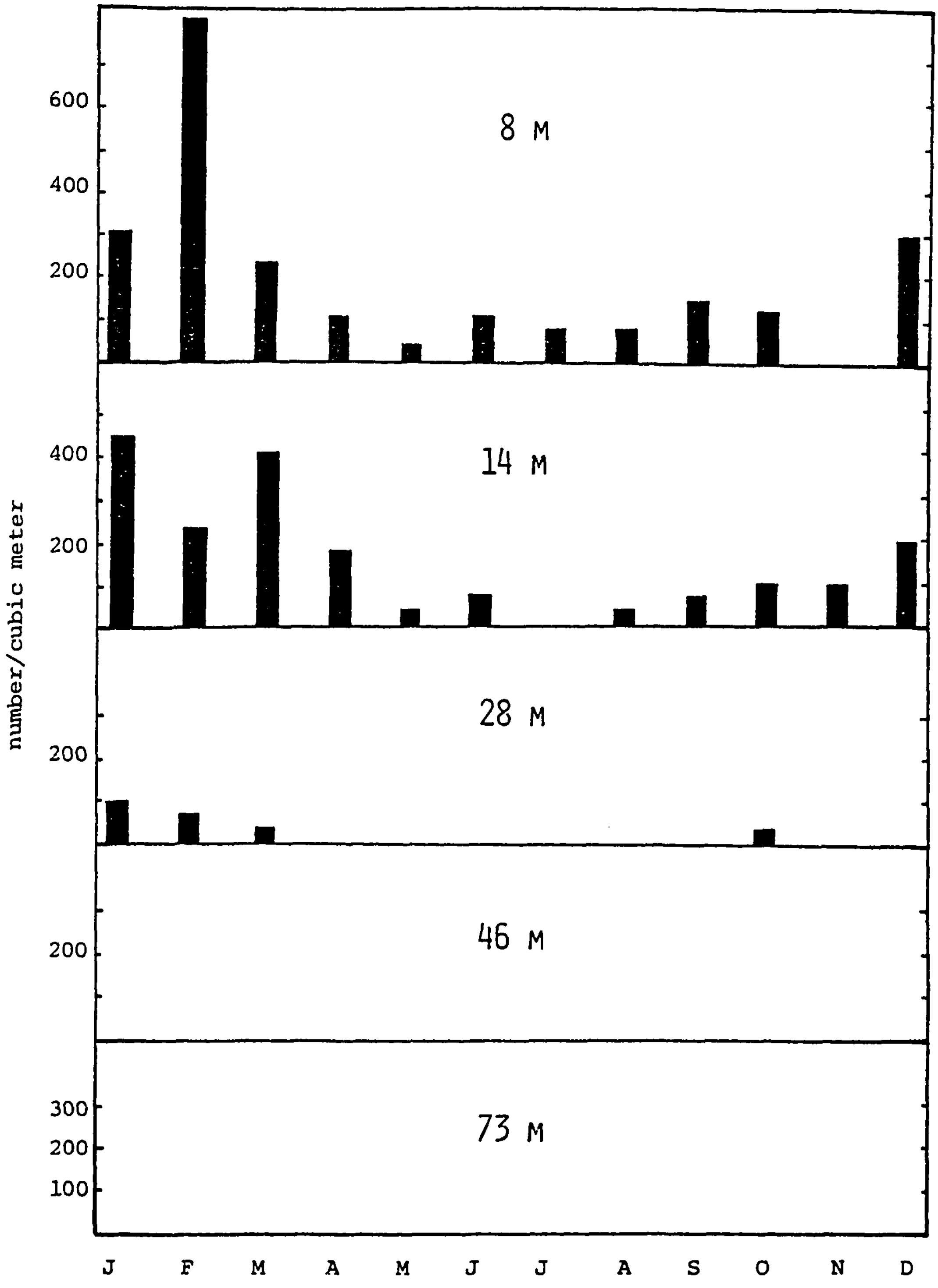


Figure 61. Mean monthly densities of *Paracalanus crassirostris* at each bottom depth sampled. Values are averaged over transects and years.

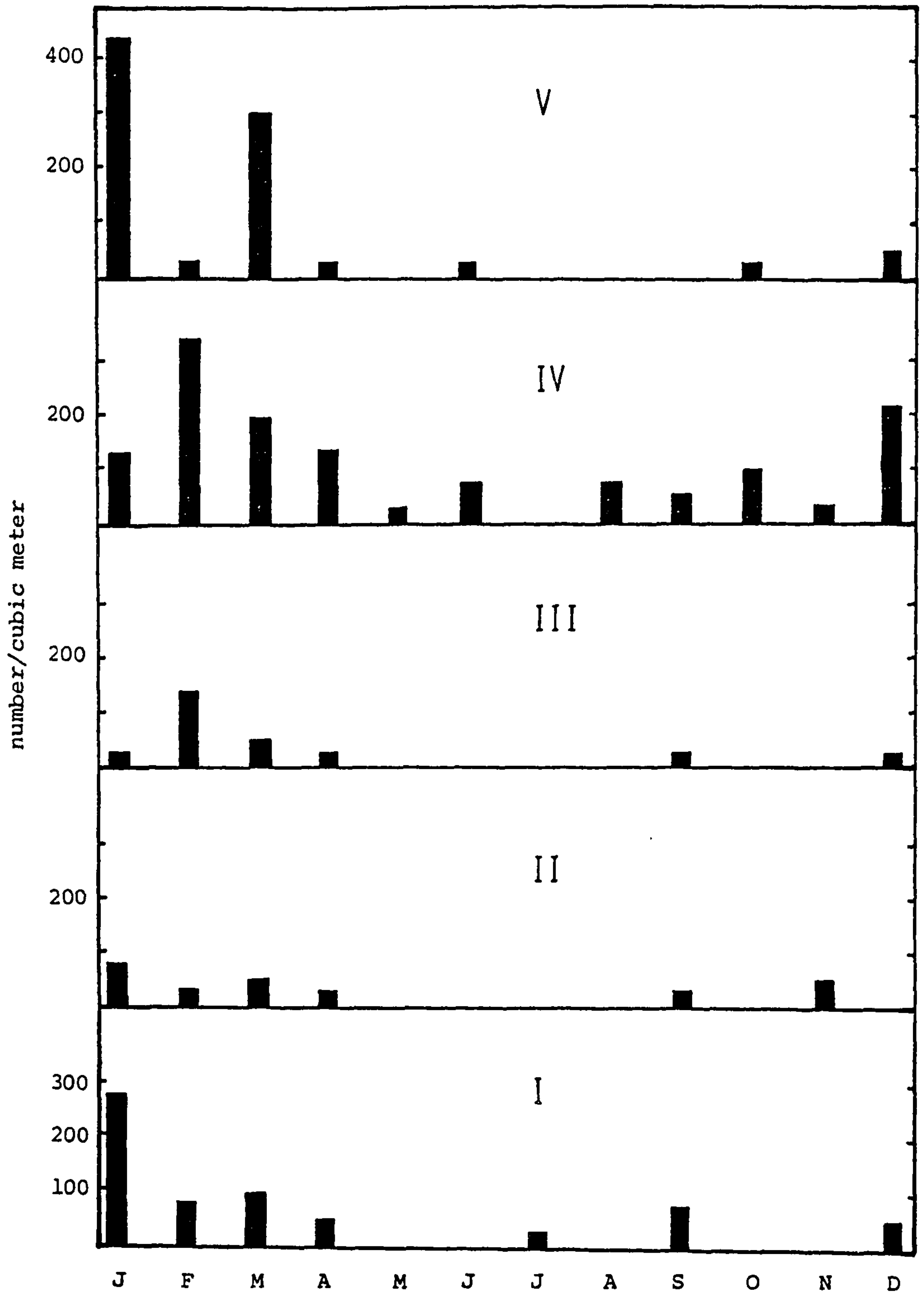


Figure 62. Mean monthly densities of *Paracalanus crassirostris* at each transect. Values are averaged over bottom depths and years.

variability. When temperature and salinity were combined in a multiple regression model the R^2 was 35.1%. Adding stability increased this to 37.4% and adding the previous month's Mississippi runoff brought this value up to 39.0%. Adding other factors did not appear to increase the fit of the multiple regression model. Figure 63 graphically shows the relationships between density and surface salinity and temperature. No obvious temperature salinity interaction was apparent in the data (Fig. 64).

Clausocalanus furcatus. This species was abundant at the 28, 46, and 73 m stations. At the deepest stations (46 and 73 m) mean densities were greatest during July and remained relatively high through December (Fig. 65). Monthly mean densities at the 28 m stations were also high during July but the fall values were lower than those at the deeper stations. At the 8 and 14 m stations this species occurred only in small numbers, mostly in the summer. The significant Month*Year interaction in the AOV can probably be attributed to the relatively high densities in 1964 from June through December.

Simple linear regression models indicated that a number of factors explained significant portions of the variability in the density of this species. Surface salinity and surface temperature were the most important factors explaining 21.5 and 11.6% of the variability, respectively. Stability and upwelling also appeared to be relatively important as simple regression variables. When temperature and salinity were combined in a multiple regression model they explained 31% of the variability. Adding stability and upwelling increased this value to 35.8%.

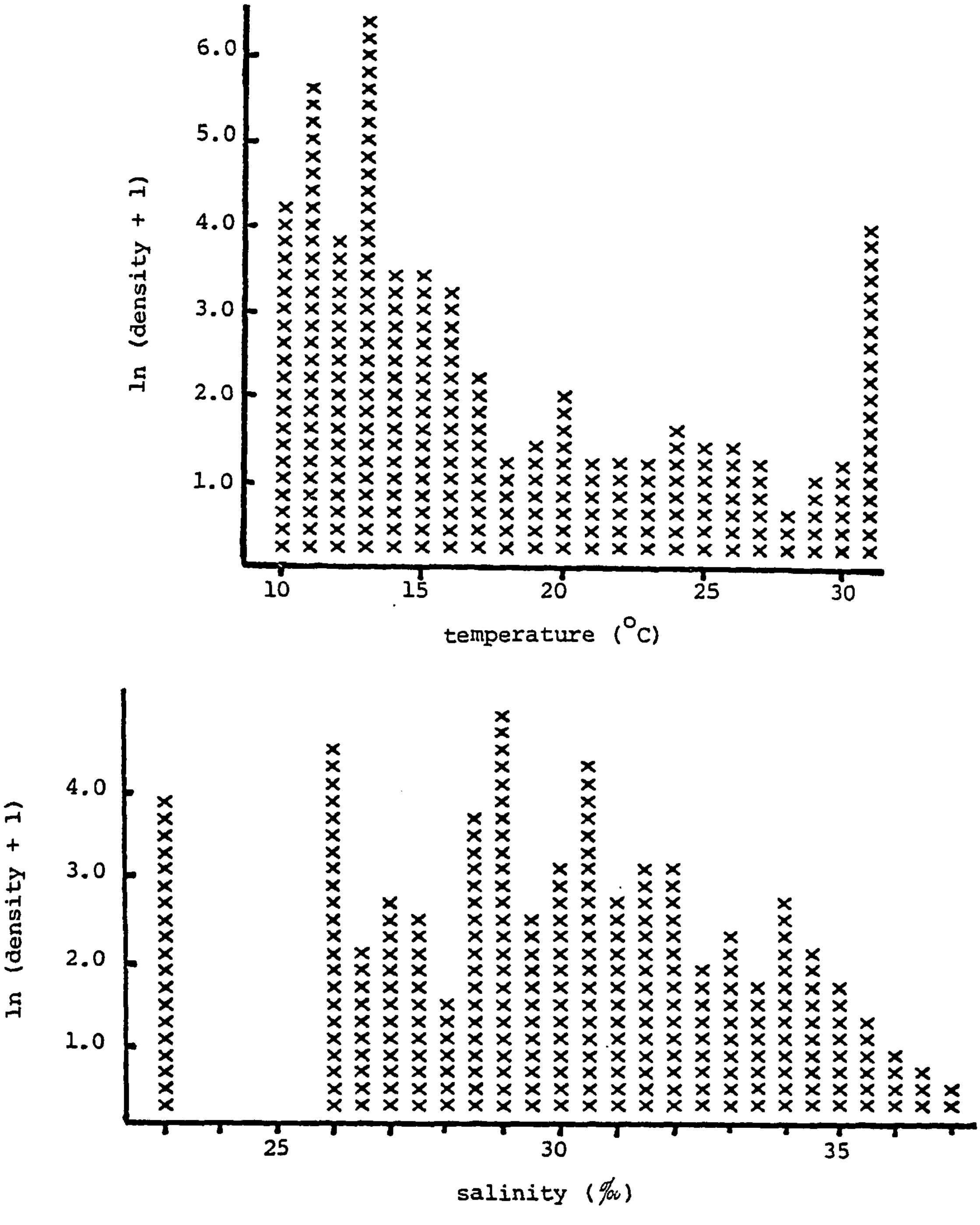


Figure 63. Density relationships with surface temperature and surface salinity for *Paracalanus crassirostris*. See legend of Figure 15 (p. 102).

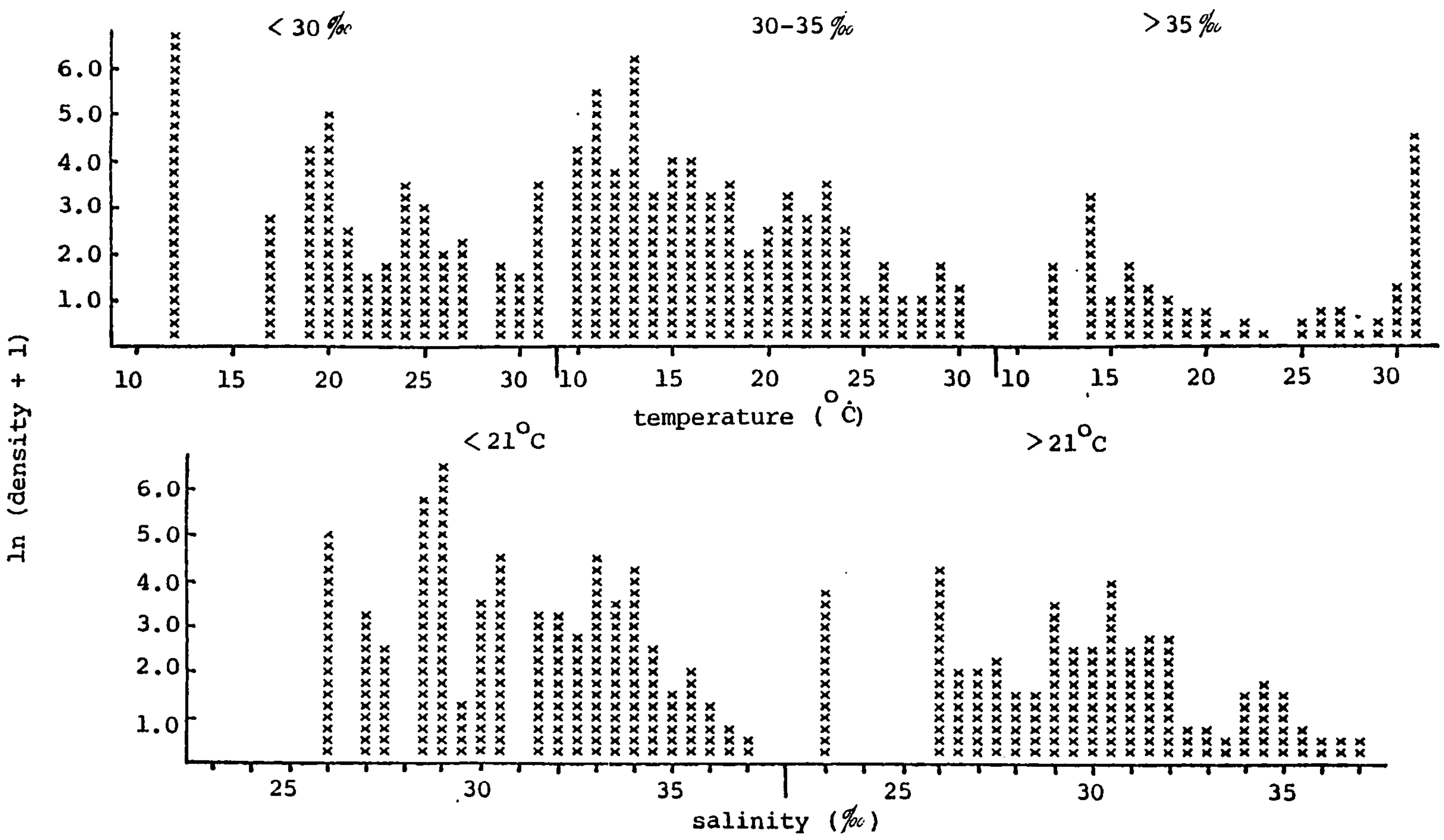


Figure 64. Densities of *Paracalanus crassirostris* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

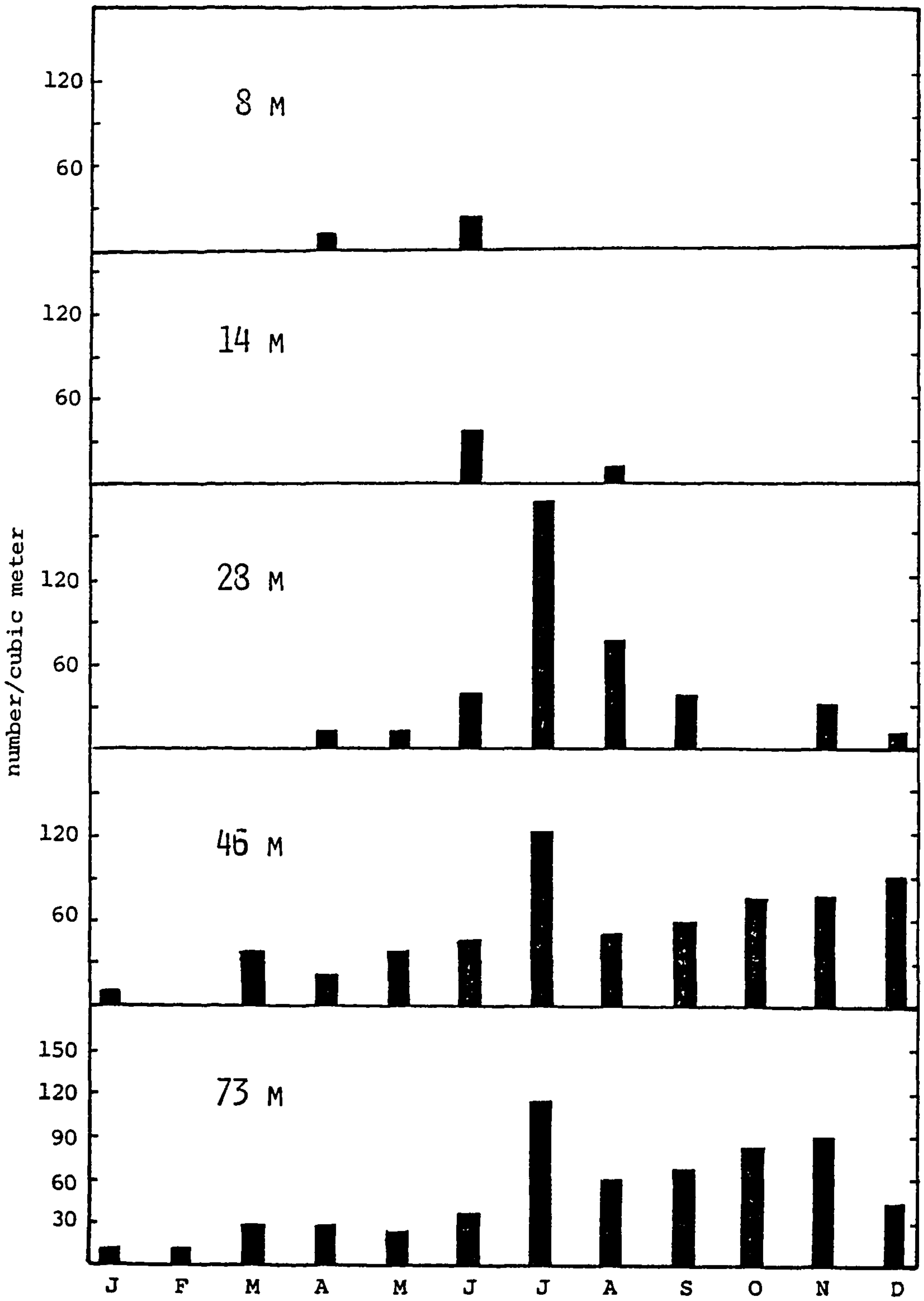


Figure 65. Mean monthly densities of *Clausocalanus furcatus* at each bottom depth sampled. Values are averaged over transects and years.

The overall regression relationship between the log of the density of this species and surface temperature was positive. Up to 23°C this relationship appears positive in Figure 66. At temperatures above 23°C however no distinct pattern was apparent. This density temperature relationship appeared to be consistent over the three salinity classes although only a few samples had temperatures below 23°C and salinities below 30°/oo (Fig. 67). The relationship with surface salinity itself was strongly positive with the highest salinities having the highest densities. No specimens were found in the 15 samples with temperatures below 21°C and salinities below 31°/oo.

Oncaea media. This species appeared to be most abundant at the 28 and 46 m stations. The Depth*Month and Transect*Month interactions were both significant at the 1% level in the AOV and seasonal variability was therefore plotted at each depth (Fig. 68) and each transect (Fig. 69). At the shallowest stations (8 and 14 m) *Oncaea media* occurred mostly in the summer months and at the 46 and 73 m stations the greatest densities occurred during the spring. No distinct seasonal pattern appeared to be consistent over transects.

A positive relationship with surface salinity explained 10.9% of the variability in the density of this species in a simple linear regression model. When all physical and chemical variables were combined in a multiple regression model it explained 22.6% of the variability. The relationship between density and salinity is shown in Figure 70. When this relationship was examined over the two temperature classes the positive trend between density and salinity seemed less distinct (Fig. 71). The relationship between density and

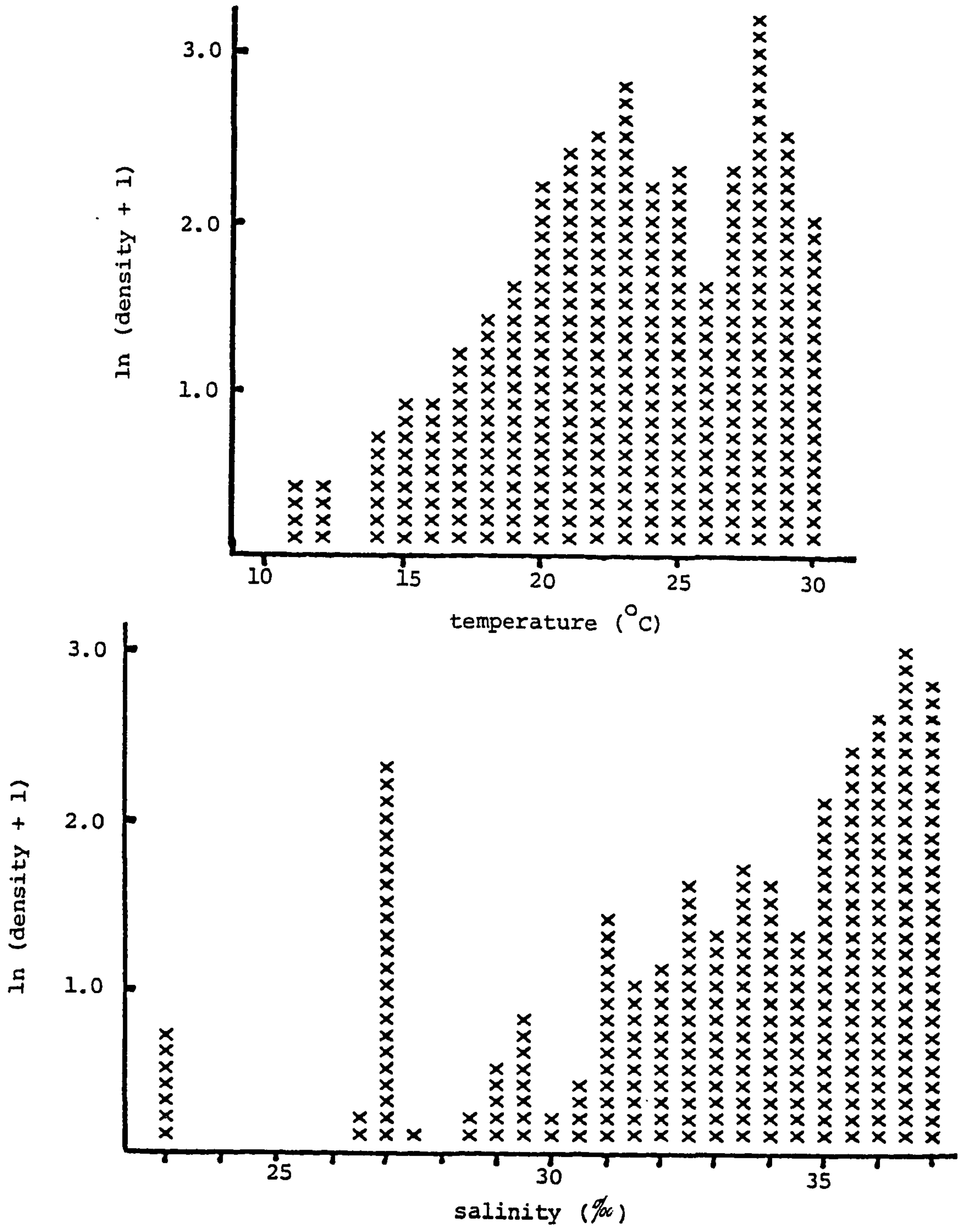


Figure 66. Density relationships with surface temperature and surface salinity for *Clausocalanus furcatus*. See legend of Figure 15 (p. 42).

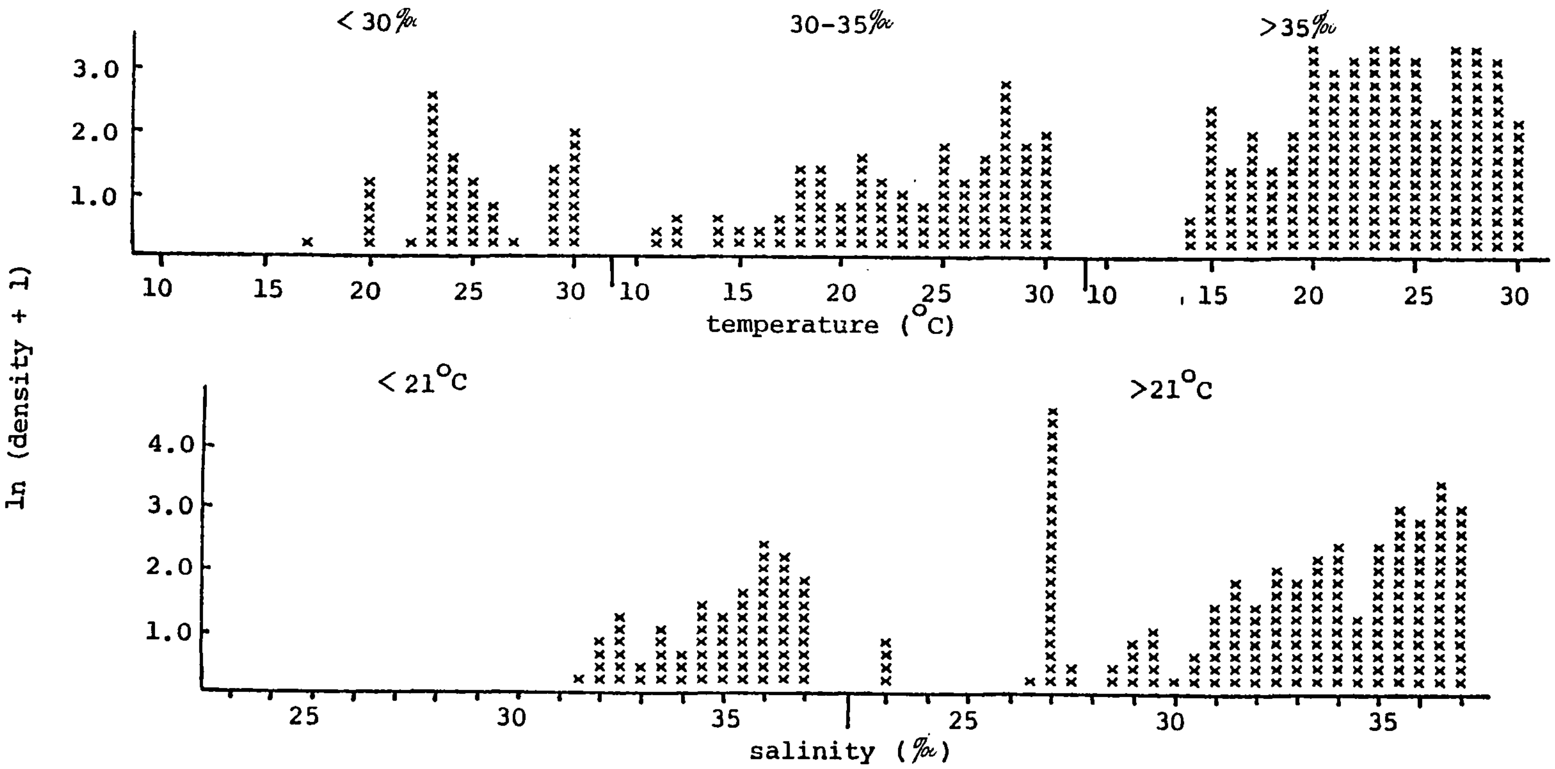


Figure 67. Densities of *Clausocalanus furcatus* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

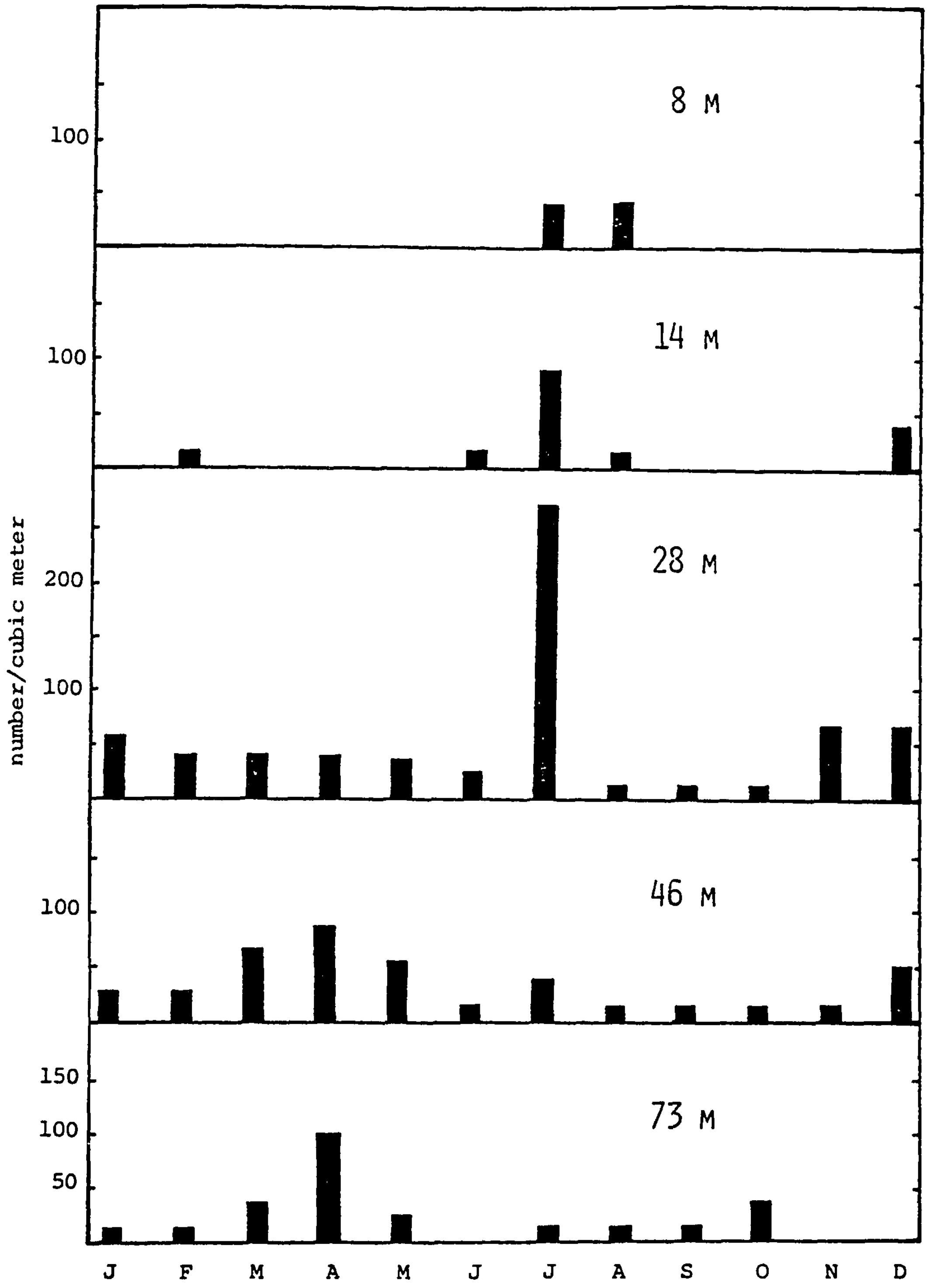


Figure 68. Mean monthly densities of *Oncaea media* at each bottom depth sampled. Values are averaged over transects and years.

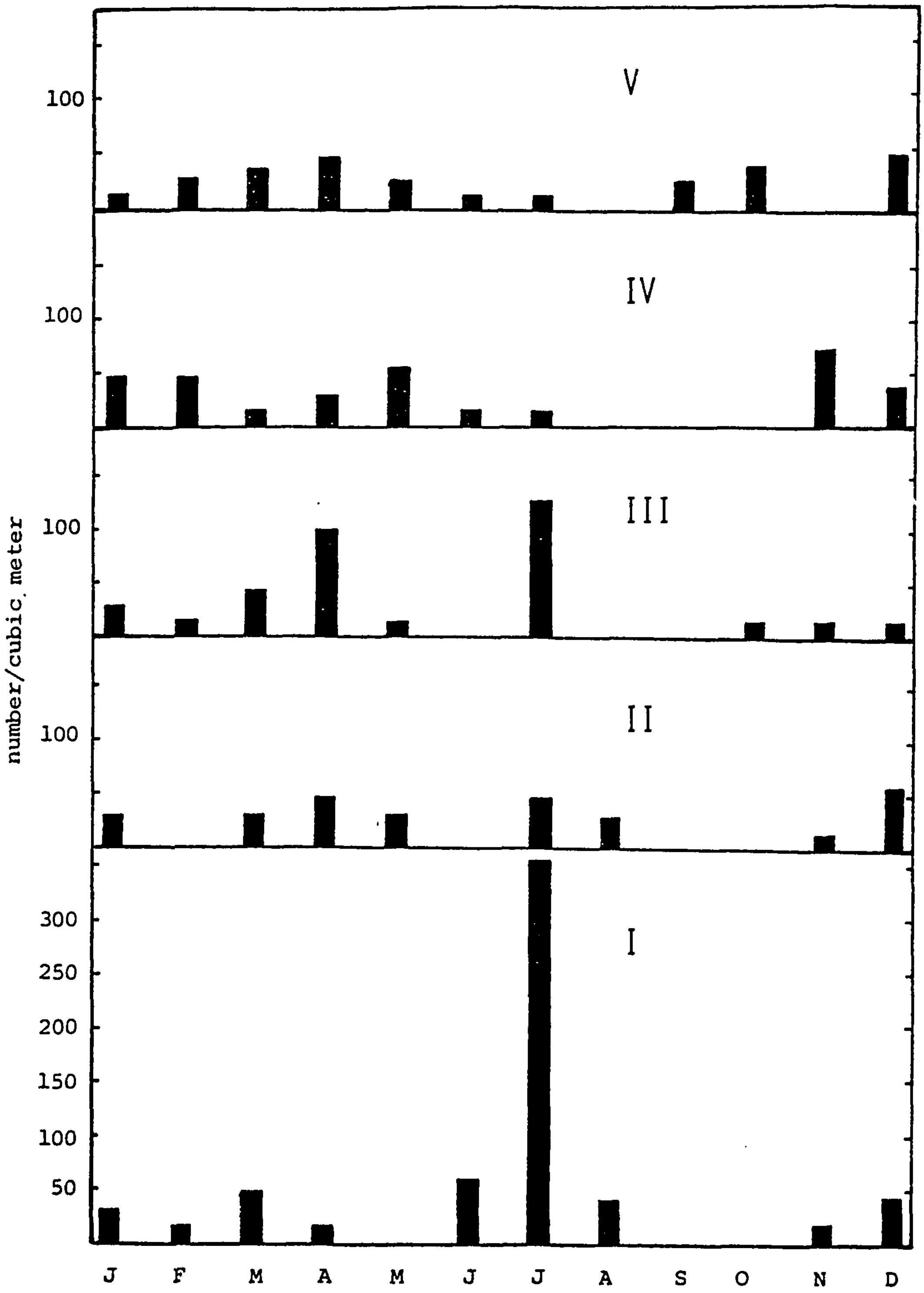


Figure 69. Mean monthly densities of *Oncaea media* on each transect. Values are averaged over bottom depths and years.

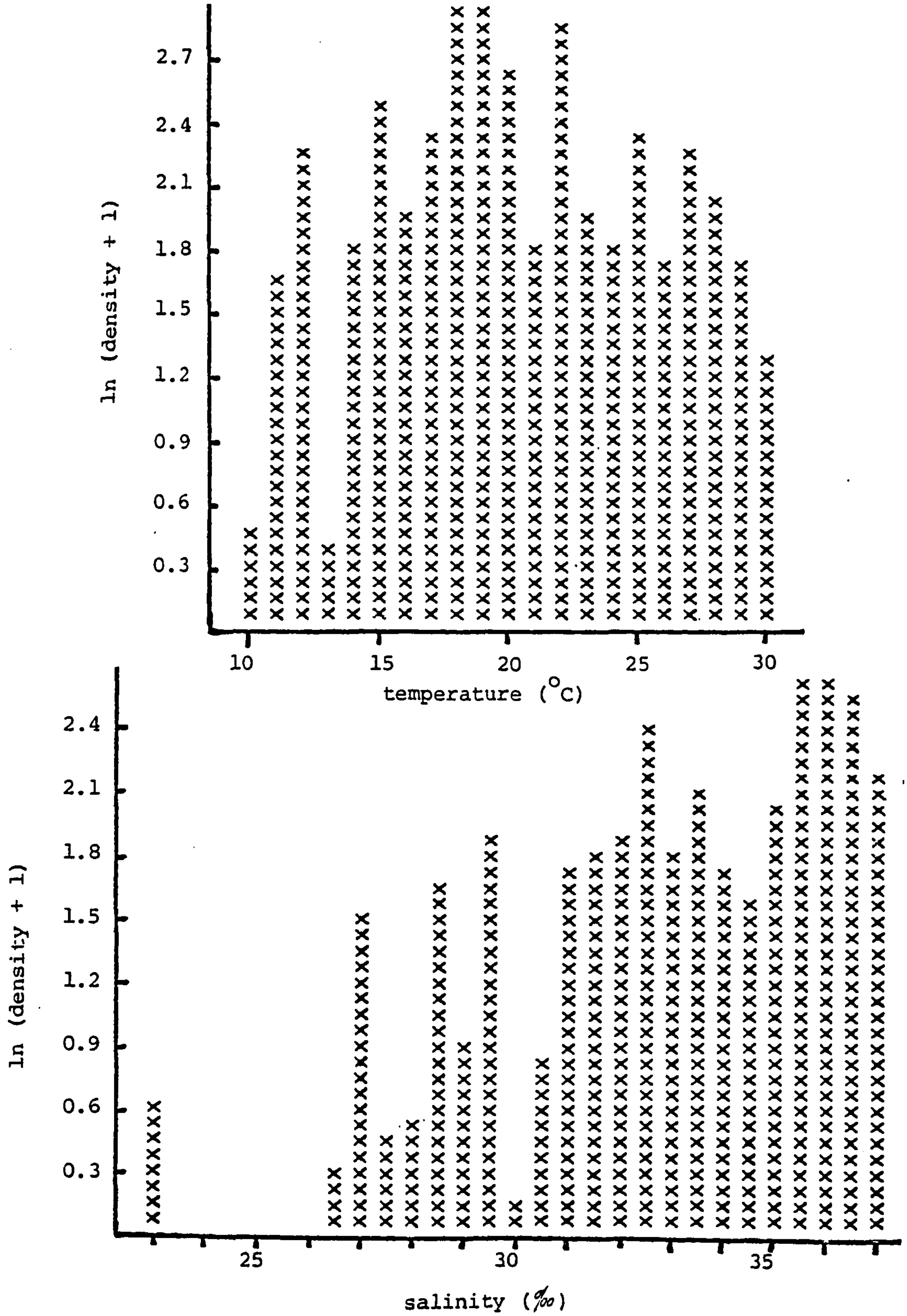


Figure 70. Density relationships with surface temperature and surface salinity for *Oncaea media*. See legend of Figure 15 (p. 42).

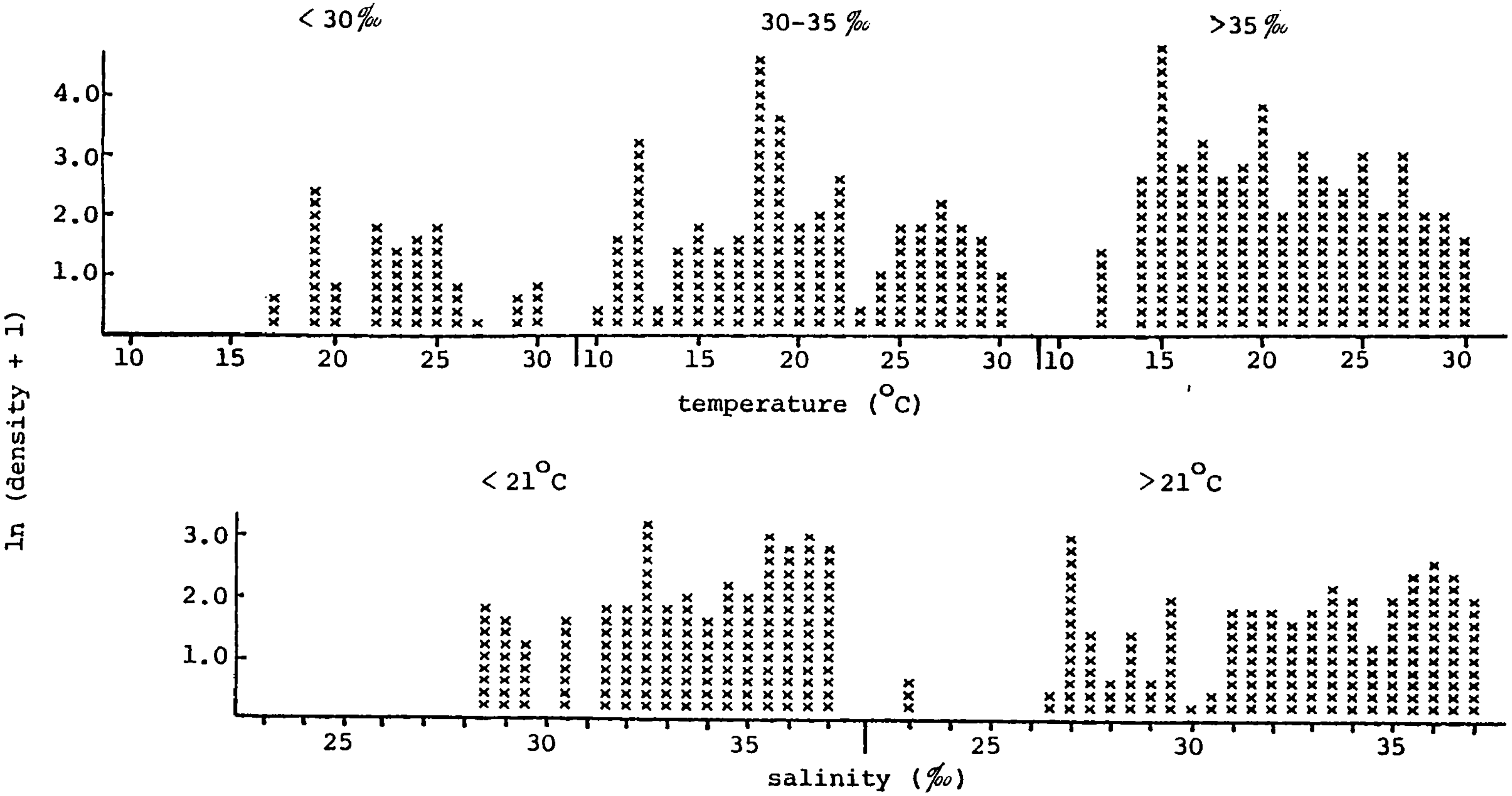


Figure 71. Densities of *Oncaea media* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

temperature itself appeared to be positive at the lower temperatures and negative at the higher values. The density peak or optimum temperature was around 18 to 19°C (Fig. 70). This pattern was also not as distinct when the different salinity classes were examined separately (Fig. 71).

Oithona nana. *Oithona nana* was one of the most abundant cyclopoids found, comprising 5.6% of all of the female copepods in the sampling area. This species was most abundant at the shallow stations and almost never present at the 46 and 73 m stations (Fig. 72). Densities were highest in the summer and the fall and the monthly variability appeared to be greatest at the 8 m stations.

Surface salinity was the only significant variable in the simple regression models with an R^2 of 7.0% (negative slope). Although the previous month's Mississippi runoff was not significant by itself, when combined with salinity in a multiple regression model, the model explained 8.9% of the variability in the density of this species. A negative trend between density and surface salinity appeared to be present at salinities above approximately 30°/oo (Fig. 73). A similar density-salinity pattern could also be seen when samples with temperatures below 21°C were examined (Fig. 74). At higher temperatures, however, the negative relationship between density and salinity was not obvious until salinities reached 34 to 35°/oo. The relationship between density and surface temperature showed no distinct pattern (Fig. 73).

When regressions with temperature and salinity were calculated for each month, September through December had high negative R^2 values for both factors. Regressions between density and temperature and salinity

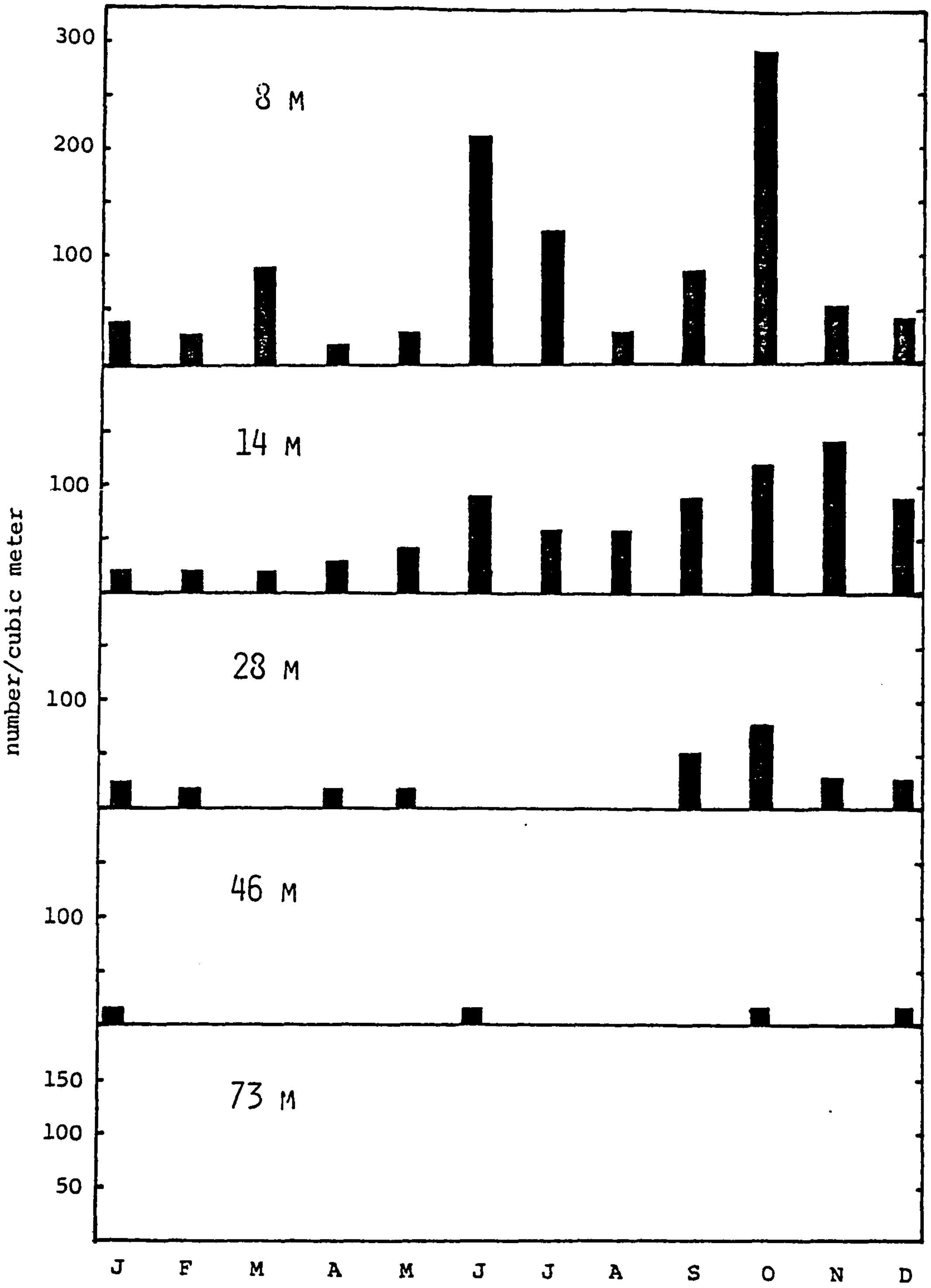


Figure 72. Mean monthly densities of *Oithona nana* at each bottom depth sampled. Values are averaged over transects and years.

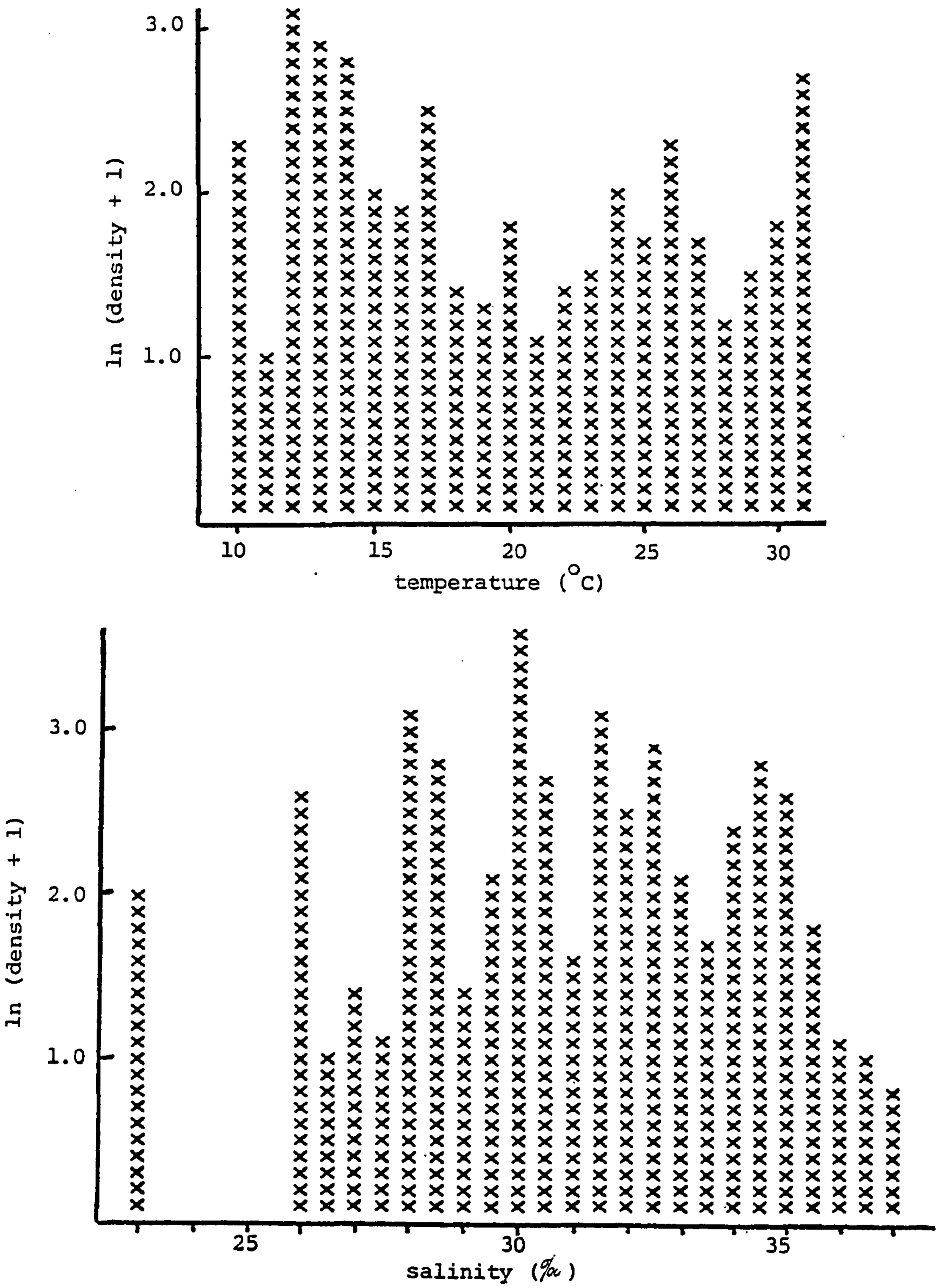


Figure 73. Density relationships with surface temperature and surface salinity for *Oithona nana*. See legend of Figure 15 (p. 42).

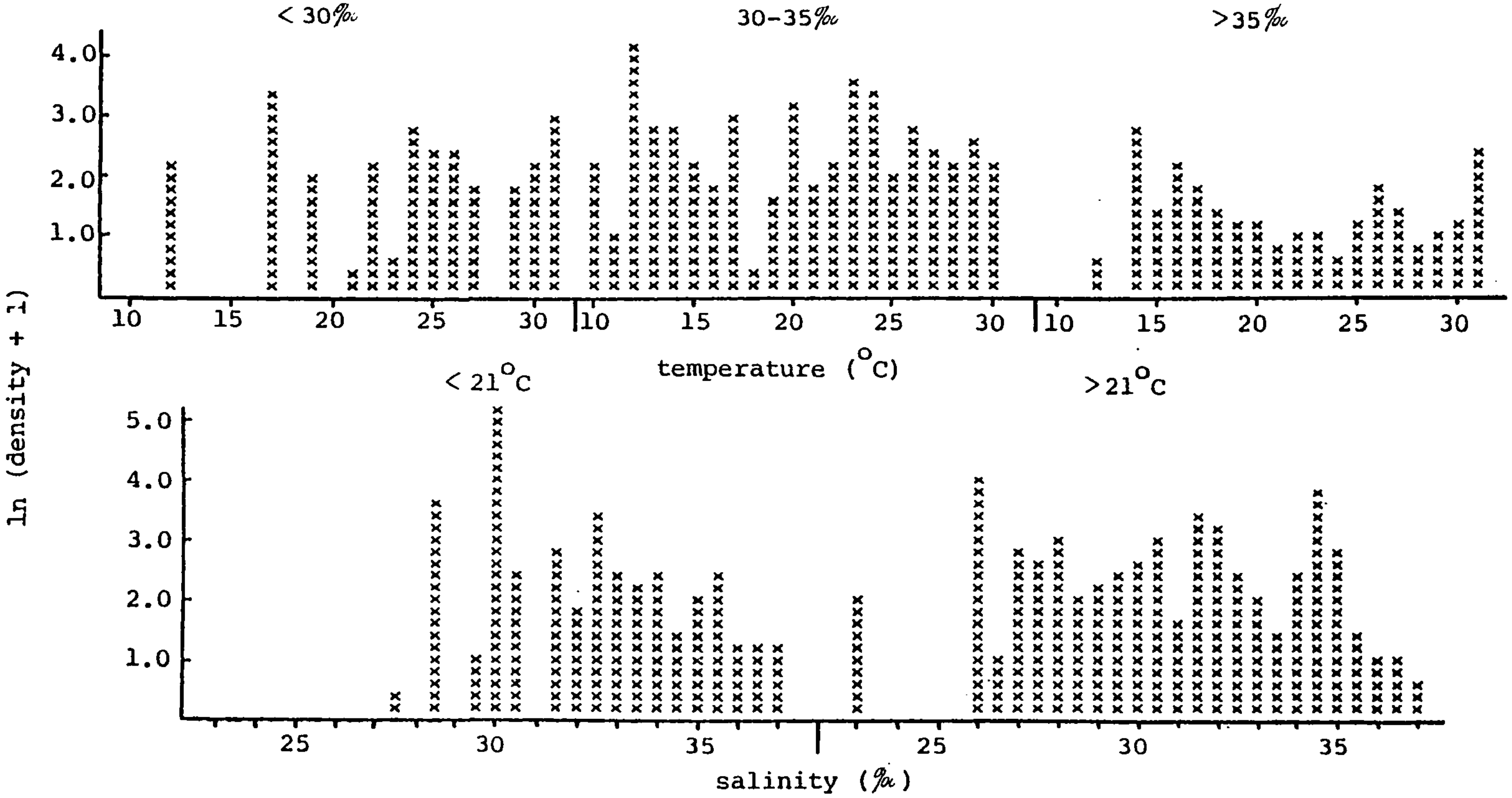


Figure 74. Densities of *Oithona nana* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

at each depth however indicated little relationship with temperature and a positive relationship with salinity at the 8 m stations (Fig. 75).

Oithona plumifera. This species was also one of the most abundant cyclopoid copepods found in the study area. Unlike *Oithona nana, O. plumifera* was most abundant at the deeper stations and was infrequently found at the 8 and 14 m depths (Fig. 76). It occurred most frequently from June through December and relatively low densities were observed in the spring. The effect of Transect was highly significant (P = 0.8%), apparently due to high density values on Transect V. The tendency for the stations on Transect V to be further offshore than the stations on the other transects probably was a contributing factor in these results. The analysis of covariance with the time of sampling as the covariate indicated a highly significant (P = 0.8%) Transect*Month interaction. This could have been due to the very low densities found during all months on Transect I. The other AOV results remained unchanged.

Results from the regression models with physical and chemical factors indicated a number of significant variables. Surface salinity (26.3%), surface temperature (11.9%), and the PMMSROFF (5.6%) all appeared to explain a significant percent of the variability in density in simple regressions. When temperature and salinity were combined the R^2 was 35.9%. The best three factor multiple regression model included these two factors and the cross shelf current and had an R^2 of 37.1%. The addition of PMMSROFF only increased this value to 37.4%. The positive relationship between density and surface salinity is shown in

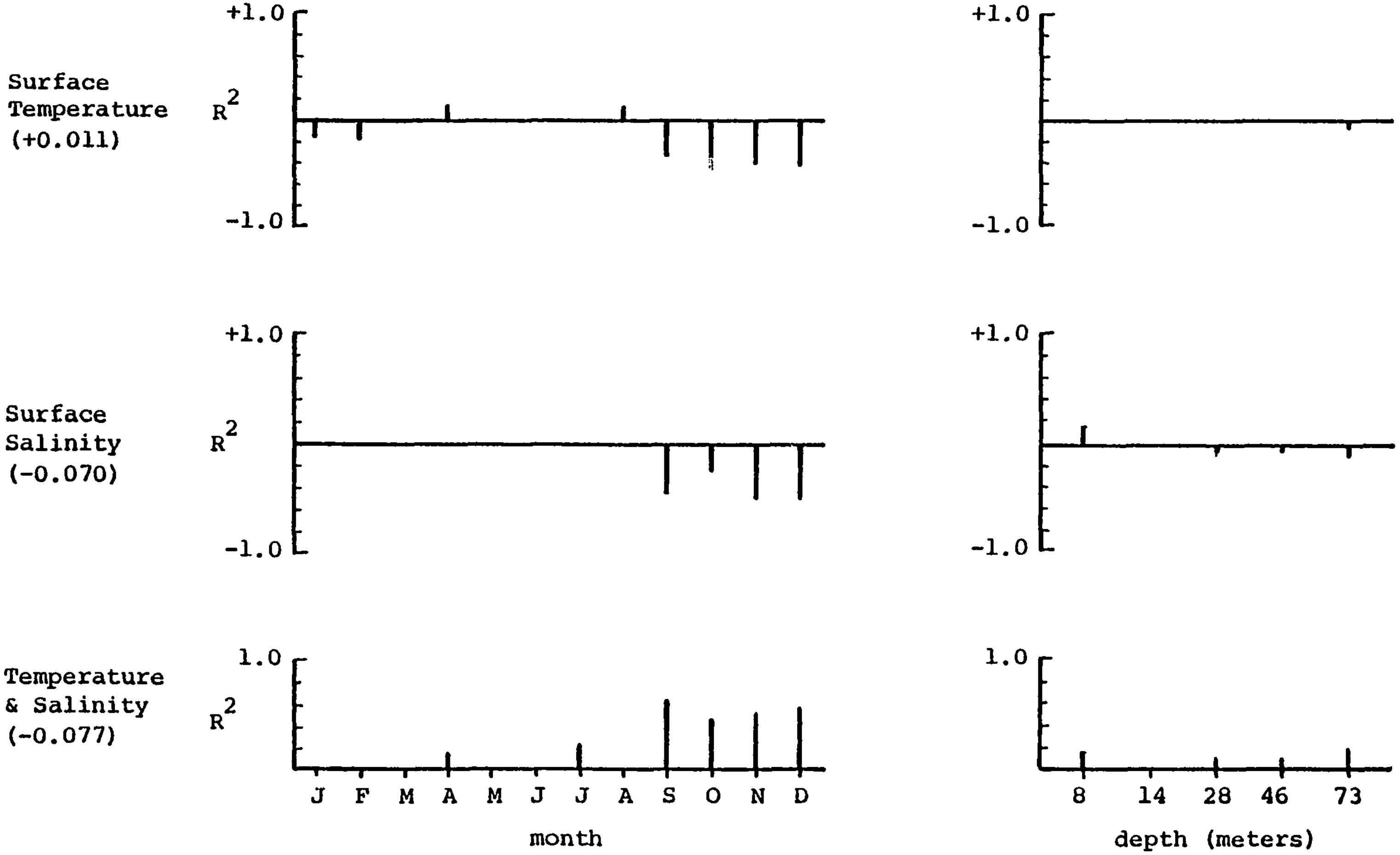


Figure 75. Regression results with surface temperature and surface salinity for *Oithona nana*. See Legend of Figure 49 (p. 102).

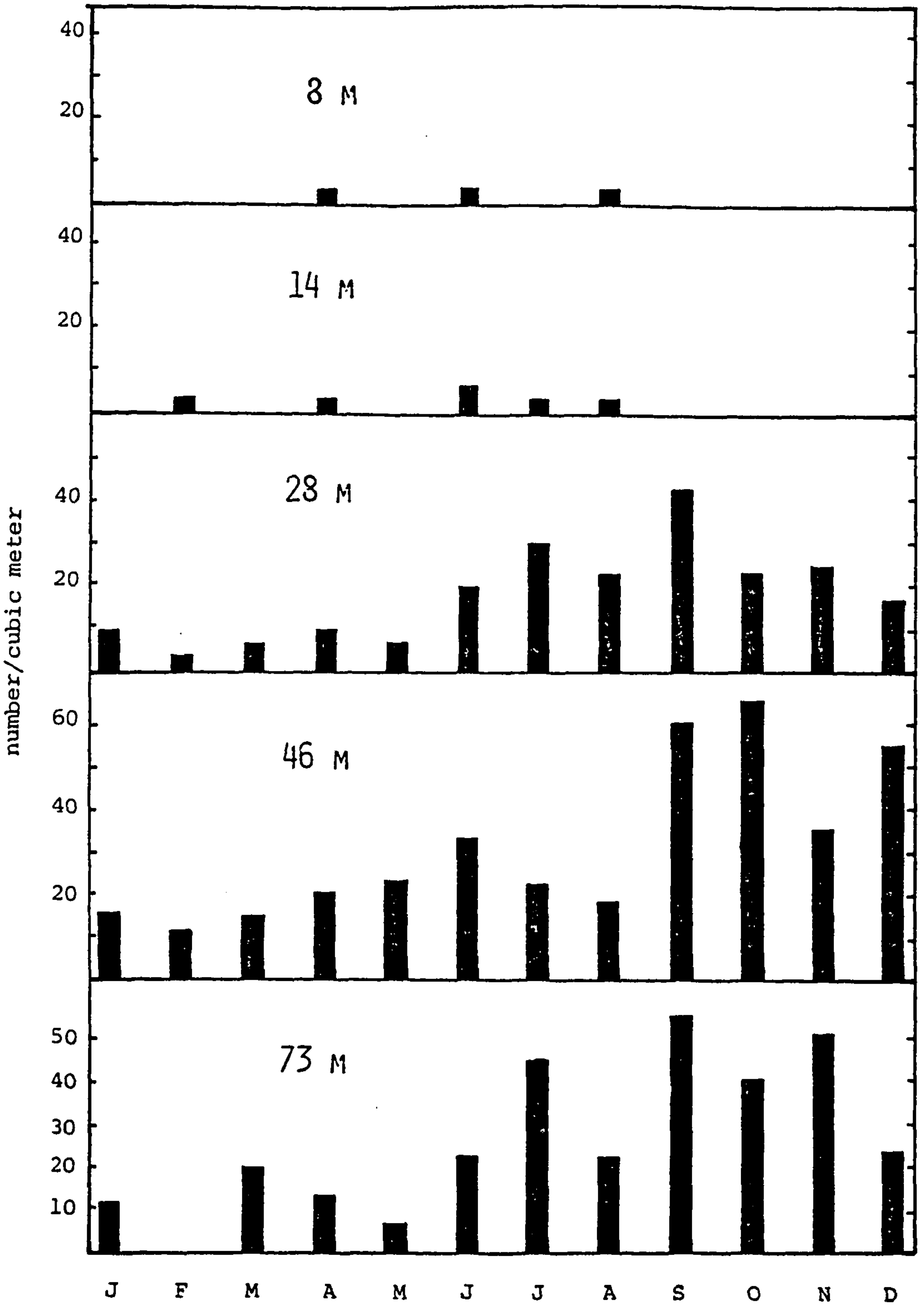


Figure 76. Mean monthly densities of *Oithona plumifera* at each bottom depth sampled. Values are averaged over transects and years.

Figure 77. The density relationship with surface temperature was also positive. At low salinities however (below 35°/oo), the positive relationship with temperature was not as apparent (Fig. 78).

The regression analyses with temperature and salinity for each month and depth are shown in Figure 79. High densities in this species appeared to be closely related to high surface temperatures and high surface salinities whether these factors were changing due to depth or season. The only negative relationships were with temperature during June and August when the highest mean surface temperatures in the sampling area were found at the 14 m stations (Fig. 3, p. 24).

Temora turbinata. *Temora turbinata* was generally most abundant at the shallow stations (8 and 14 m) and its density appeared to decrease with the depth of the water at the other stations (Fig. 80). Averaged over transects, depths, and years, mean monthly density values peaked in July and also in the fall months. The July density peak was mainly due to high densities in 1963 (Fig. 81). High fall densities were present during all 3 years. When mean monthly densities were examined on each transect (Fig. 82) the above seasonal distribution was not as evident.

The regression models did not appear to explain much of the variability in the density of this species. The stability of the water column appeared to be most important and only explained 2.3% of the variability. All variables combined explained less than 10% of the variability in a multiple regression model. The histograms of density versus surface salinity indicated a slight negative relationship at

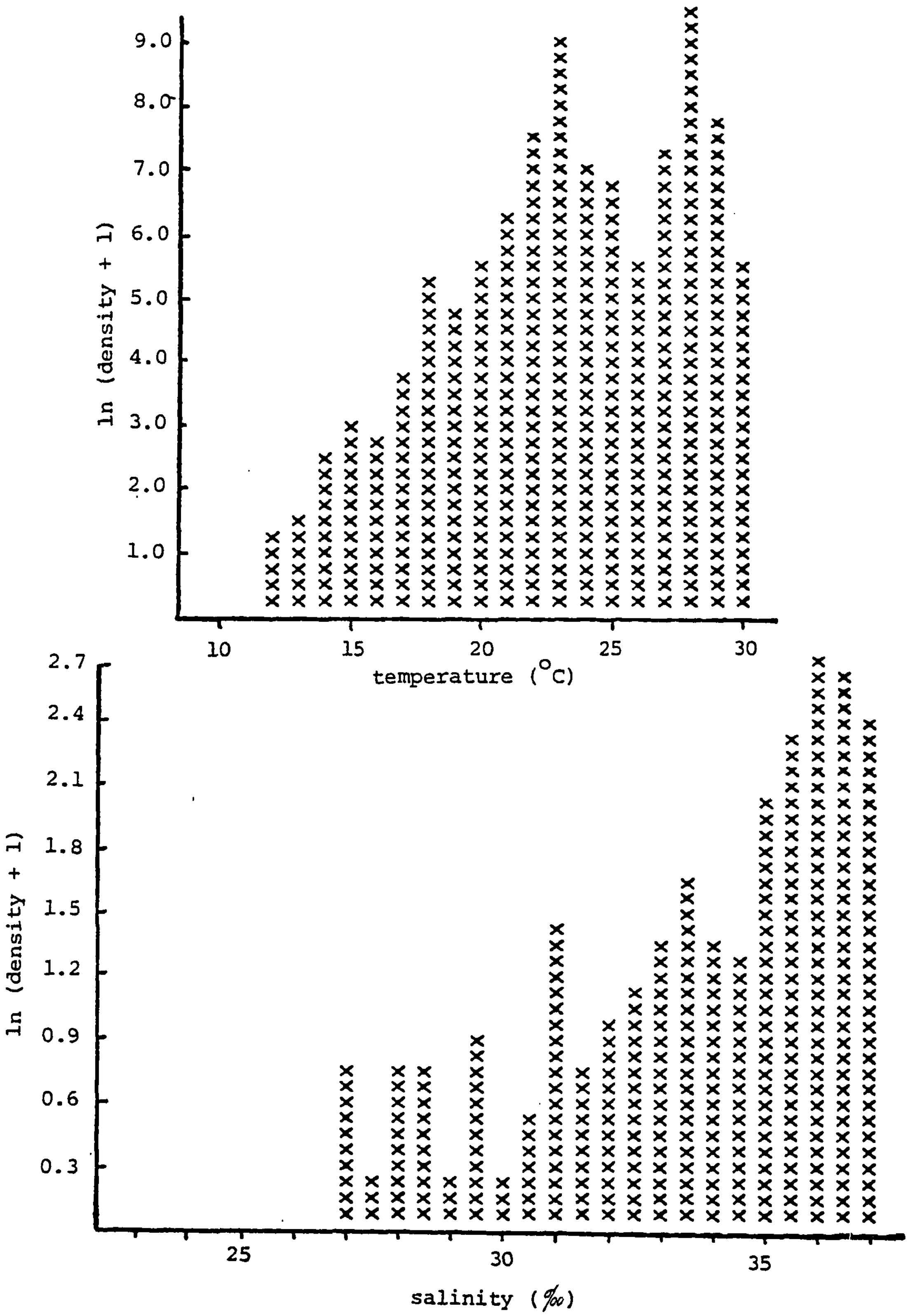


Figure 77. Density relationships with surface temperature and surface salinity for *Oithona plumifera*. See legend of Figure 15 (p. 42).

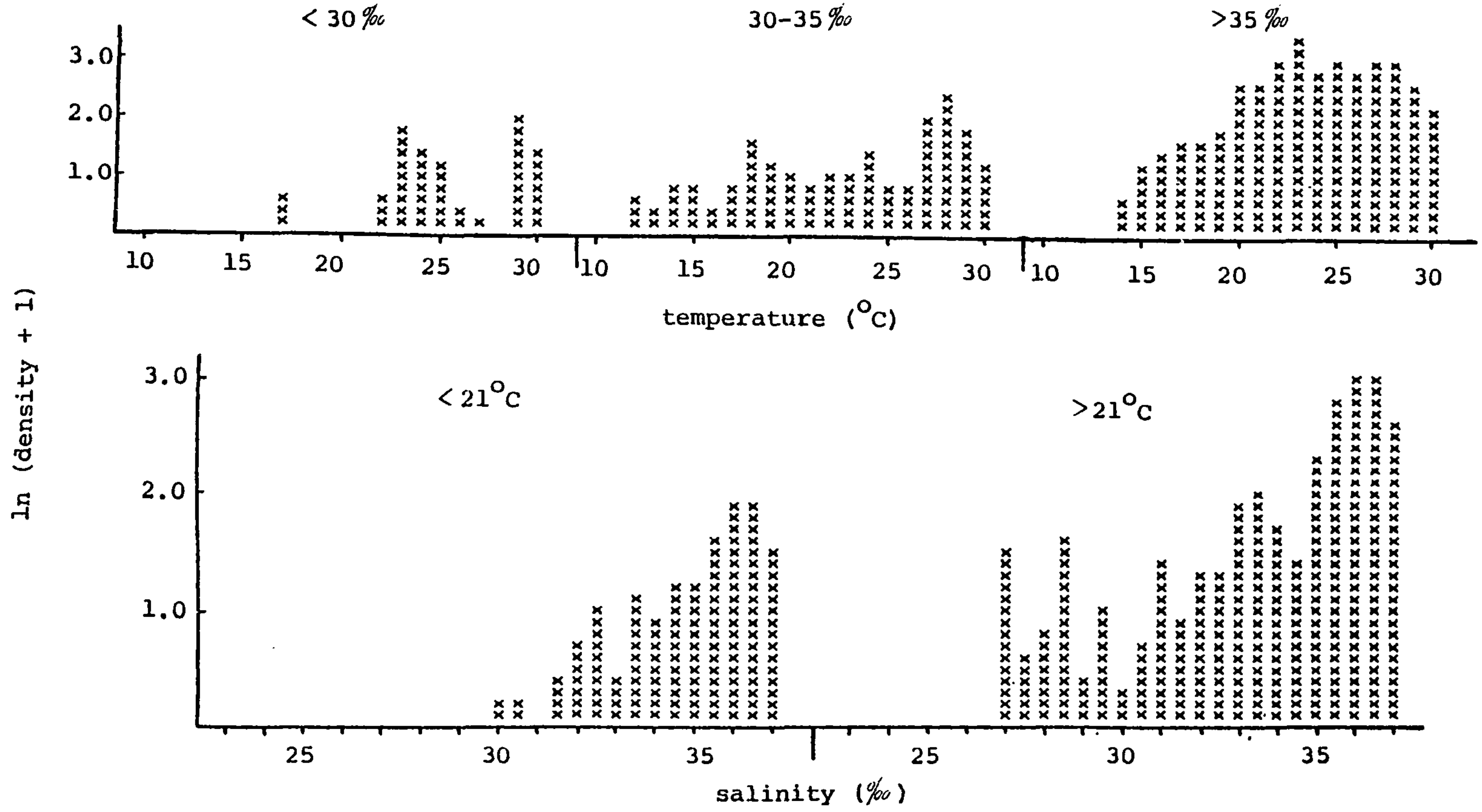


Figure 78. Densities of *Oithona plumifera* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

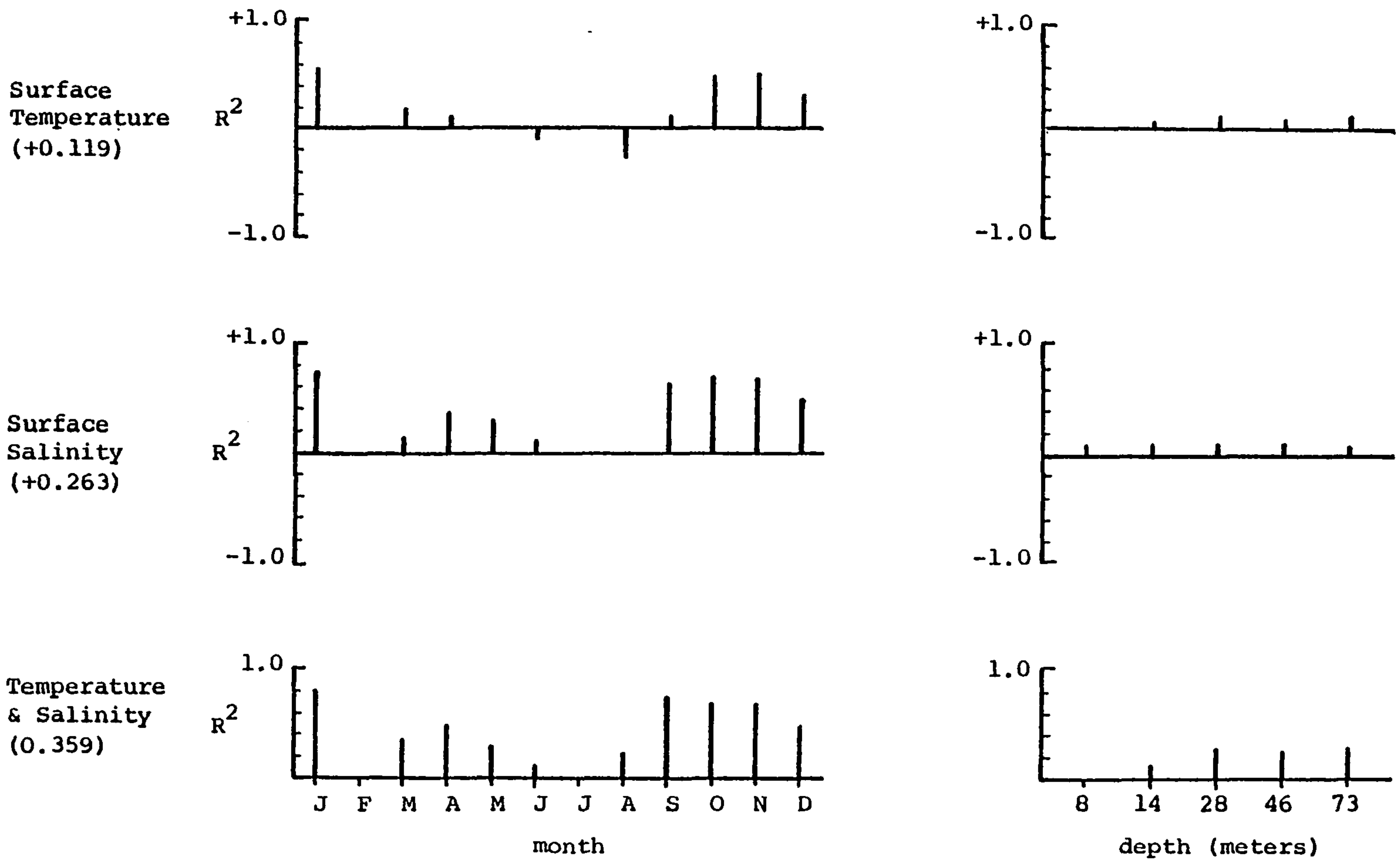
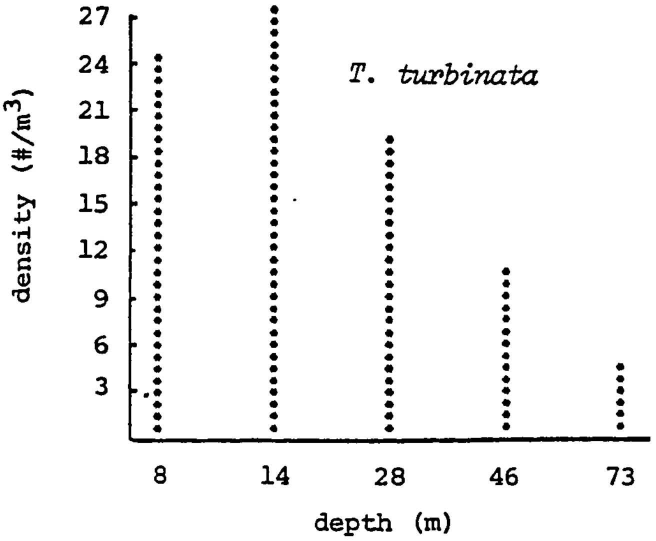


Figure 79. Regression results with surface temperature and surface salinity for *Oithona plumifera*. See legend of Figure 49 (p. 102).



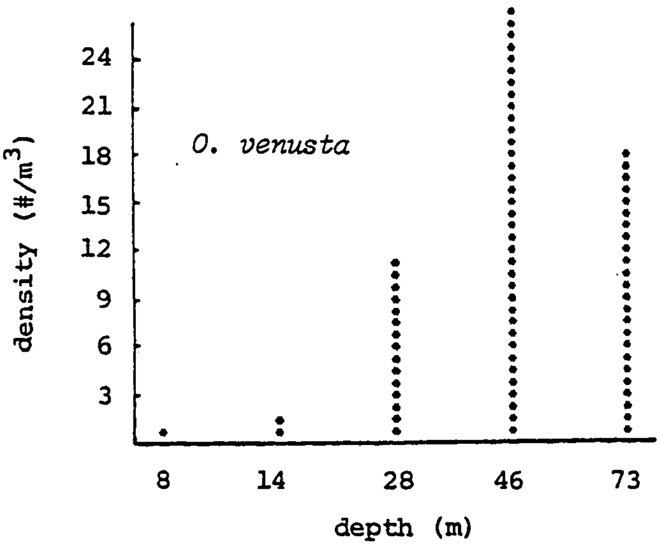


Figure 80. Mean densities of *Temora turbinata* and *Oncaea venusta* at each bottom depth.

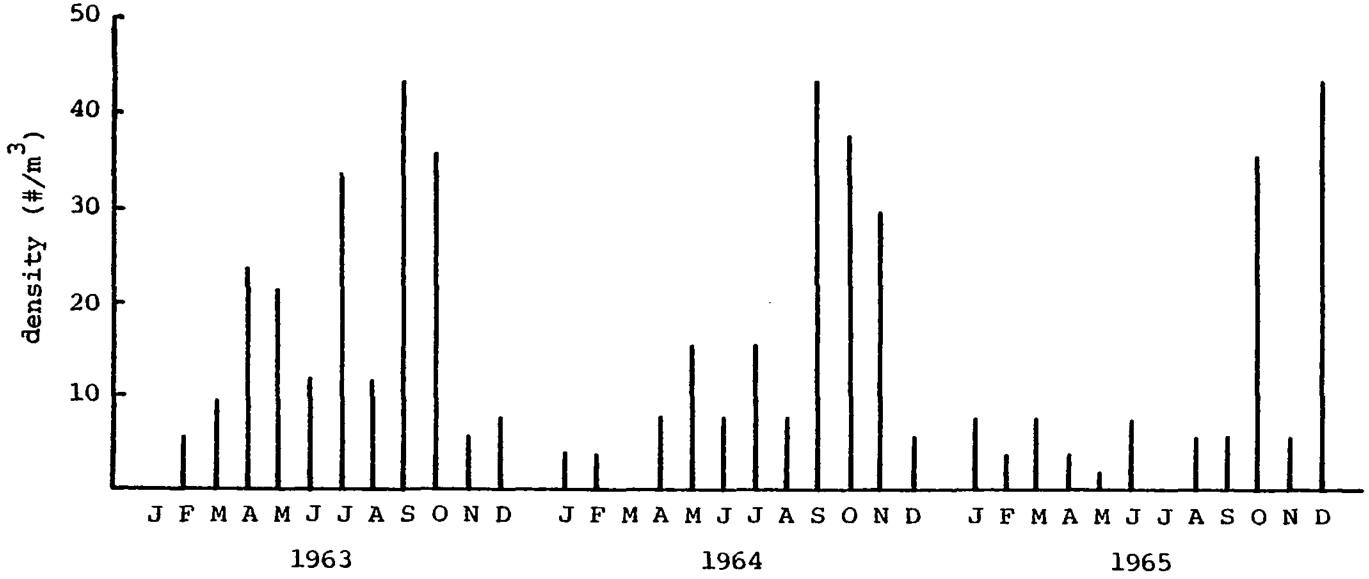


Figure 81. Mean monthly densities of *Temora turbinata* over the entire sampling area for the three years of the study. Values are averaged over transects and bottom depths.

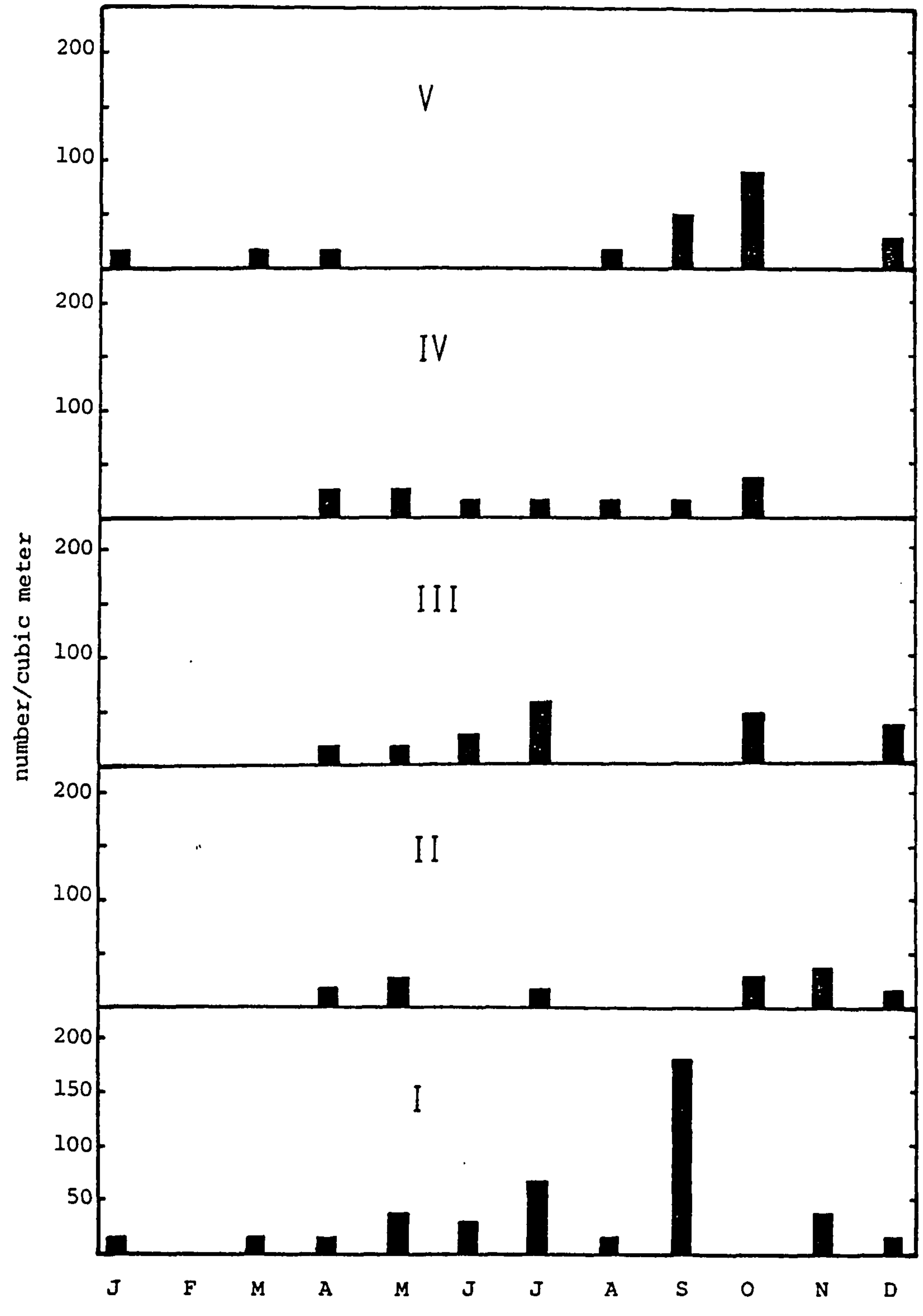


Figure 82. Mean monthly densities of *Temora turbinata* on each transect. Values are averaged over bottom depths and years.

high salinities (Fig. 83). Densities did not appear to be related to surface temperature.

Oncaea venusta. This species was most abundant at the offshore stations. Stations with a depth of 46 m averaged the highest densities (Fig. 80, p. 141). When densities were averaged over depths, transects, and years, the seasonal distribution appeared to show peaks of abundance in the late summer and early winter months. Although this seasonal distribution was present during 1964 and 1965, a distinct fall peak was not present in 1963 (Fig. 84). The greatest overall densities occurred in 1964.

Simple regression models indicated that surface salinity and temperature were important factors explaining 14.7 and 10.3% of the variability in the density of this species, respectively. These two variables combined in a multiple regression model explained 23.3% of the variability. All of the variables combined had an R^2 of 27.6%. The relationships between density and surface temperature and salinity were both positive (Fig. 85). No interactions between temperature and salinity could be distinguished.

Paracalanus aculeatus. *Paracalanus aculeatus* generally occurred from June through December at the 28 and 46 m stations (Fig. 86). It was found only in very small numbers at the other depths except for a density peak at Station 60 (8 m, Transect I) in October, 1964. The seasonal distribution was examined on each transect due to a significant (P = 1.0%) Transect*Month interaction. These monthly distributions on each transect appeared similar except for a very large density peak on

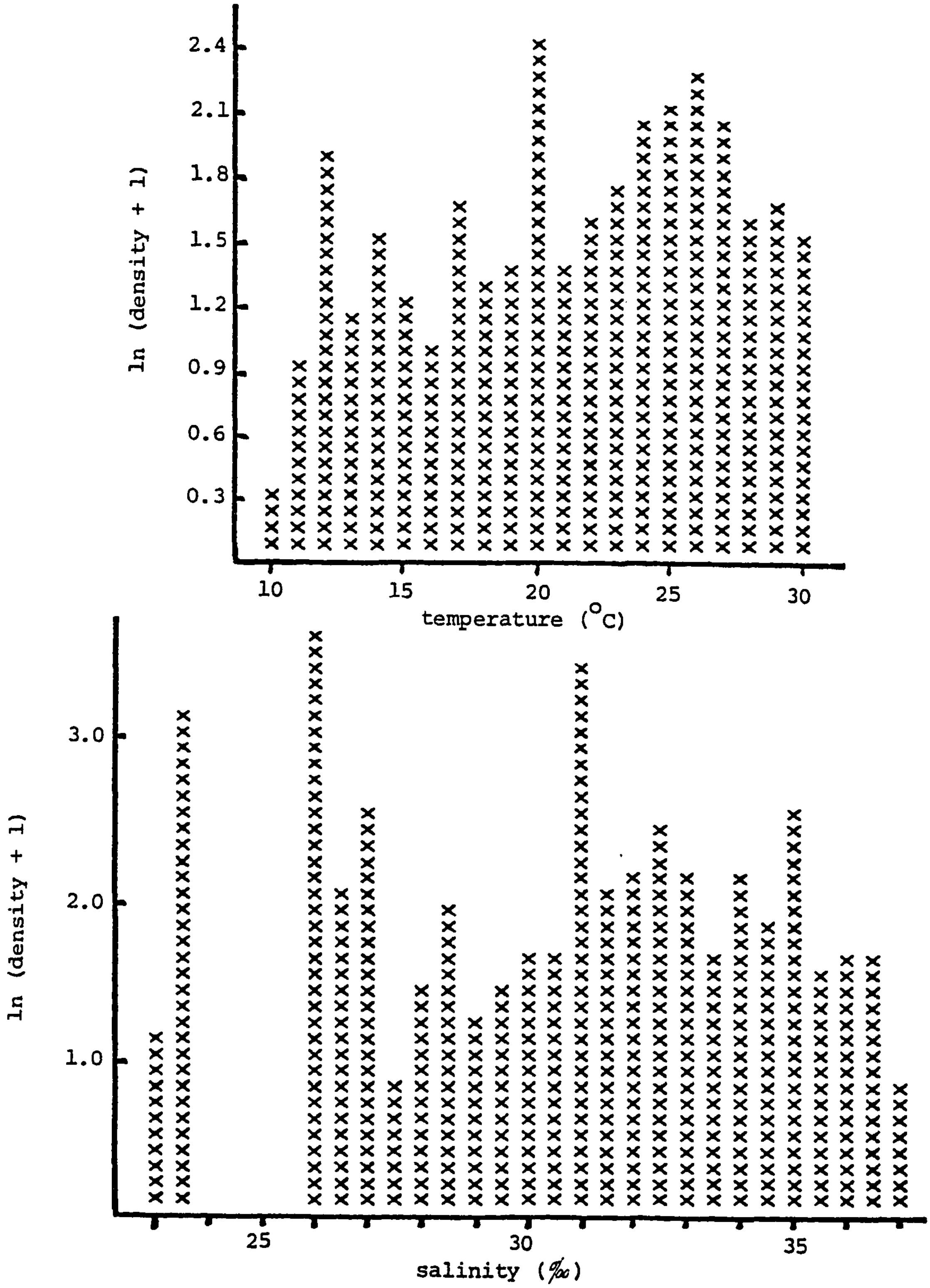


Figure 83. Density relationships with surface temperature and surface salinity for *Temora turbinata*. See legend of Figure 15 (p. 42).

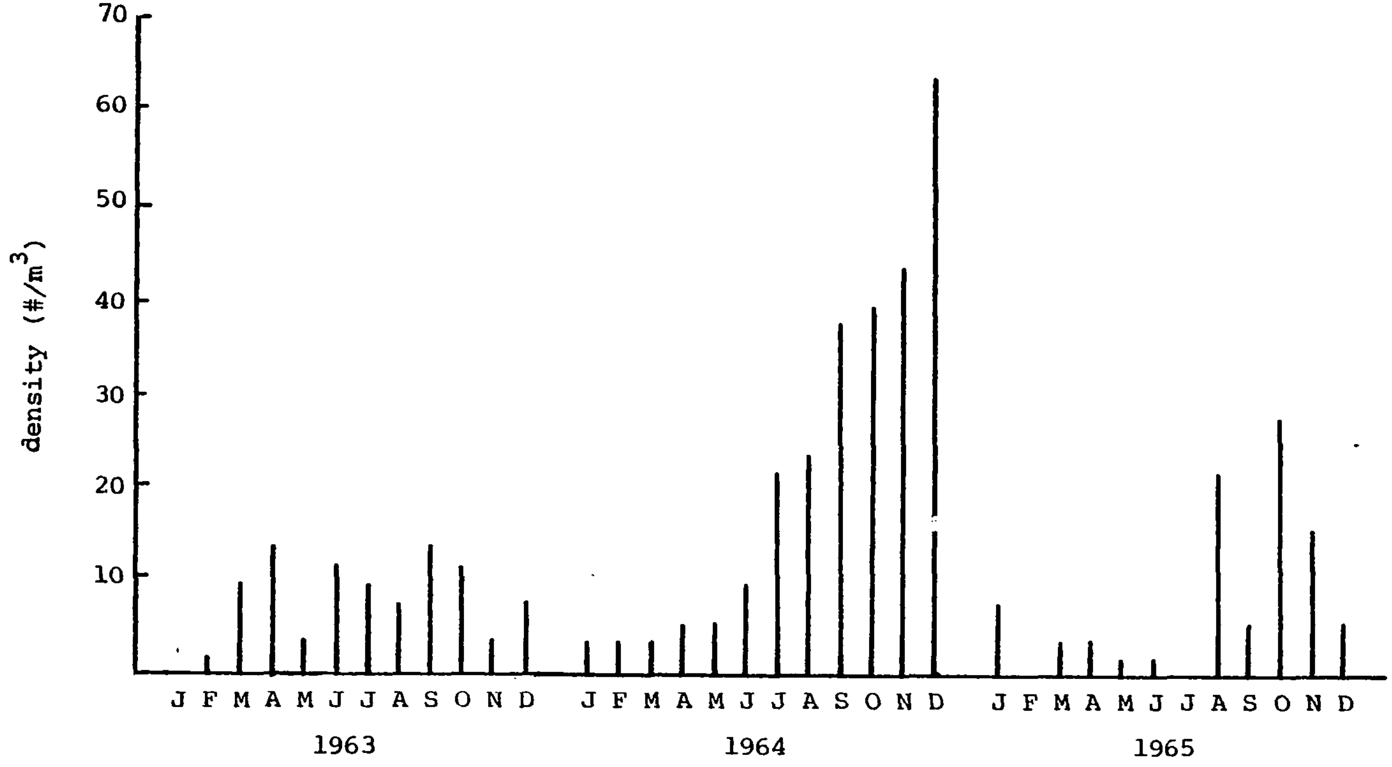


Figure 84. Mean monthly densities of *Oncaea venusta* over the entire sampling area for the three years of the study. Values are averaged over transects and bottom depths.

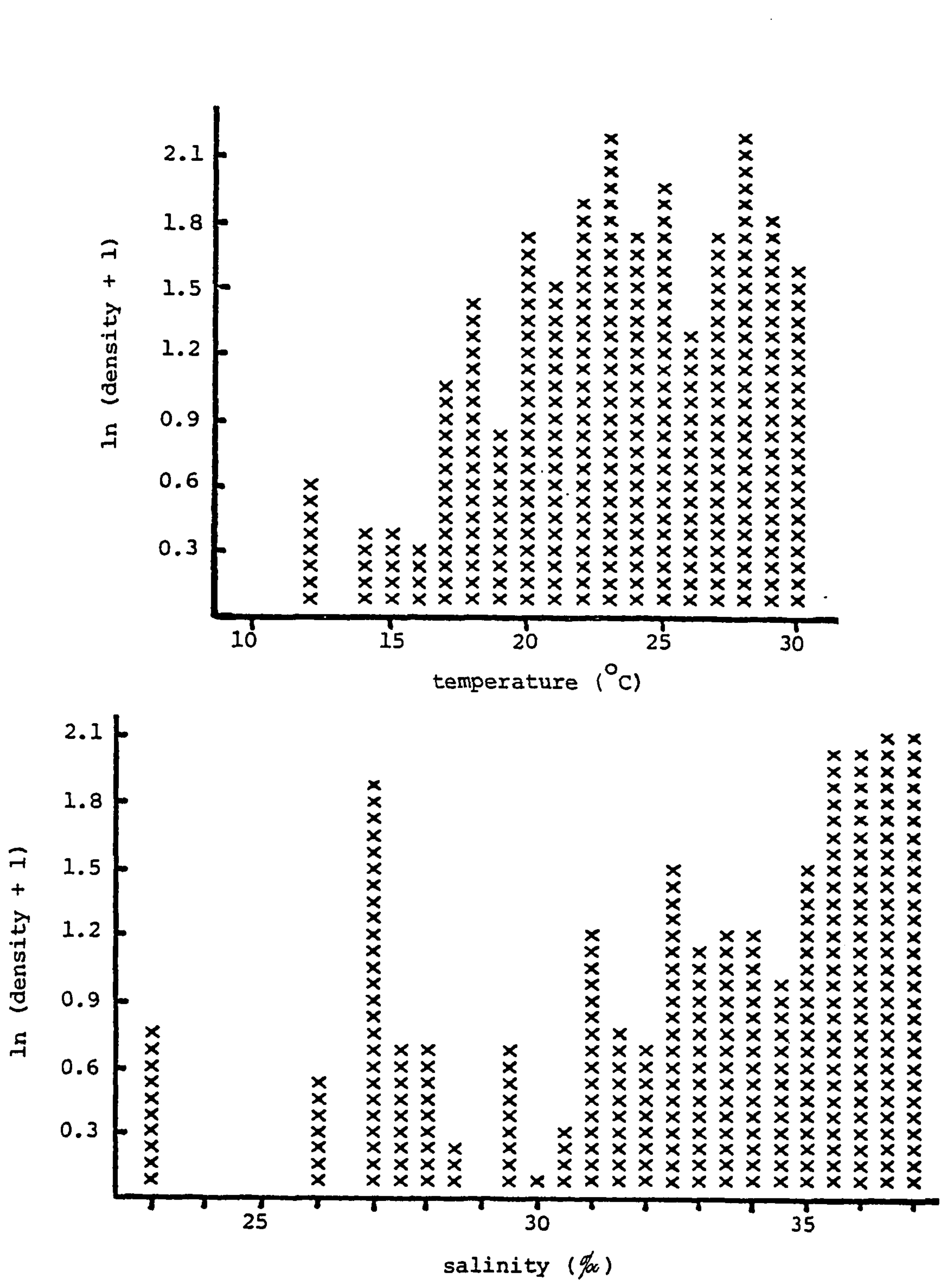


Figure 85. Density relationships with surface temperature and surface salinity for *Oncaea venusta*. See legend of Figure 15 (p. 42).

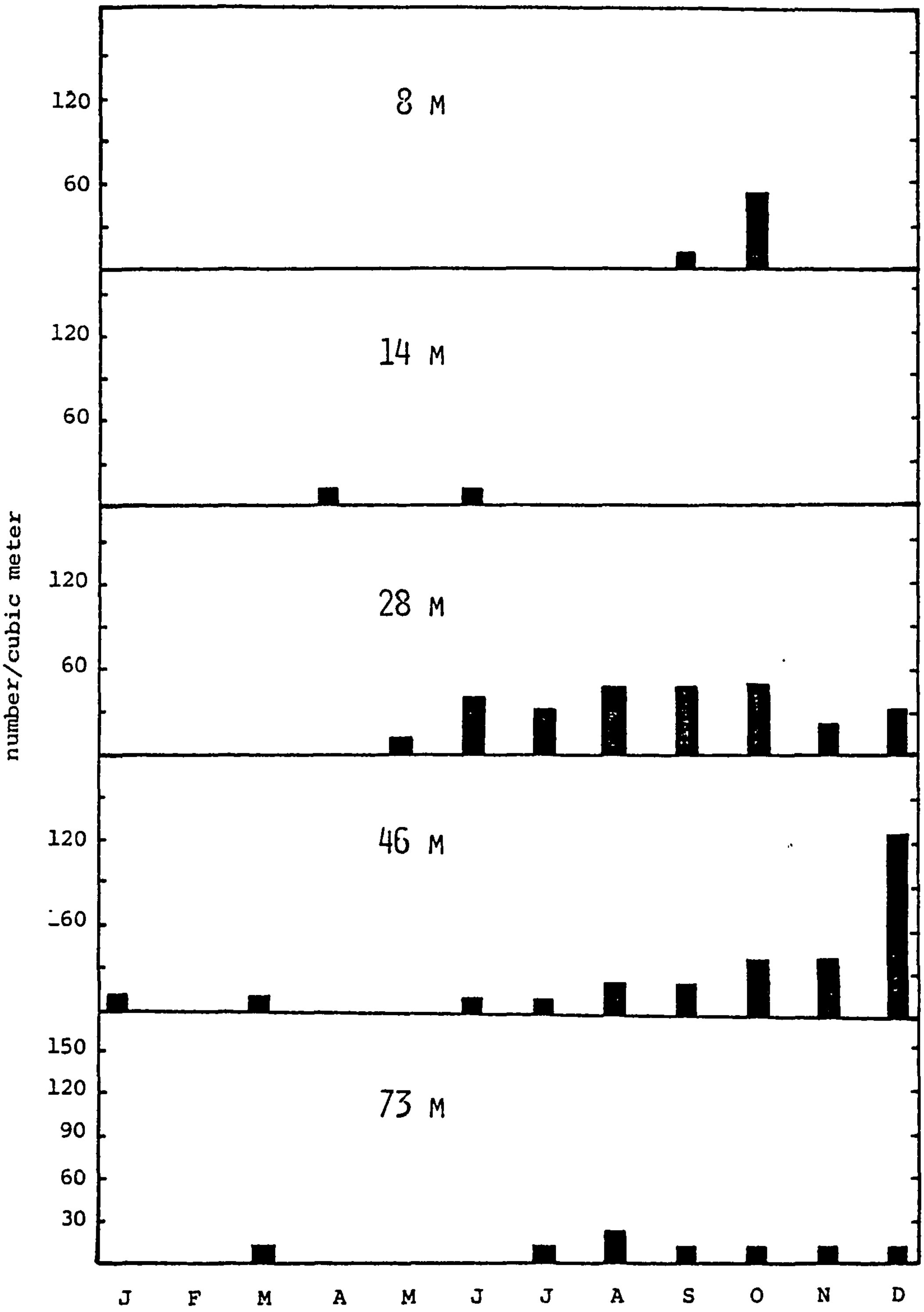


Figure 86. Mean monthly densities of *Paracalanus aculeatus* at each bottom depth sampled. Values are averaged over transects and years.

Transect V in December (Fig. 87). This was due to a high density value at Station 10 in 1964. The density of this species also appeared to be related to sampling time with the greatest densities occurring when sampling was conducted at night. The AOCOV showed only one major change in the distribution results. The effect of Transect became highly significant (P = 0.5%) which appeared to be due to the high mean densities found on Transect V.

The important physical and chemical variables in the simple regression models were surface salinity, surface temperature, and the PMMSROFF explaining 14.9, 10.4, and 6.3% of the variability in the density of this species, respectively. When these three factors were combined in a multiple regression model they explained 26.3% of the variability. The positive relationships between density and surface temperature and salinity are shown in Figure 88. There did not appear to be any meaningful temperature salinity interactions (Fig. 89).

Acartia lilljeborgi. This species was most abundant at the 8 m stations where it occurred in large numbers during the fall (Fig. 90). At the deeper stations it appeared occasionally, usually during the fall, except at the 73 m stations where no specimens were captured. Although the Transect*Month interaction was significant (P = 0.1%) it appeared that any apparent transect effect (Fig. 91) could be explained by the density distribution over depth.

Few variables appeared to be important in the regression analysis. The previous month's Mississippi runoff (PMMSROFF) was the most significant factor in the simple regressions and it only explained 2.6% of the variability in density. The best two factor multiple regression

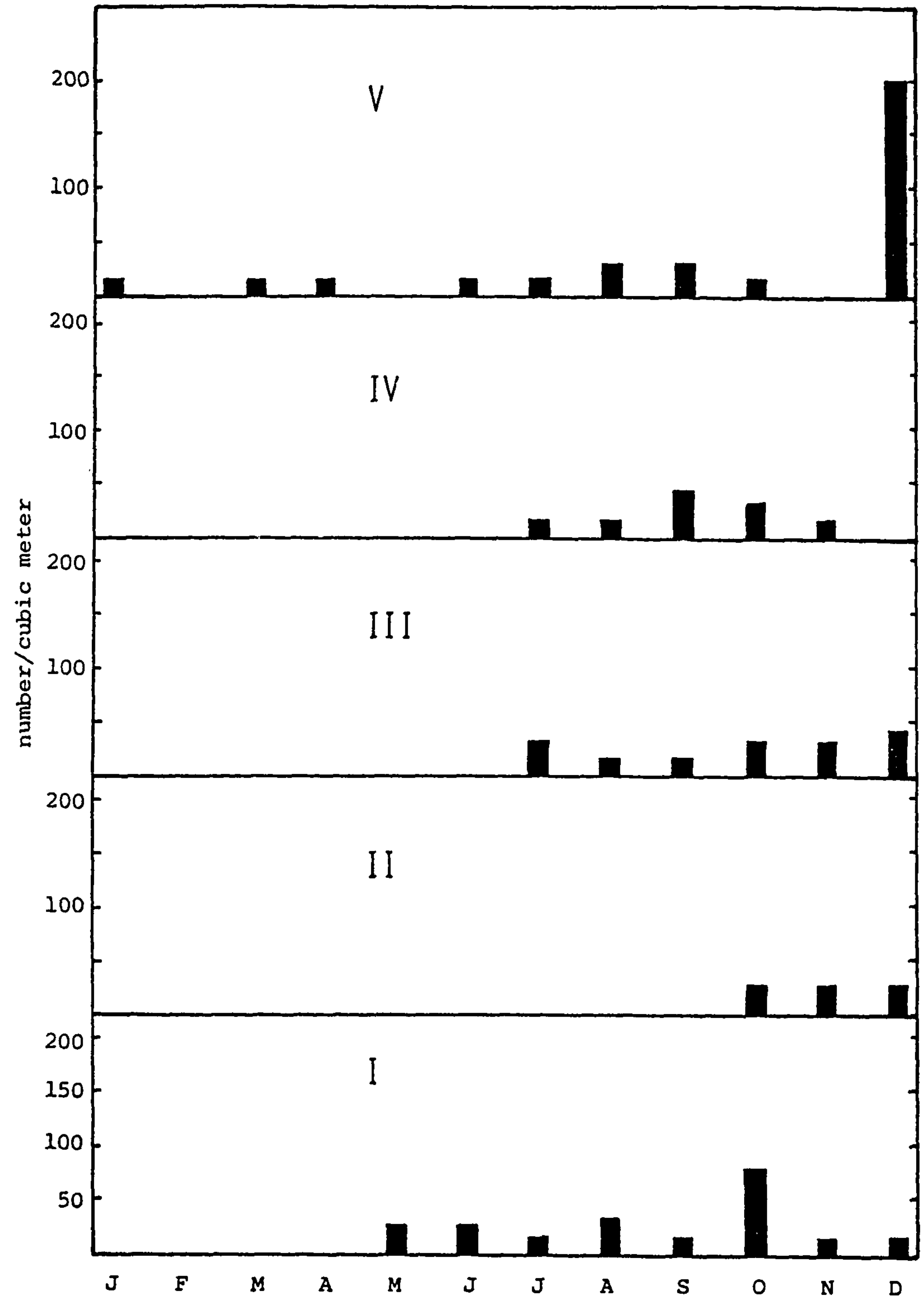


Figure 87. Mean monthly densities of *Paracalanus aculeatus* on each transect. Values are averaged over bottom depths and years.

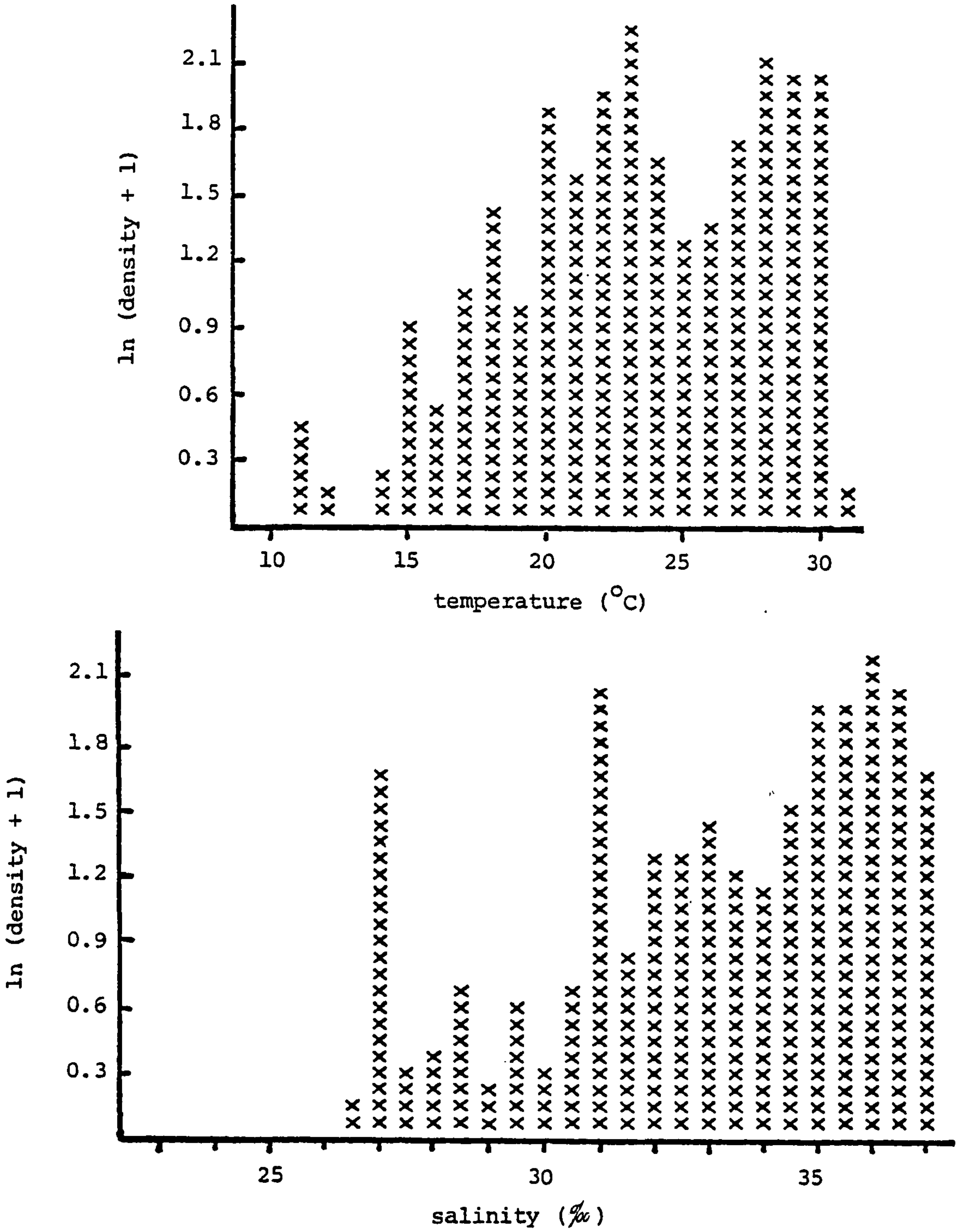


Figure 88. Density relationships with surface temperature and surface salinity for *Paracalanus aculeatus*. See legend of Figure 15 (p. 42).

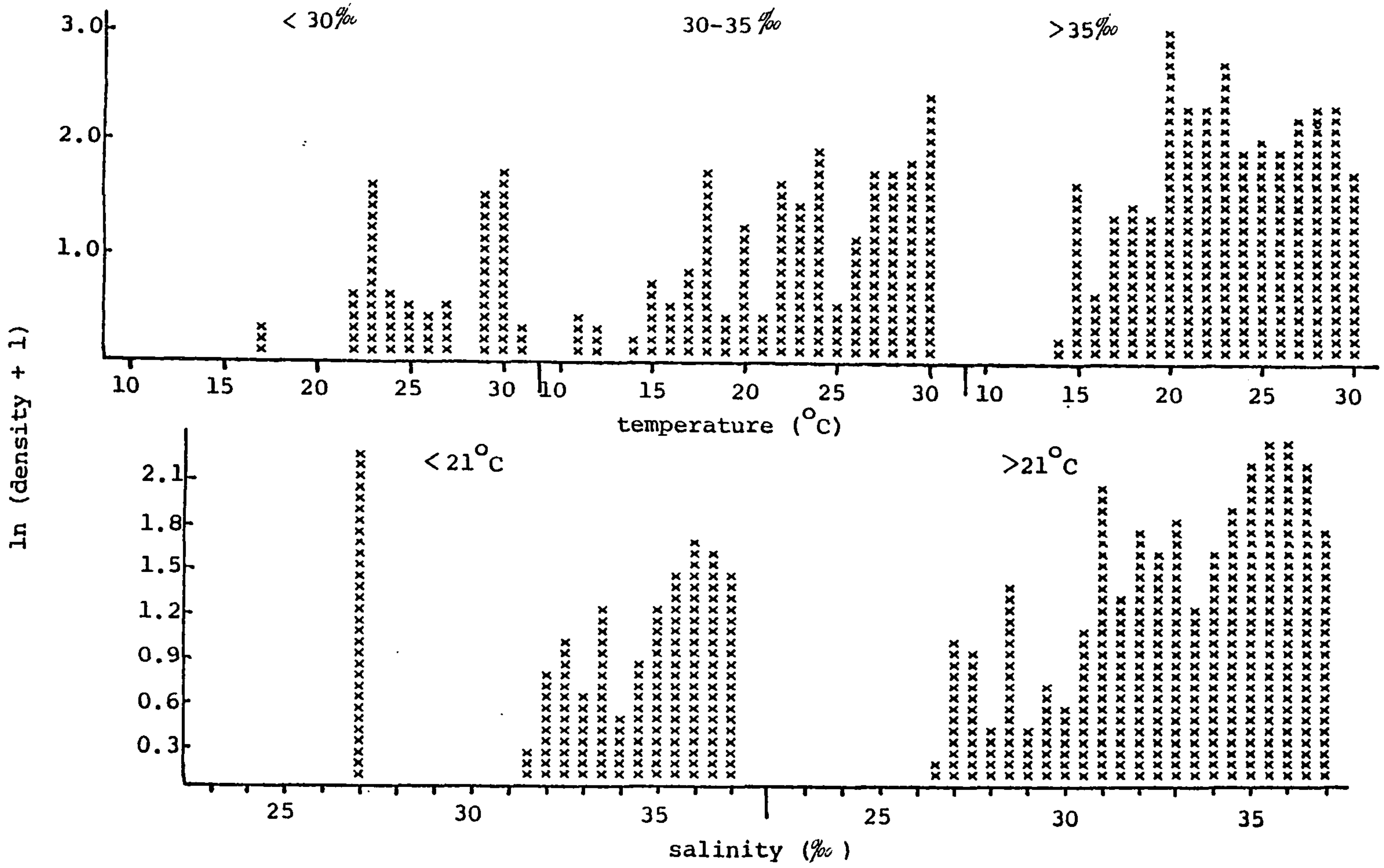


Figure 89. Densities of *Paracalanus aculeatus* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

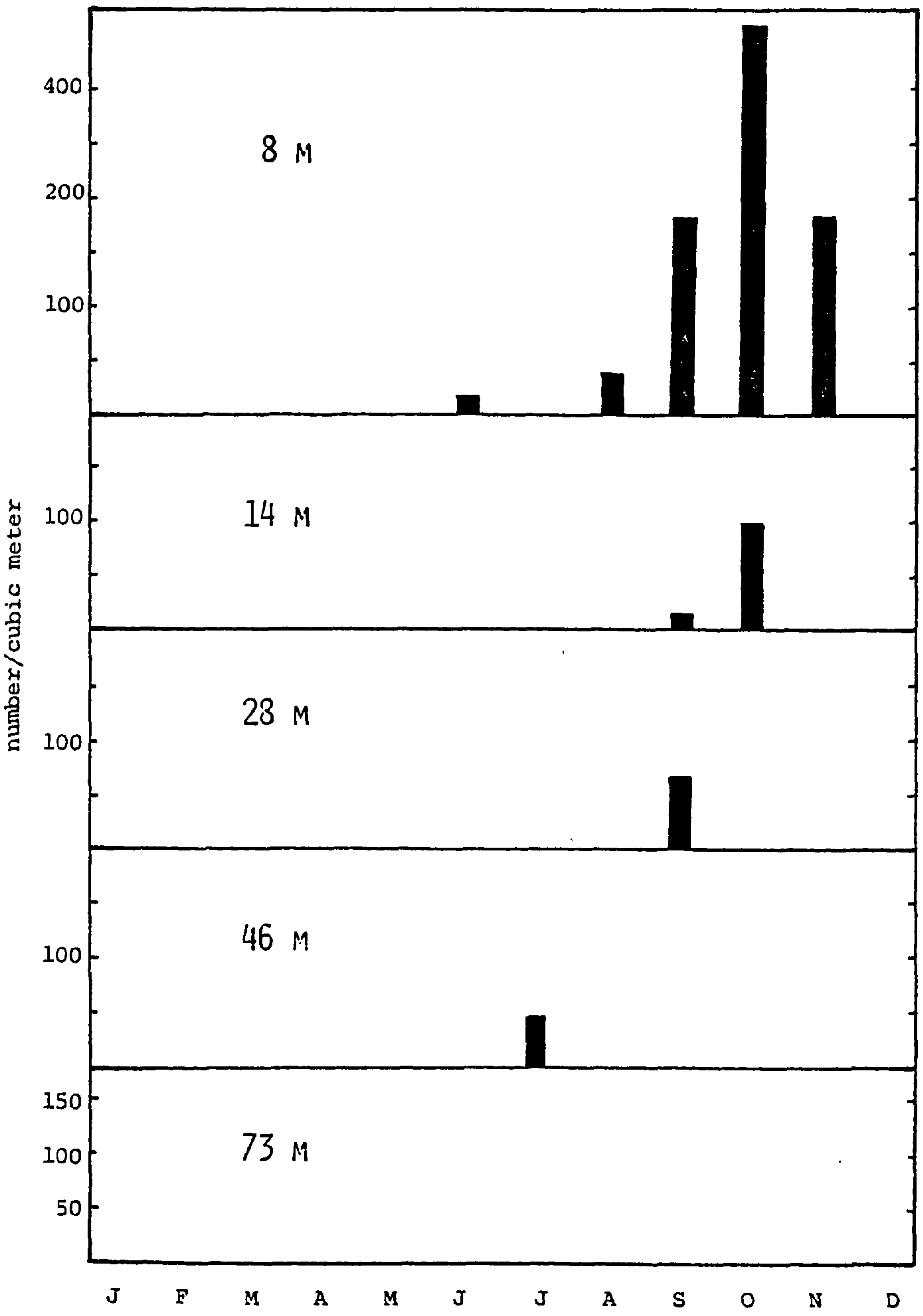


Figure 90. Mean monthly densities of *Acartia lilljeborgi* at each bottom depth sampled. Values are averaged over transects and years.

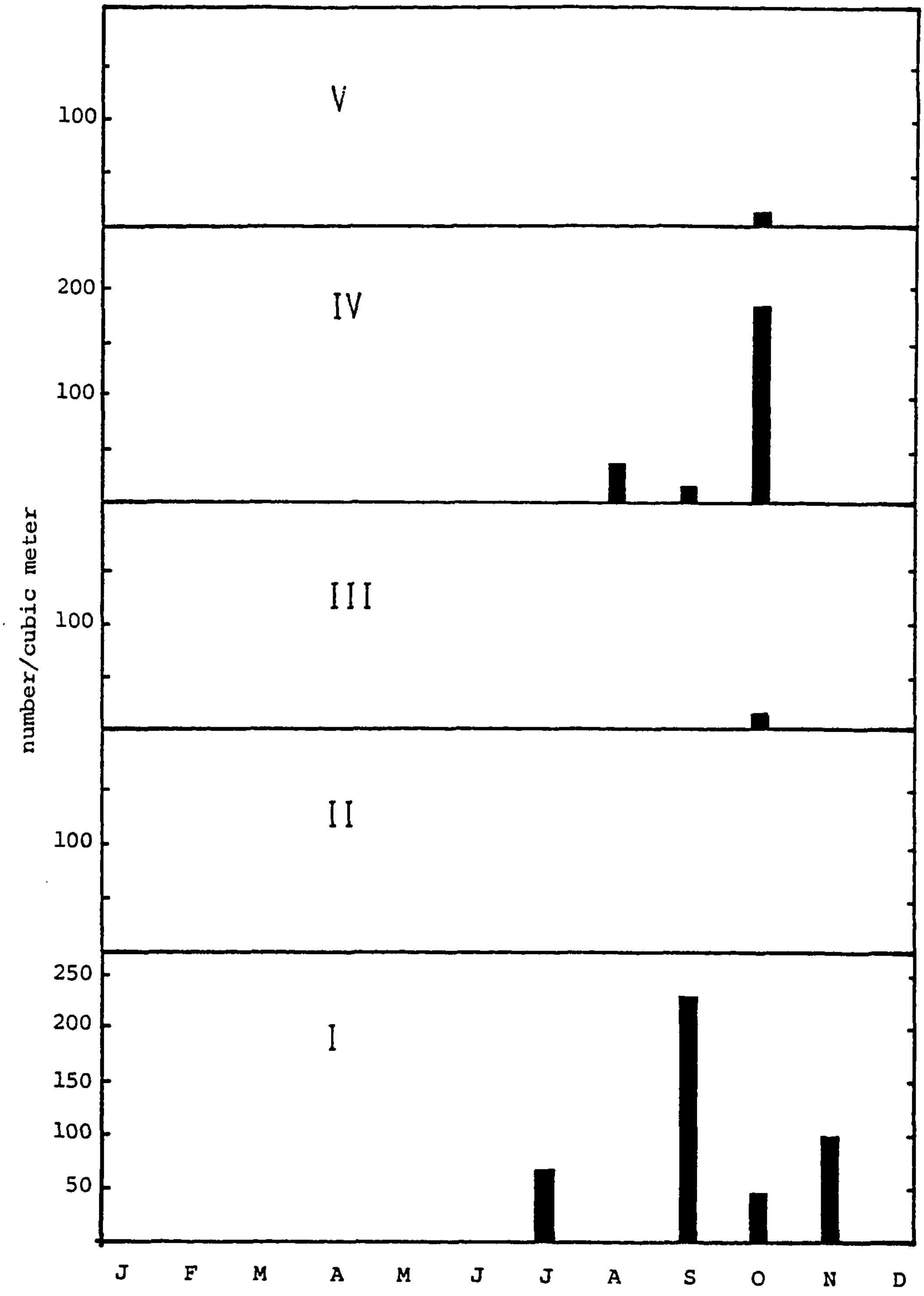
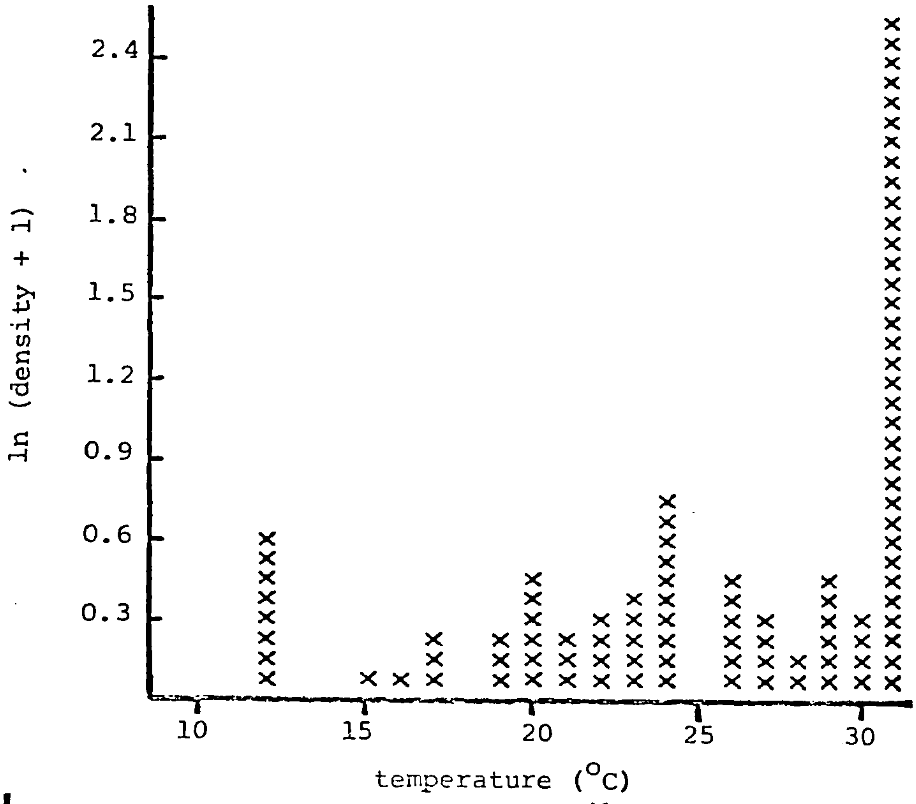


Figure 91. Mean monthly densities of *Acartia lilljeborgi* on each transect. Values are averaged over bottom depths and years.

model combined surface salinity and PMMSROFF and explained 6.3% of the variability. When surface temperature was added to the model the R^2 increased to 8.0% and the inclusion of the vertical stability of the water column further increased this value to 9.7%.

The histograms of density versus surface temperature and salinity are shown in Figure 92. The relationship with temperature was difficult to interpret. The optimum temperature appeared to be around 24°C. When this relationship was examined for the three salinity classes (Fig. 93), it was apparent that the overall relationship between density and temperature was mostly influenced by samples with salinities between 30 and 35°/oo. At higher salinities (above 35°/oo) no specimens were found at temperatures below 23°C, although 98 samples had this temperature salinity combination. This species was never found in samples with salinities less than 28°/oo and the greatest mean density occurred in samples with a salinity of approximately 31°/oo. In samples with temperatures below 21°C, most specimens were found at salinities between 32 and 35°/oo (Fig. 93).

Corycaeus amazonicus. *Corycaeus amazonicus* was fairly evenly distributed over the sampling area. A slight tendency for a decrease in density with depth was exhibited however and the 73 m stations had the lowest mean densities. Seasonal peaks of density occurred in the spring and the fall although the spring peaks appeared later in the year at the shallow stations and the fall peak was absent at the 73 m stations (Fig. 94). Although this seasonal pattern was not as distinct when mean monthly density values were examined at each transect, no really anomalous seasonal distribution could be seen (Fig. 95). The analysis of



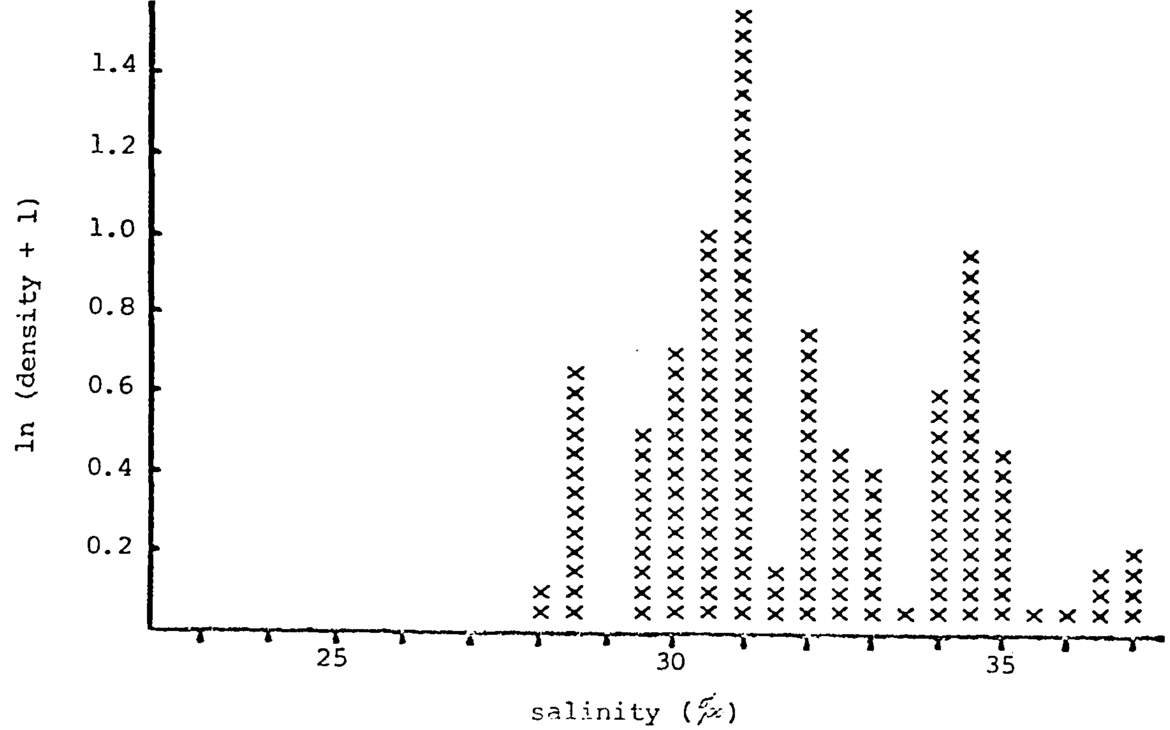


Figure 92. Density relationships with surface temperature and surface salinity for *Acartia lilljeborgi*. See legend of Figure 15 (p. 42).

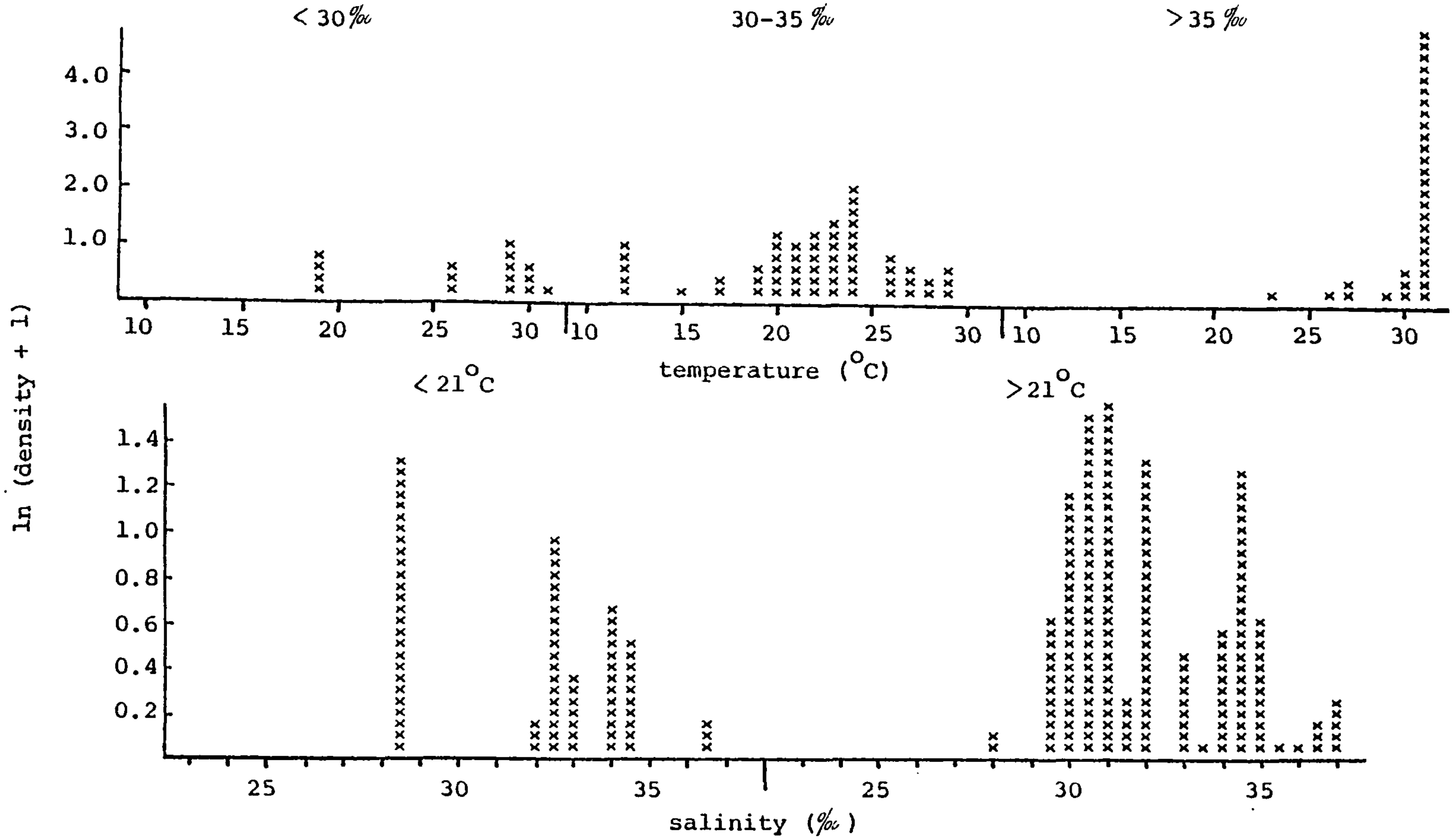


Figure 93. Densities of *Acartia lilljeborgi* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

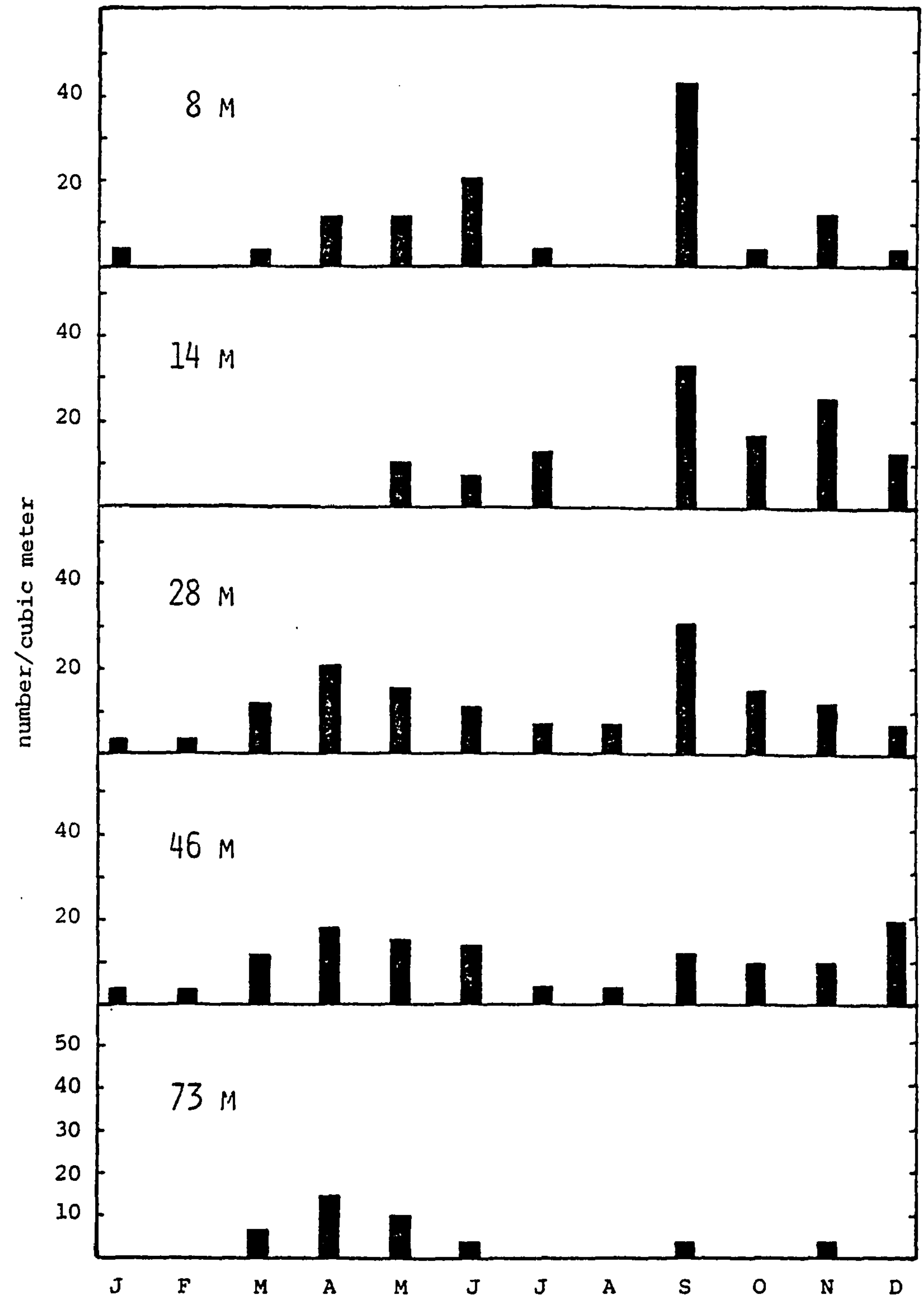


Figure 94. Mean monthly densities of *Corycaeus amazonicus* at each bottom depth sampled. Values are averaged over transects and years.

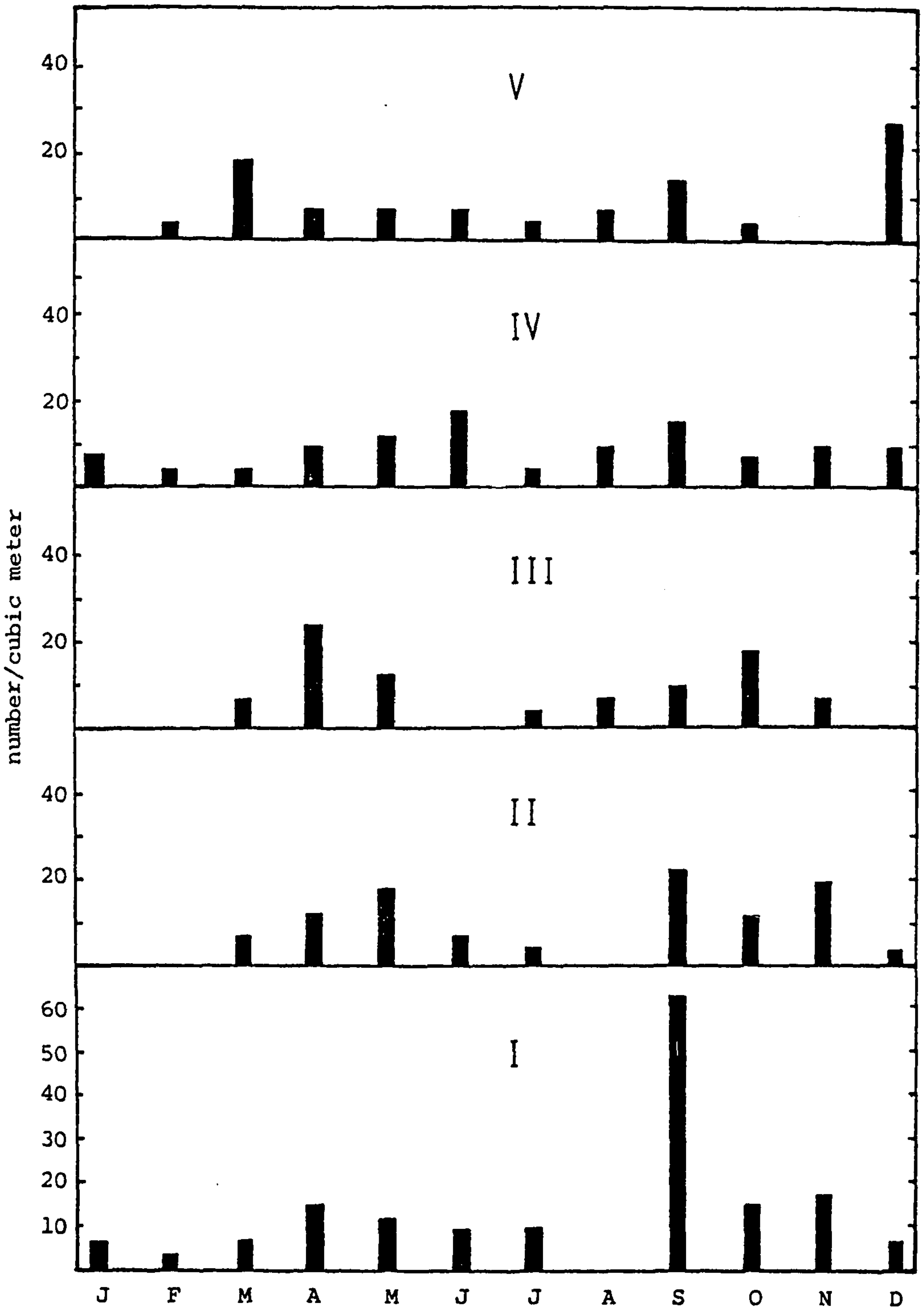


Figure 95. Mean monthly densities of *Corycaeus amazonicus* on each transect. Values are averaged over bottom depths and years.

covariance used to examine the effect of sampling time on these results did not appear to alter the probability values in the AOV table.

The results from the regression models indicated little relationship between the density of this species and the physical and chemical factors examined. The most important single factors appeared to be surface temperature and the PMMSROFF. Both of these variables explained approximately 1.4% of the variability in density. All of the factors combined in a multiple regression model only explained 6.5% of this variability. The graphical representation of density versus surface salinity also showed little apparent relationship (Fig. 96). There did appear to be a positive relationship between density and surface temperature up to 26°C. Above this temperature mean densities declined. The overall regression slope was positive. No obvious temperature salinity interaction was apparent (Fig. 97).

Farranula gracilis. *Farranula gracilis* was most abundant at the deeper stations and appeared infrequently in samples from the 8 and 14 m stations. Seasonally, this species had a mean density peak in July and was relatively abundant throughout the summer and fall (Fig. 98). Only a few specimens were captured in the sampling area between December and May. The general seasonal distribution was present during 1964. The density peak occurred slightly earlier in the year in 1963 (June and July) and apparently occurred later in 1965, although no July samples were available for this year of the study. The AOV indicated that there was no significant Transect effect or Transect interaction.

Surface temperature, surface salinity, and stability all appeared to be important variables in the simple regression models, explaining

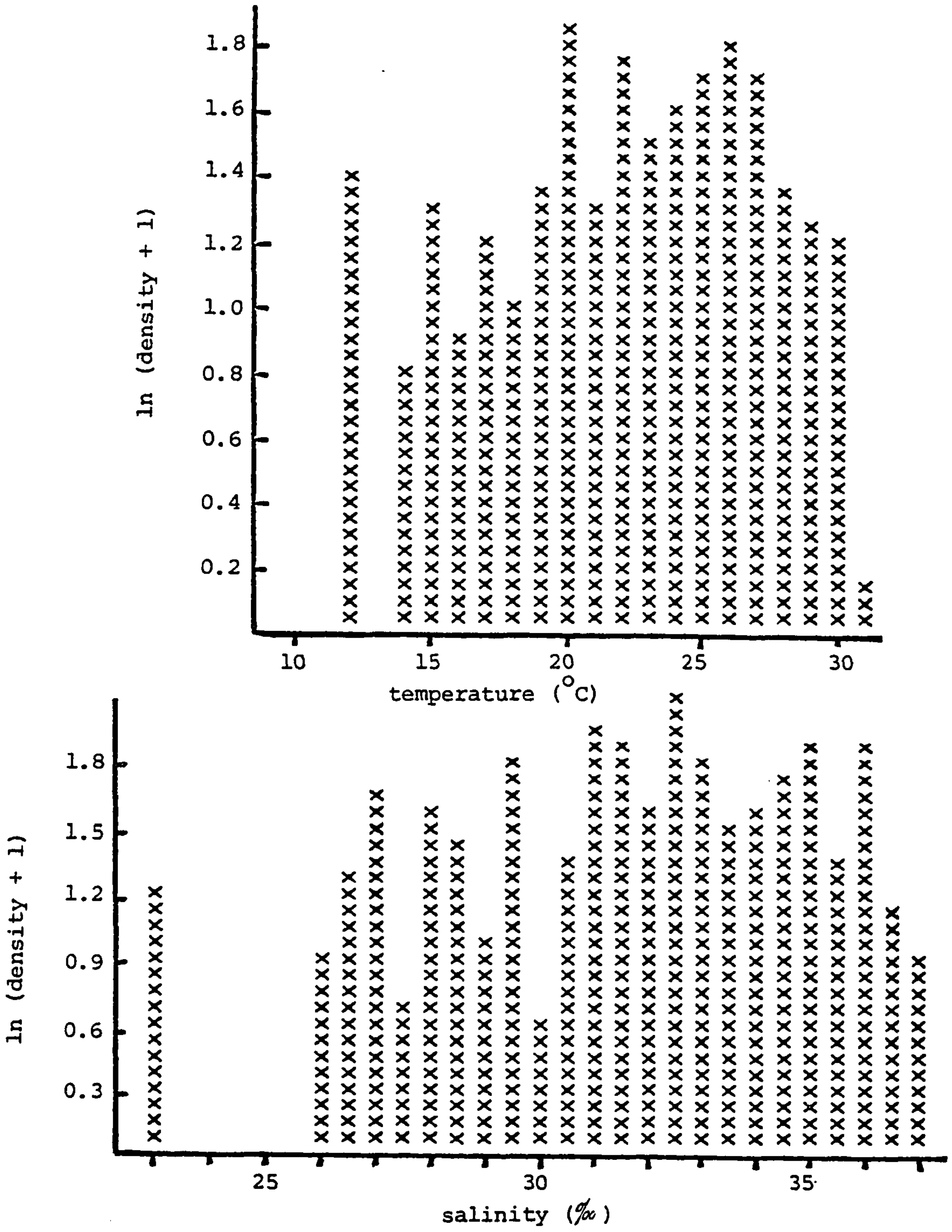


Figure 96. Density relationships with surface temperature and surface salinity for *Corycaeus amazonicus*. See legend of Figure 15 (p. 42).

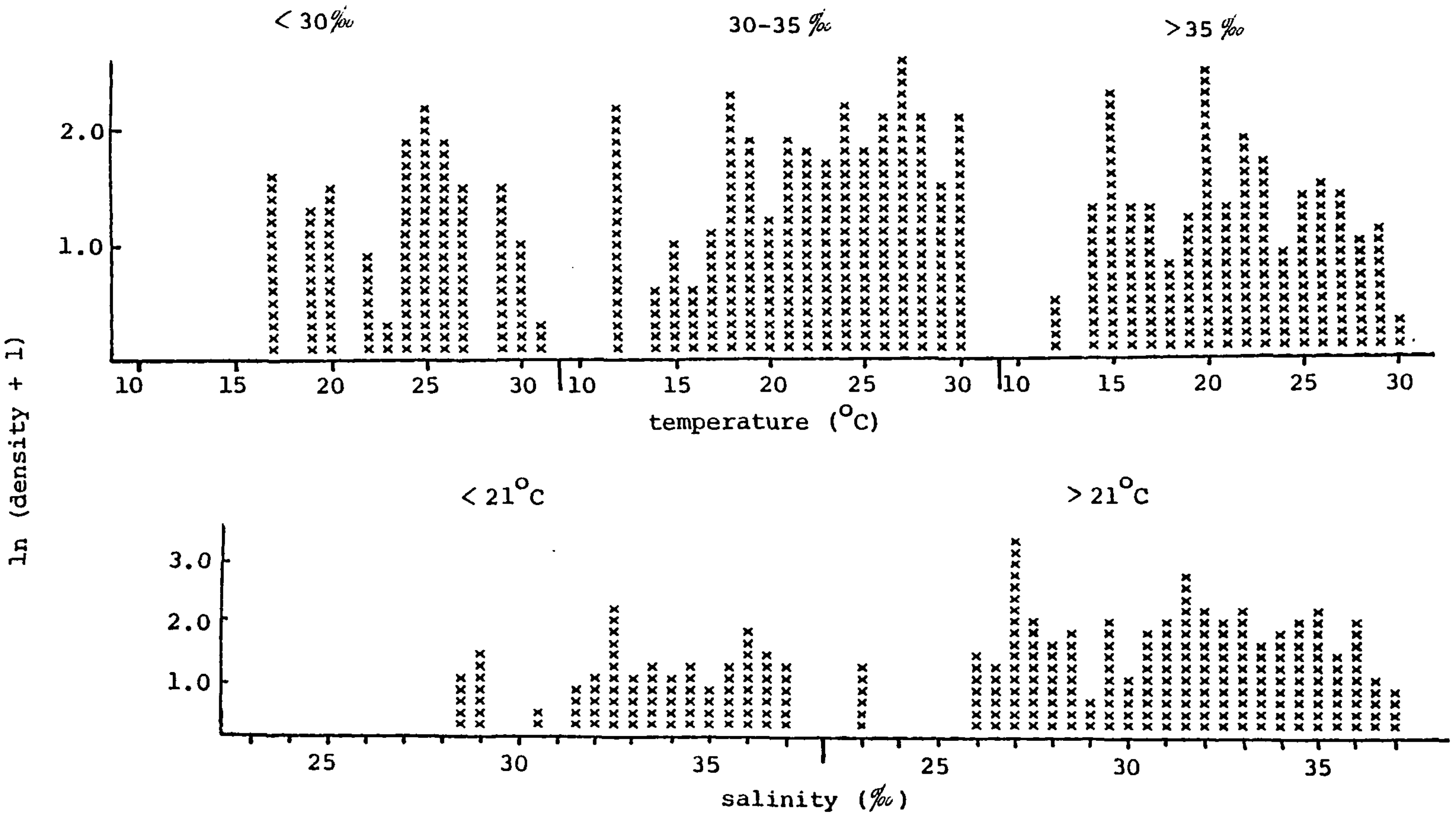


Figure 97. Densities of *Corycaeus amazonicus* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

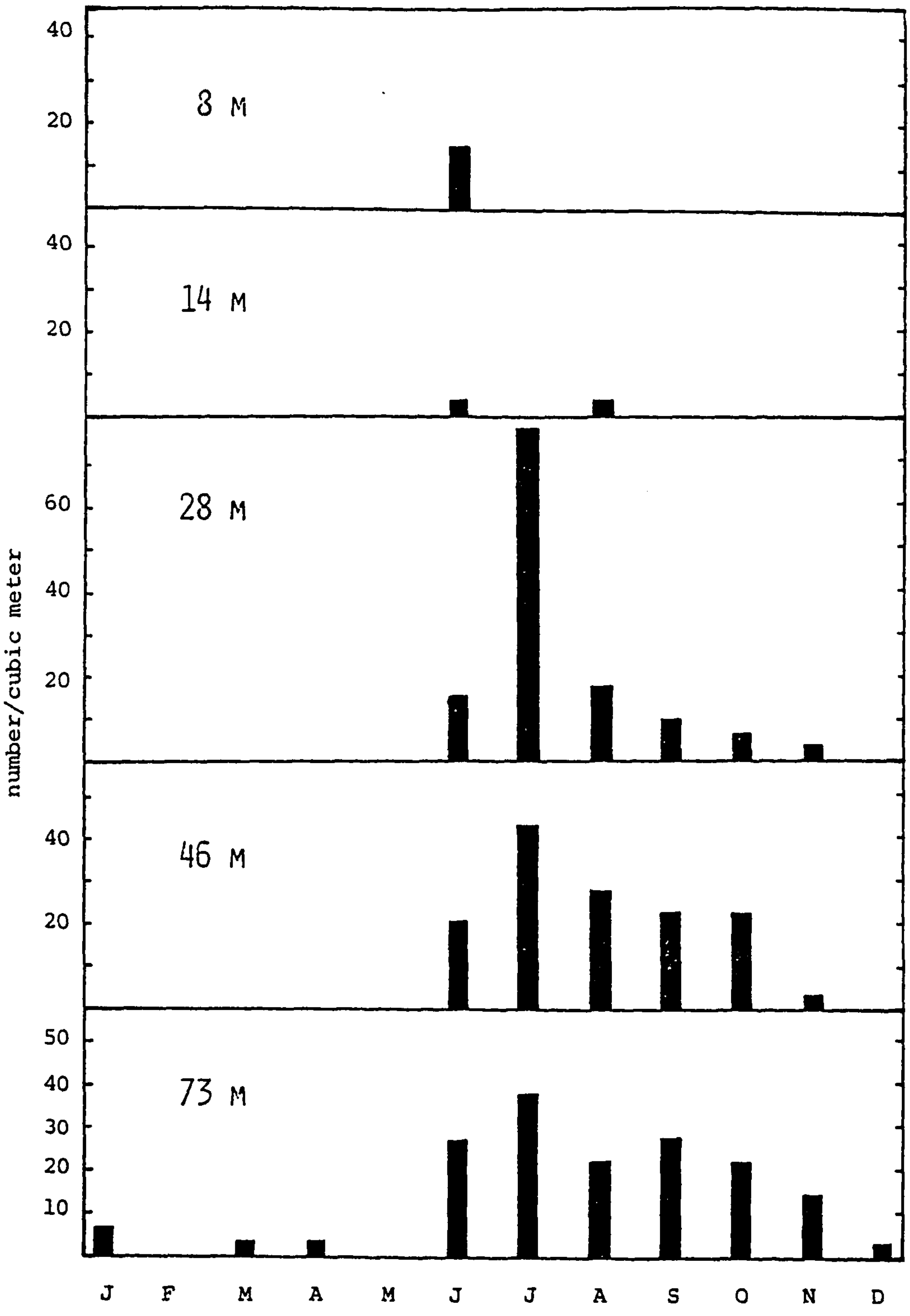
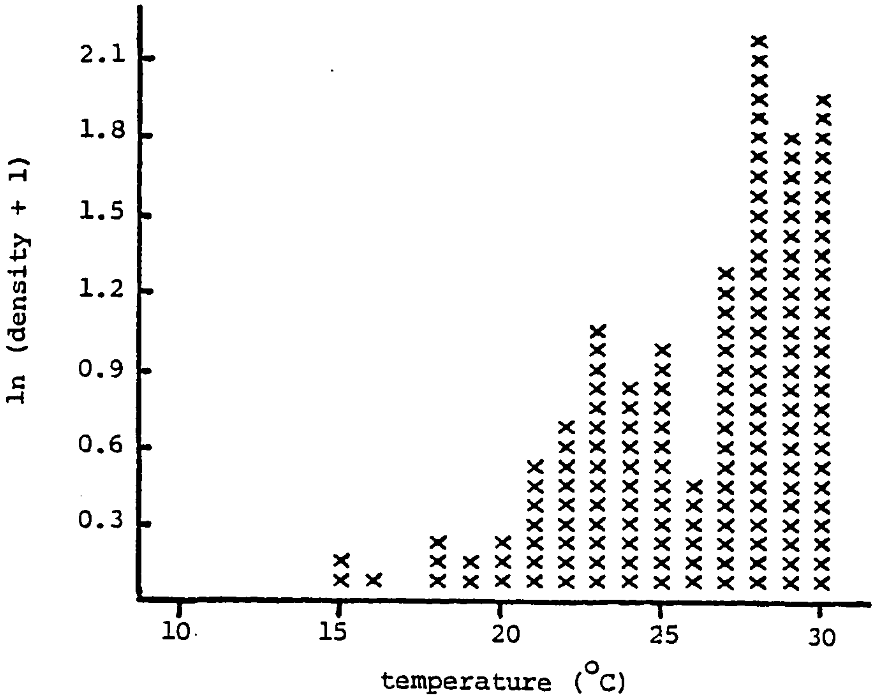


Figure 98. Mean monthly densities of *Farranula gracilis* at each bottom depth sampled. Values are averaged over transects and years.

22.2, 13.4, and 11.7% of the variability in density, respectively. The best two factor multiple regression model included temperature and salinity and had an R^2 of 33.3%. Including stability increased this value to 36.4%. All of the variables combined in a regression model explained 42.8% of the variability in the density of this species. The relationship between density and surface temperature was positive and the greatest mean densities occurred at temperatures between 28 and 30°C. The relationship between density and surface salinity was also positive with the greatest mean densities occurring in samples with the highest salinities recorded (approximately 37°/oo) (Fig. 99). Few specimens were observed in samples with low temperature and low salinity combinations (Fig. 100).

Corycaeus americanus. The density of *Corycaeus americanus* did not appear to be closely related to the bottom depth of the station. The seasonal distribution at each depth is shown in Figure 101. Low densities occurred from August through October at all depths and there was some tendency for abundance peaks to be present in the spring. Late fall and early winter density peaks also occurred sporadically at all depths except at the 73 m stations, where few representatives were found during this part of the year.

Simple regression models indicated a significant negative relationship between the density of this species and the surface temperature which explained 11.8% of the variability. The best two factor multiple regression model combined temperature and PMMSROFF and had an R^2 of 15.7%. These two variables appeared to be the only significant physical factors. All variables combined in a multiple regression model only had



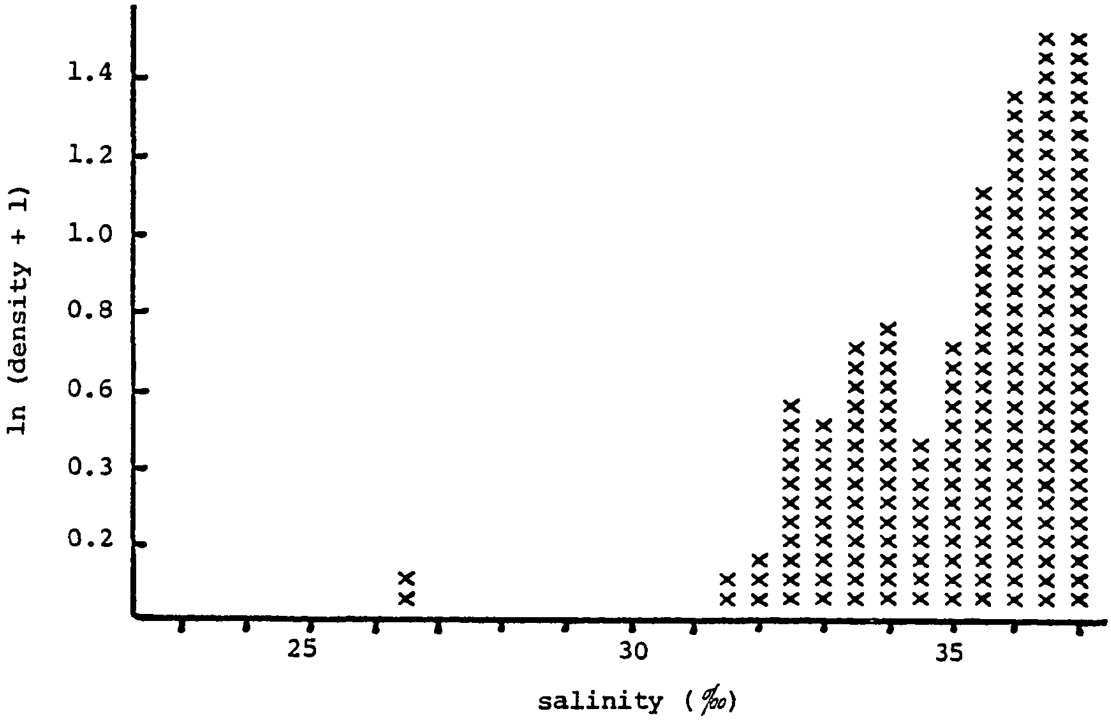


Figure 99. Density relationships with surface temperature and surface salinity for *Farranula gracilis*. See legend of Figure 15 (p. 42).

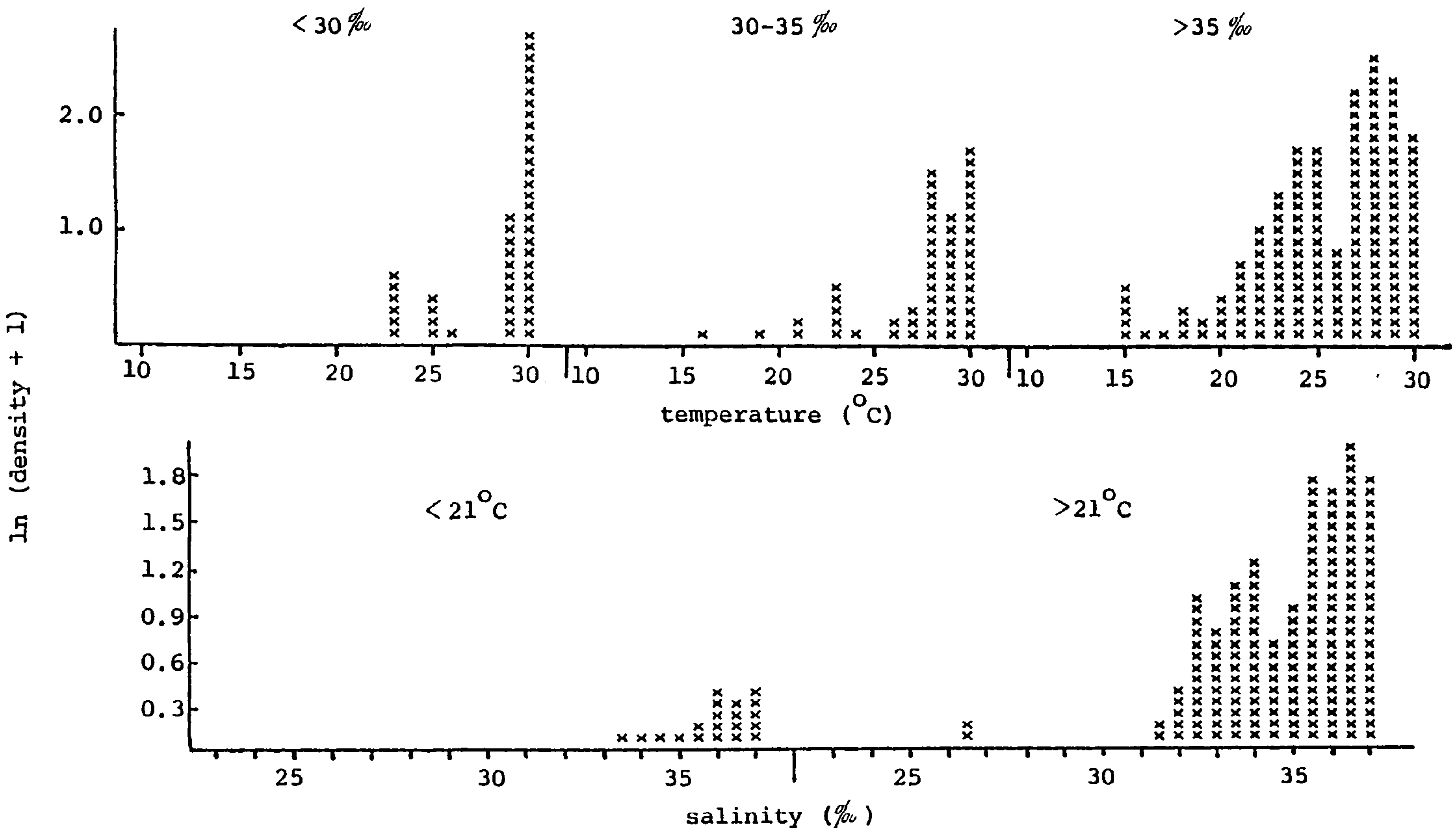


Figure 100. Densities of *Farranula gracilis* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

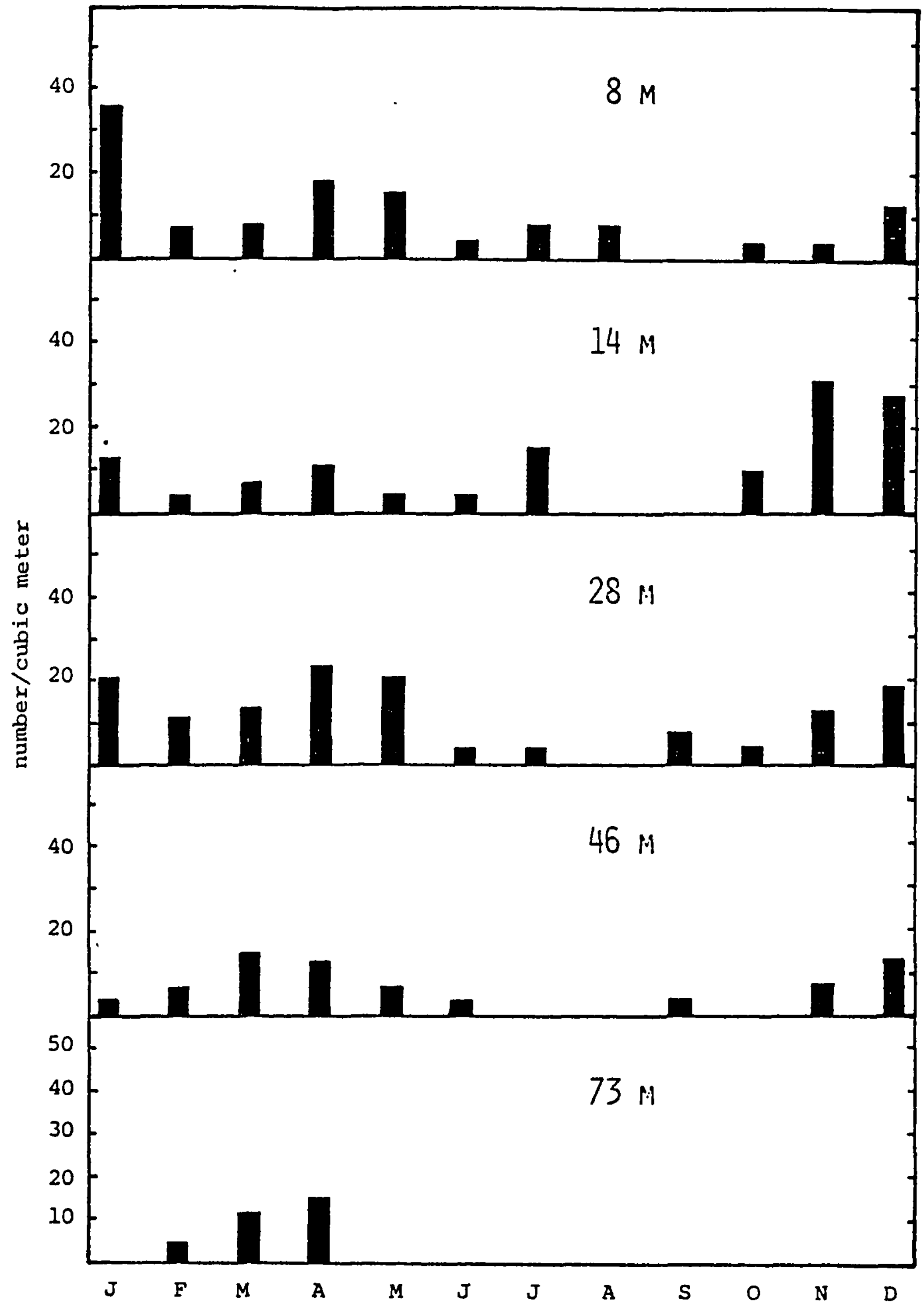


Figure 101. Mean monthly densities of *Corycaeus americanus* at each bottom depth sampled. Values are averaged over transects and years.

an R^2 of 16.6%. The relationship between density and surface temperature is shown in Figure 102. Although surface salinity did not appear to be significant in the linear regression models, Figure 102 indicates that above 32.5°/oo densities appeared to decrease as salinity increased. There was no apparent temperature salinity interaction.

Centropages velificatus. The density of *Centropages velificatus* generally decreased with the bottom depth of the station. Highest densities occurred at the 8 m stations and few specimens were found in samples taken at the 73 m stations (Fig. 103). Seasonally, the greatest numbers were collected from June through October. Specimens were rarely captured from January through April. The effect of Transect was significant in the AOV (P = 0.7%) and the mean density on Transect I was relatively high. The depth distribution of the stations on each transect, however, could explain this elevation in density. Transect I had an 8 m station and no 73 m station.

The single regression models indicated that surface temperature was the only highly significant factor explaining 14.2% of the variability in the density of this species. The other factors did not appear to be important by themselves but when they were added into a multiple regression model with temperature, the model explained 22.6% of the variability. The positive relationship between density and temperature is shown graphically in Figure 104. There did not appear to be any change in this trend at different salinities.

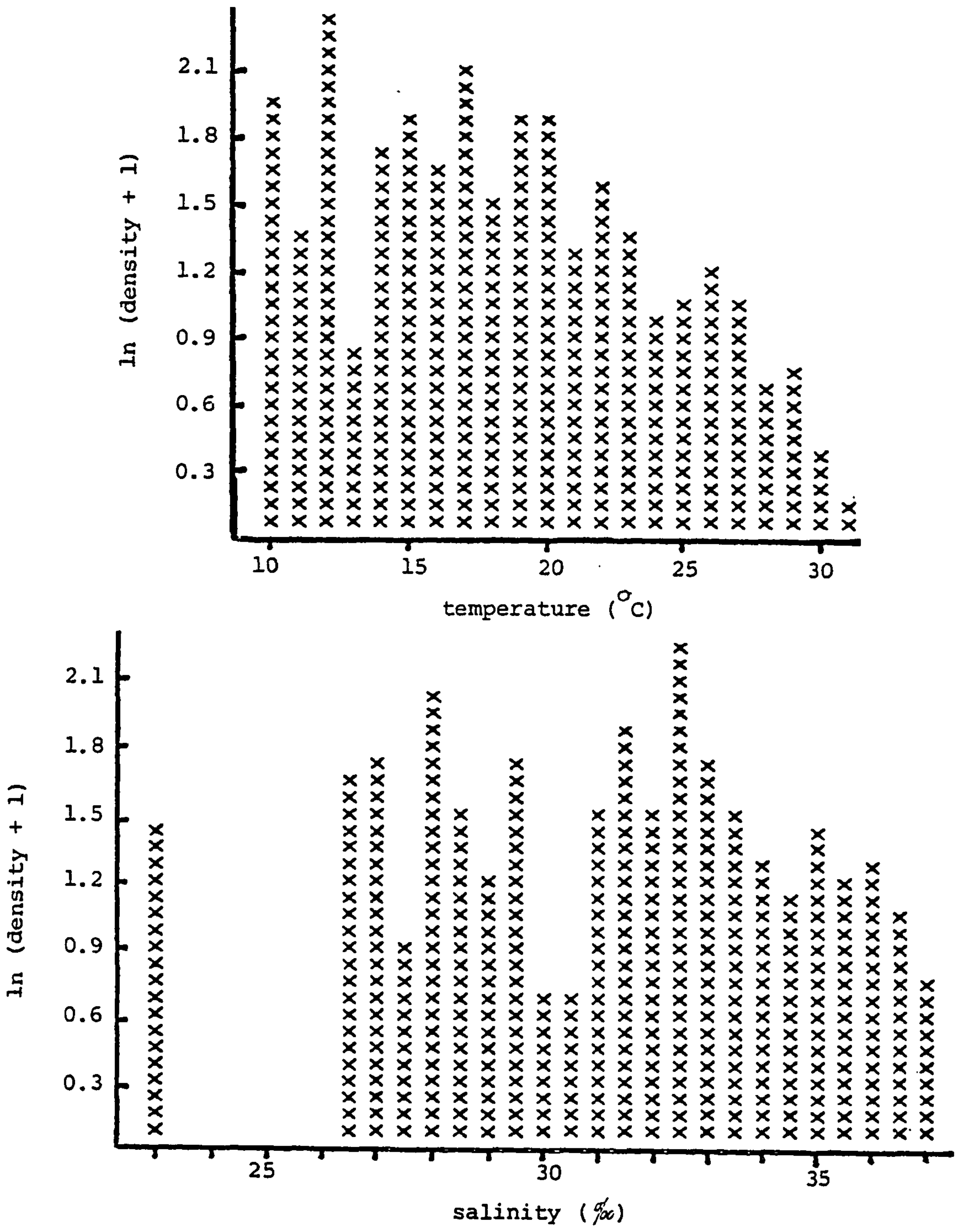


Figure 102. Density relationships with surface temperature and surface salinity for *Corycaeus americanus*. See legend of Figure 15 (p. 42).

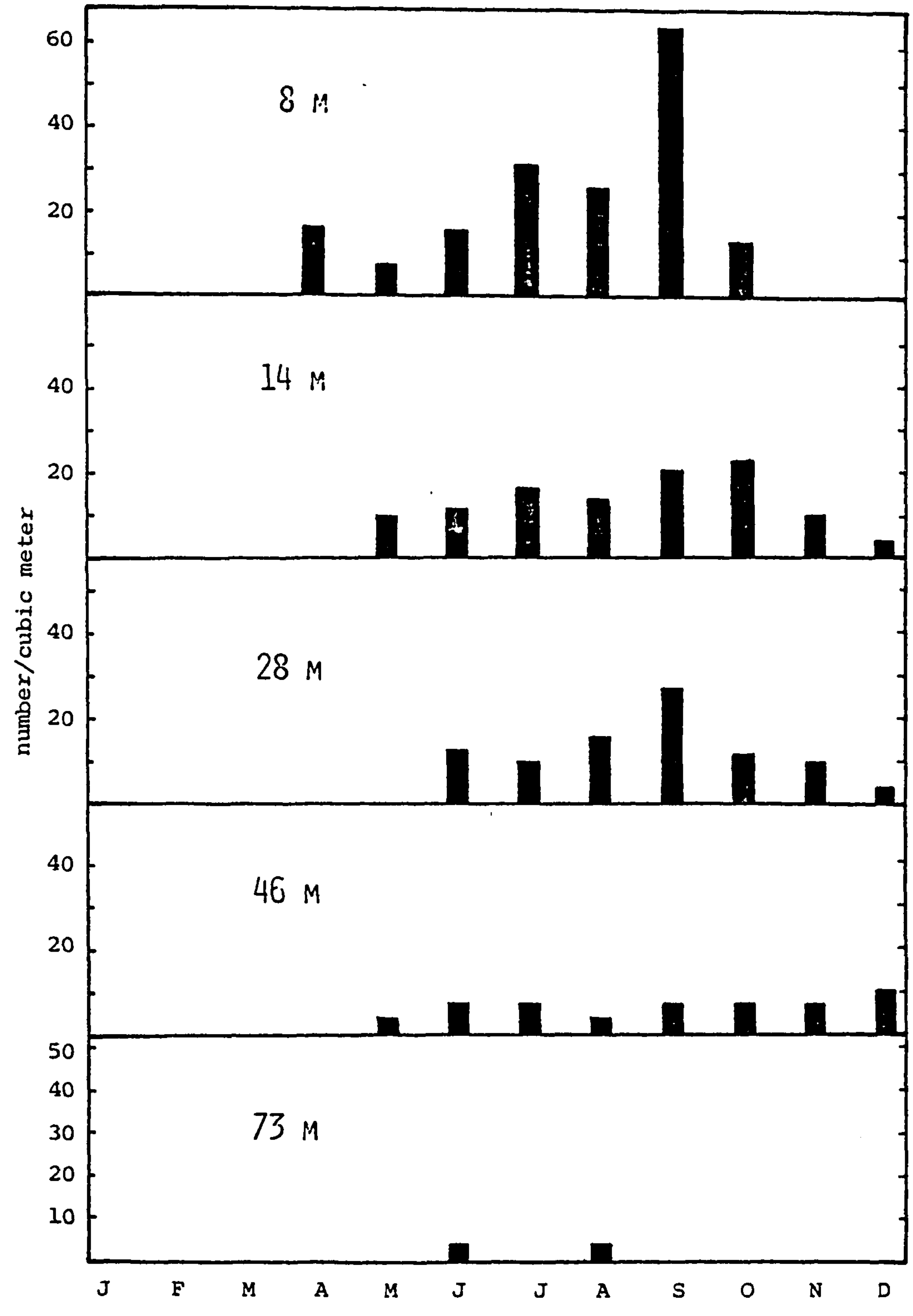
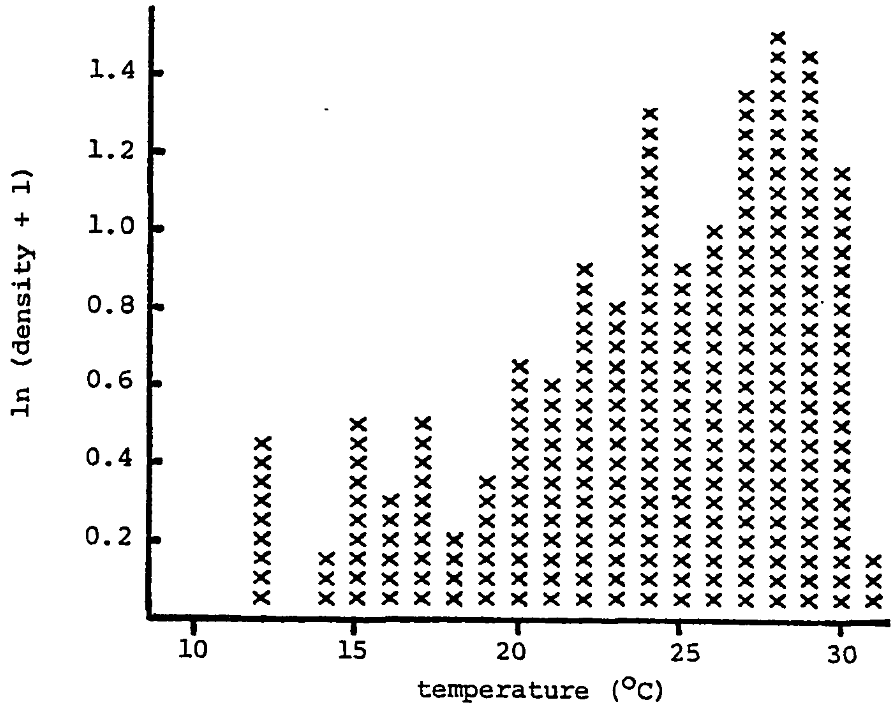


Figure 103. Mean monthly densities of *Centropages velificatus* at each bottom depth sampled. Values are averaged over transects and years.



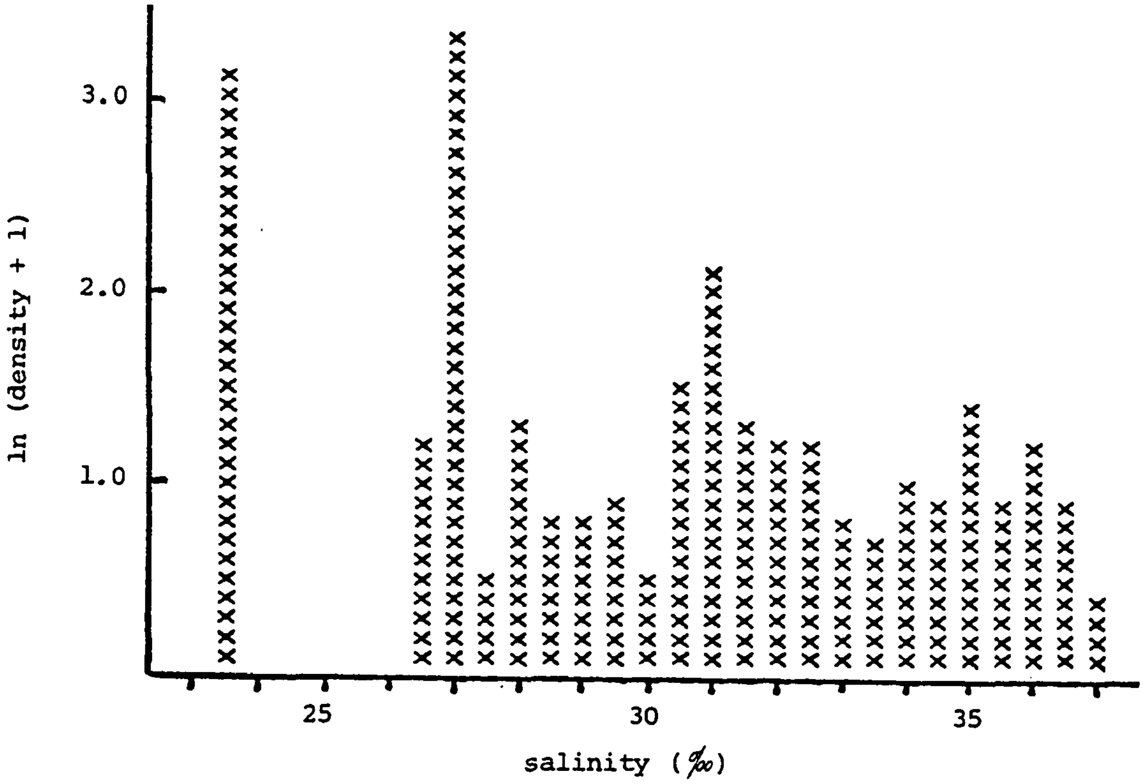


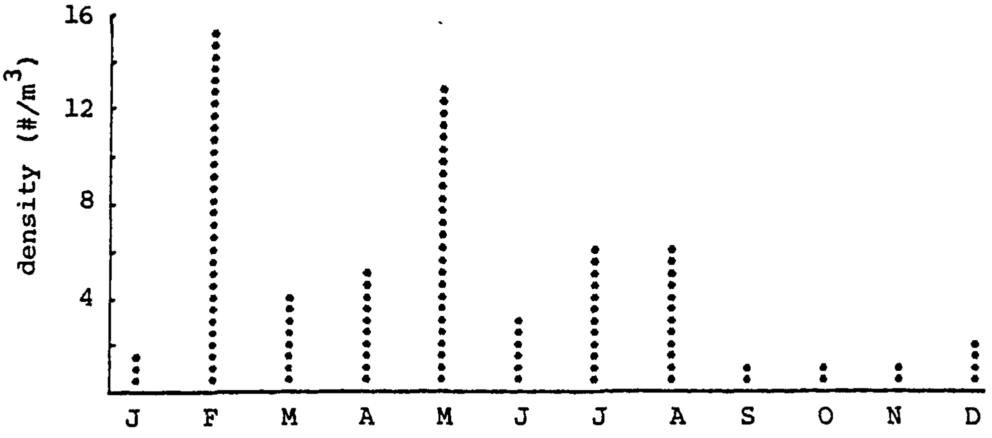
Figure 104. Density relationships with surface temperature and surface salinity for *Centropages velificatus*. See legend of Figure 15 (p. 42).

Clausocalanus jobei. This species was frequently found in large numbers at the offshore stations. Relatively few specimens were captured at the 8, 14, and 28 m stations. The overall seasonal distribution as indicated by mean monthly densities averaged over depth, transect, and year showed the greatest densities occurring between February and August (Fig. 105). Although this pattern generally remained unchanged when the seasonal distribution was examined at each transect, the month of peak density was variable (Fig. 106).

The regression models and the histograms (Fig. 107) both indicated that surface temperature and salinity did not relate very well to density for this species. Simple regression models with other physical factors generally had low R^2 values with stability (8.9%), PMMSROFF (3.3%), and upwelling (3.0%) being the most important variables. When these factors were combined with surface salinity (R^2 = 3.0%) and surface temperature in a multiple regression model it explained 22.9% of the variability in density.

Oncaea mediterranea. The results of the AOV indicated that even at the 5% significance level, depth was the only significant factor in the temporal and spatial distribution of this species. Mean densities increased dramatically with bottom depth (Fig. 108) and the greatest densities were found at the 73 m stations. This was one of the few species or groups of organisms that showed no significant effect of Month or any Month interactions. This indicated a relatively stable population throughout the year (Fig. 108).

Simple regression models indicated that stability of the water column (R^2 = 8.4%), salinity (R^2 = 8.1%), and upwelling (R^2 = 3.4%)



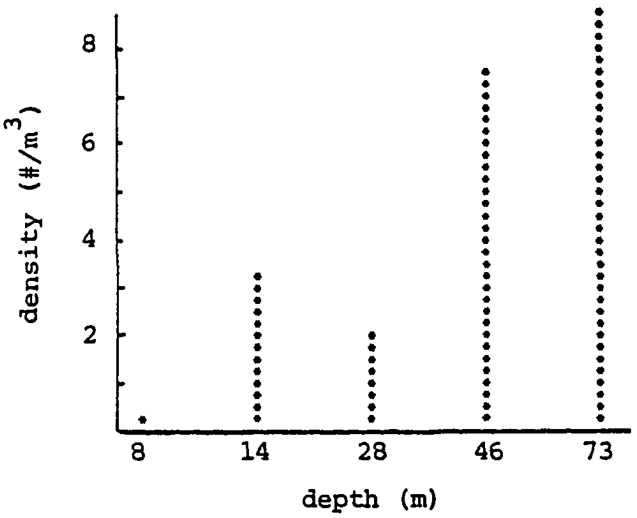


Figure 105. Mean density of *Clausocalanus jobei* for each month and bottom depth.

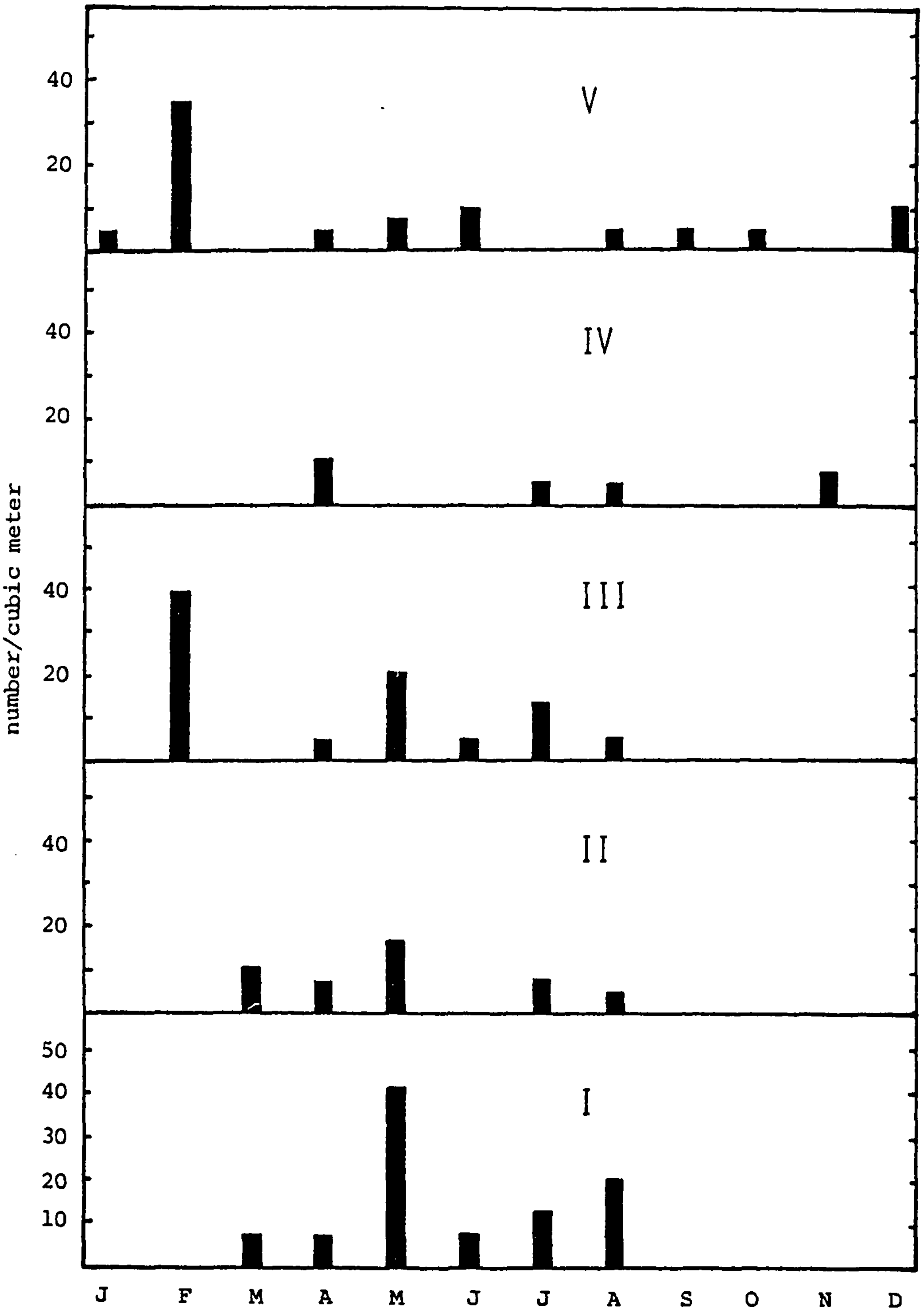


Figure 106. Mean monthly densities of *Clausocalanus jobei* on each transect. Values are averaged over bottom depths and years.

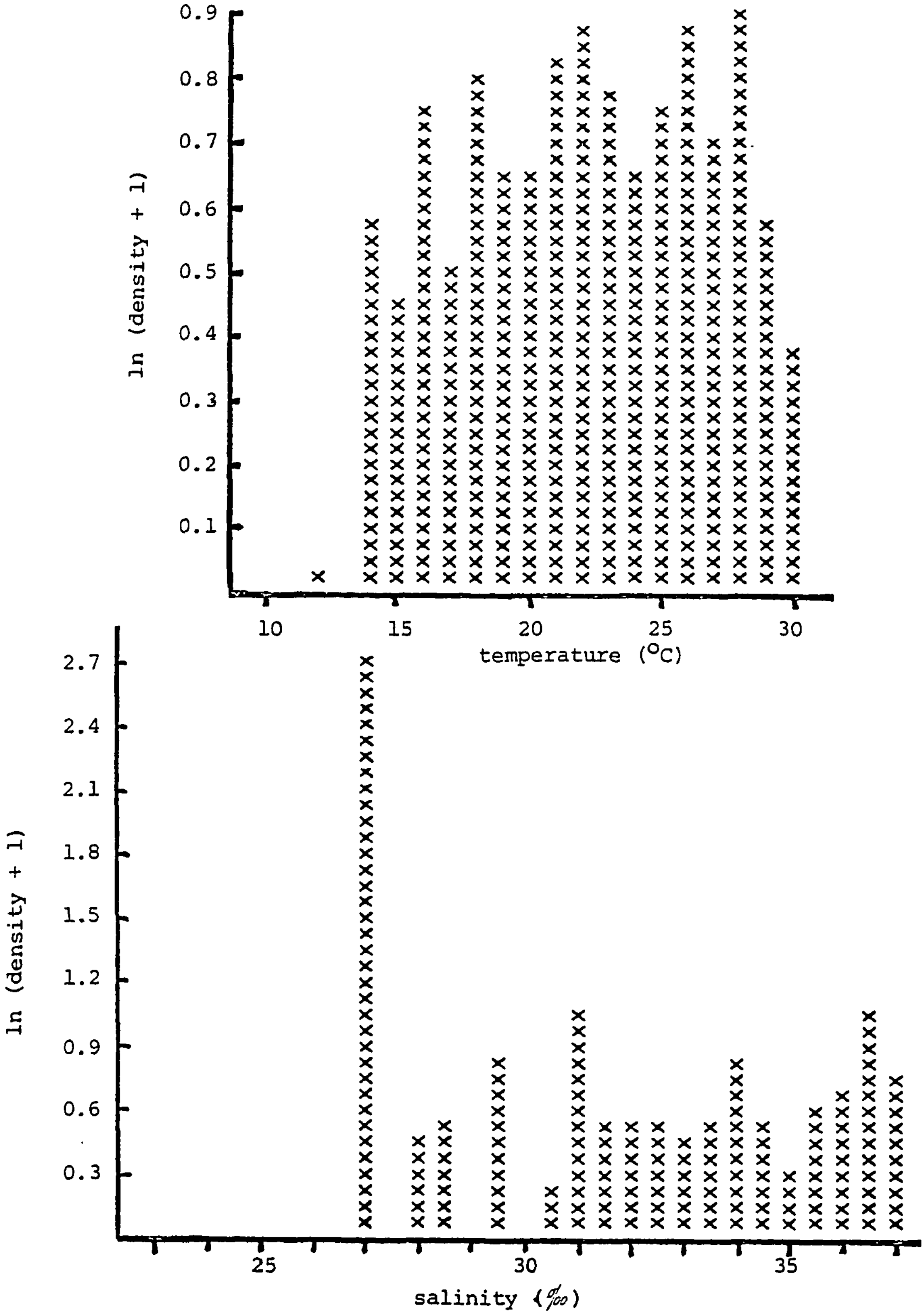
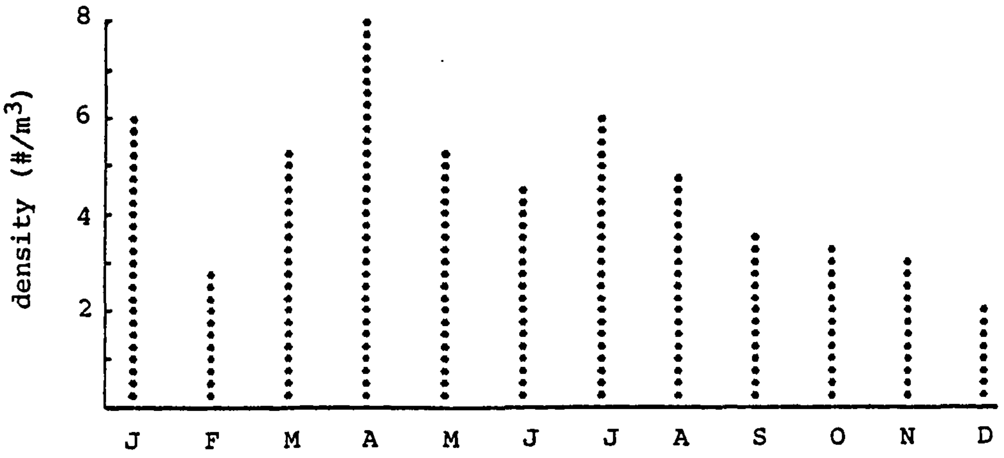


Figure 107. Density relationships with surface temperature and surface salinity for *Clausocalanus jobei*. See legend of Figure 15 (p. 42).



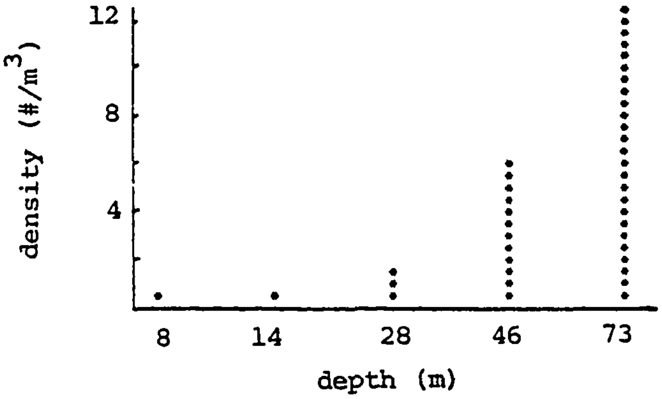


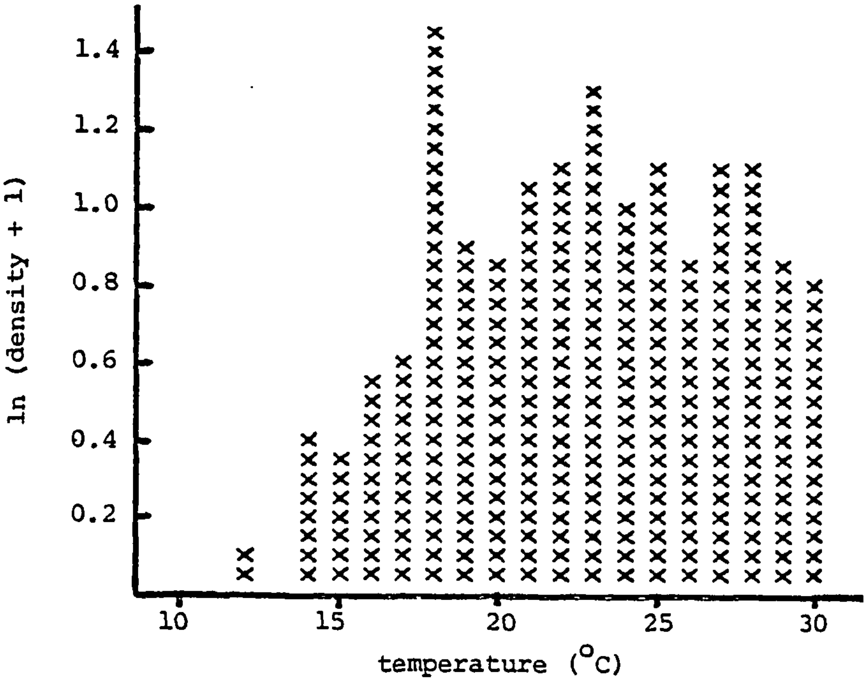
Figure 108. Mean density of *Oncaea mediterranea* for each month and bottom depth.

were important physical and chemical factors. Combined with surface temperature in a multiple regression model these factors explained 22.4% of the variability in the density of this species. The overall regression slope for density and salinity was positive. The histogram of density and salinity showed this general trend of increasing density with salinity (Fig. 109). This pattern however was much more apparent in the samples with temperatures below 21°C (Fig. 110). The histograms of density and temperature showed no distinct relationships.

Species Diversity

Species diversity was measured by the number of species of adult female copepods found in the subsample analyzed from each sample. The relationship between the number of specimens examined and the number of species found is shown in Figure 111 for all of the samples combined and for samples grouped by bottom depth. Subsamples with over 150-250 females appeared to include most of the species. Only 50 subsamples contained fewer than 150 adult females.

The monthly mean number of species is shown in Figure 112 for each depth. The greatest number of species was found at the 73 m stations and the diversity generally decreased at the shallower stations. At the deepest stations (46 and 73 m) the greatest diversity occurred during the winter. The largest mean number was found in January at 73 m (51 species). At the 28 m stations diversity was high in the winter and the summer and at the shallow stations the highest diversities were found in the summer months. This seasonal distribution with depth implied a positive relationship with surface salinity (see Fig.



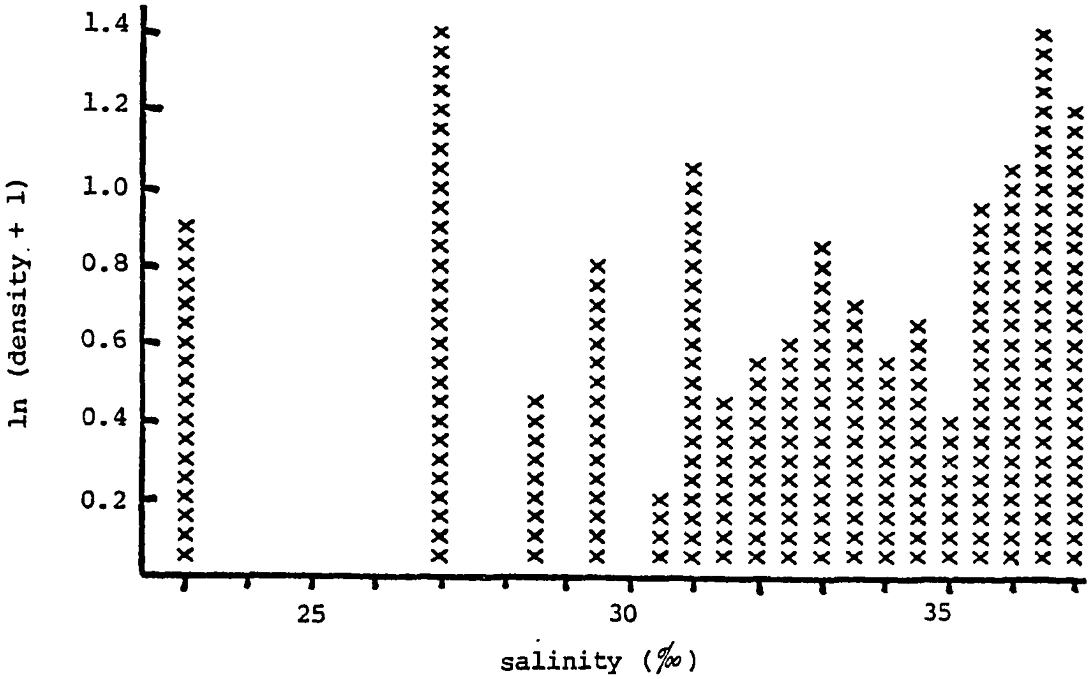


Figure 109. Density relationships with surface temperature and surface salinity for *Oncaea mediterranea*. See legend of Figure 15 (p. 42).

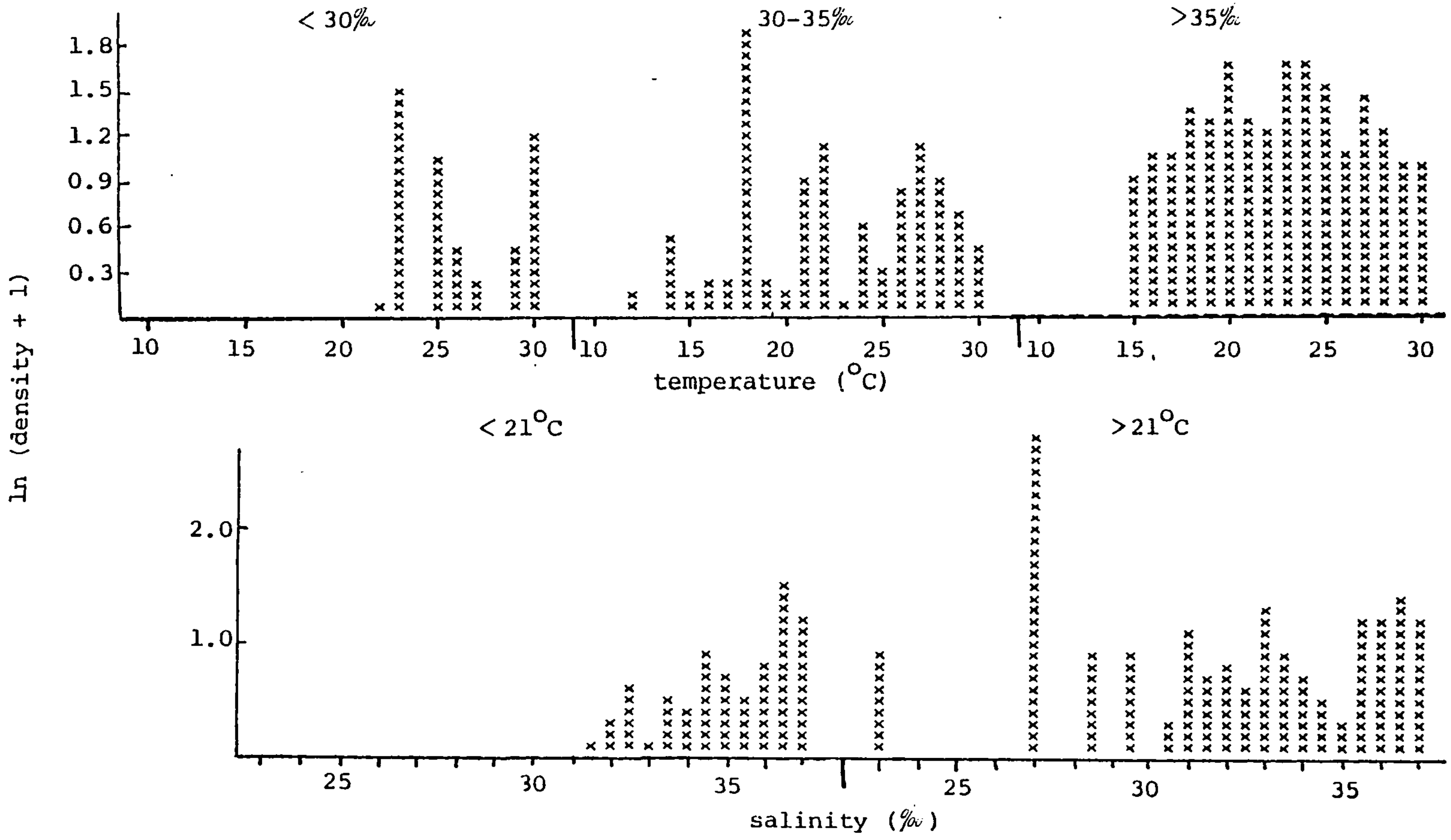
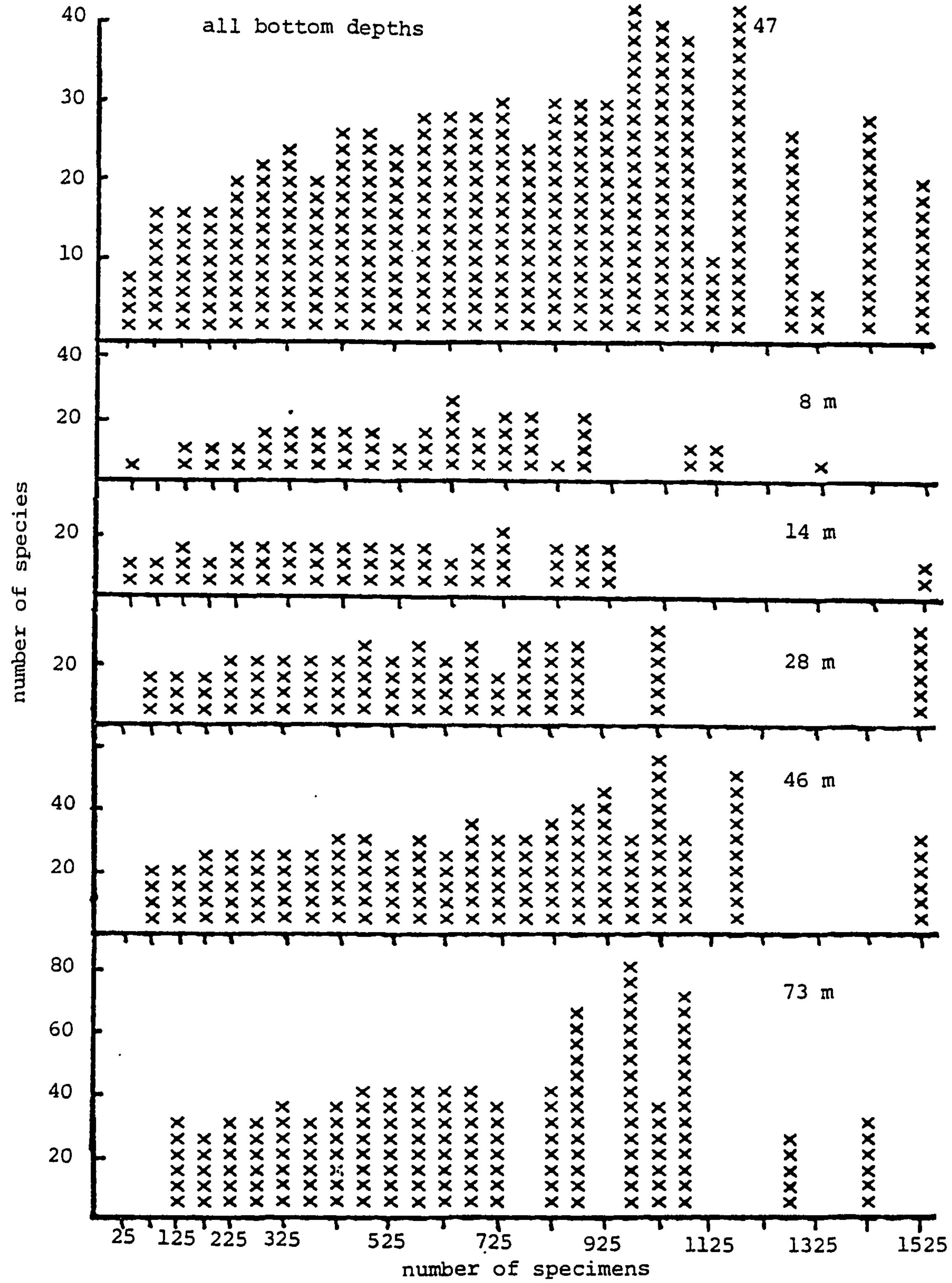


Figure 110. Densities of *Oncaea mediterranea* at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

Figure 111. The relationship between the number of species found and the number of specimens examined for adult female copepods. This relationship is shown for all bottom depths combined and for stations grouped by bottom depth. Each bar represents an interval of 50 specimens examined in a subsample. The height of the bar represents the mean number of species identified from these subsamples.


all bottom depths
47
8 m
14 m
28 m
46 m
73 m
number of species
40
30
20
10
40
20
20
20
40
20
80
60
40
20
25
125
225
325
525
725
925
1125
1325
1525
number of specimens

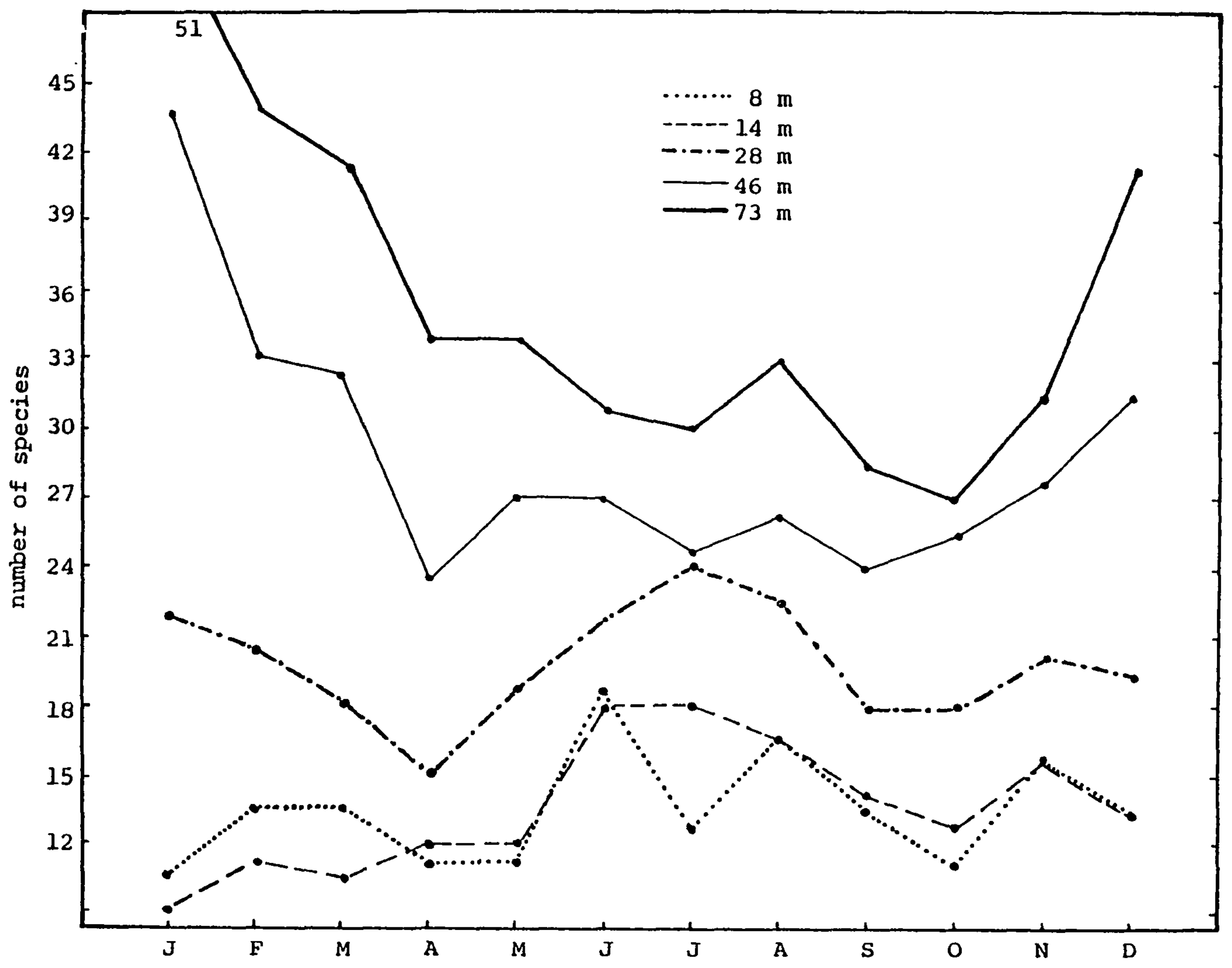


Figure 112. Monthly mean number of species of adult female copepods at each bottom depth sampled.

9, p. 31). The seasonal intrusion of oceanic waters into inshore areas, as evidenced by high salinities, probably increases the number of species in these areas. Seasonal changes in diversity at the deepest stations however may be more complex. Diversity was low during the summer months at these stations although salinities were relatively high. This indicates that some other factors may also be involved in controlling species numbers in these offshore areas. Histograms indicated a general positive relationship between the number of species and surface salinity (Fig. 113) which was most prominent in samples with temperatures below 21°C (Fig. 114).

Grice (1957) found differences in the number of species collected with latitude along the west coast of Florida but inshore-offshore and seasonal trends were apparently not distinct. From samples taken in February and March in the coastal and oceanic waters of the Gulf, Livingston (1974) reported a trend of decreasing species numbers of calanoids with bottom depth. Caldwell and Maturo (1976), using the Shannon-Wiener index, reported increasing diversity offshore and the highest diversities in the fall. Organisms were seldom identified to species, however, and a wide variety of taxa were included in the analysis. Off of South Texas, Park (1979) reported the greatest number of species at offshore stations. At stations with bottom depths comparable to the intermediate and offshore GUS III stations, the number of species of copepods appeared to be greatest during the winter and the summer. Off of the eastern coast of the United States, a trend of increasing species numbers with bottom depth has been reported by Bowman (1971) and Malone (1977). Malone also reported the greatest

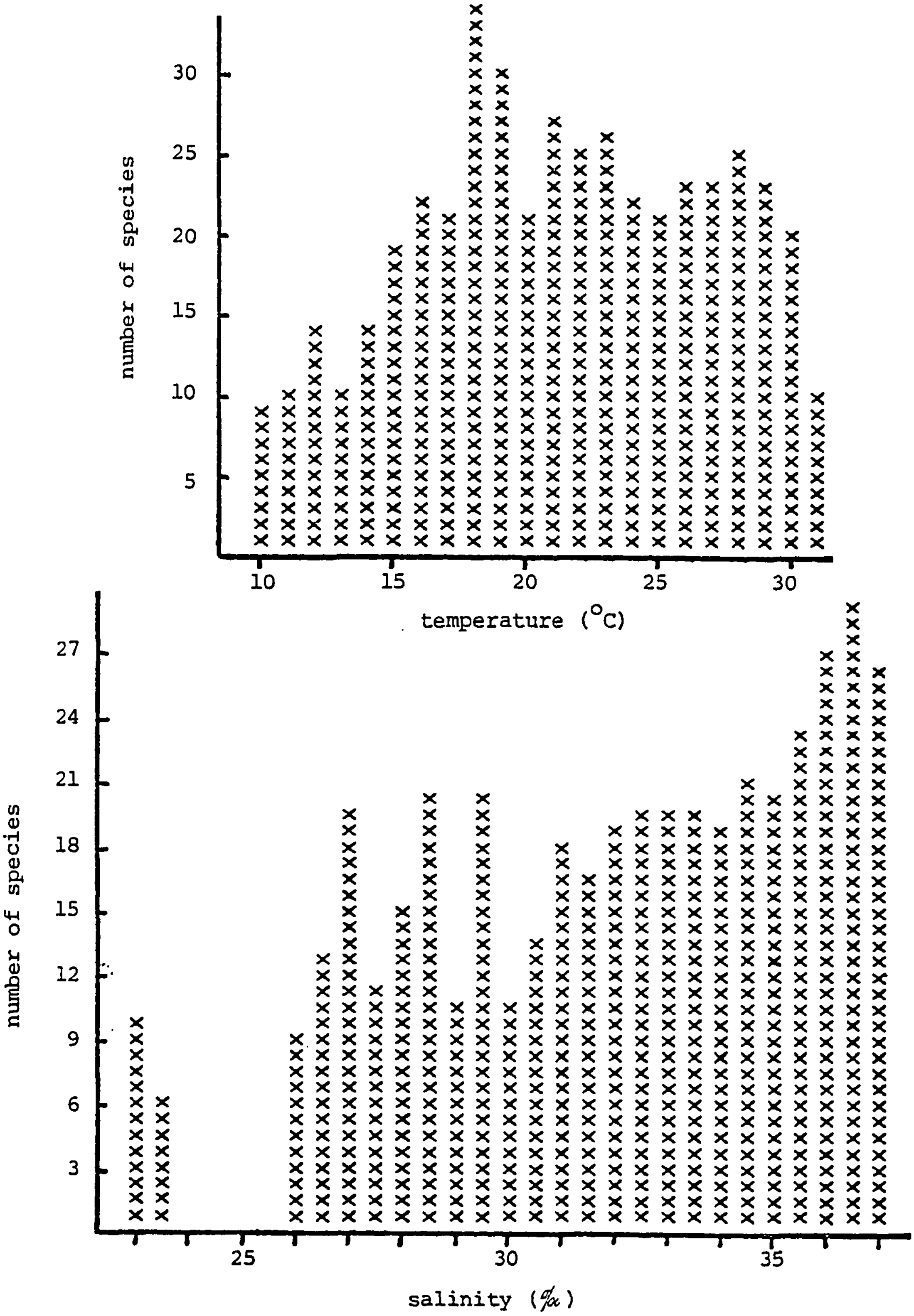


Figure 113. The relationships between the number of species of adult female copepods and the surface temperature and surface salinity. See legend of Figure 15 (p. 42).

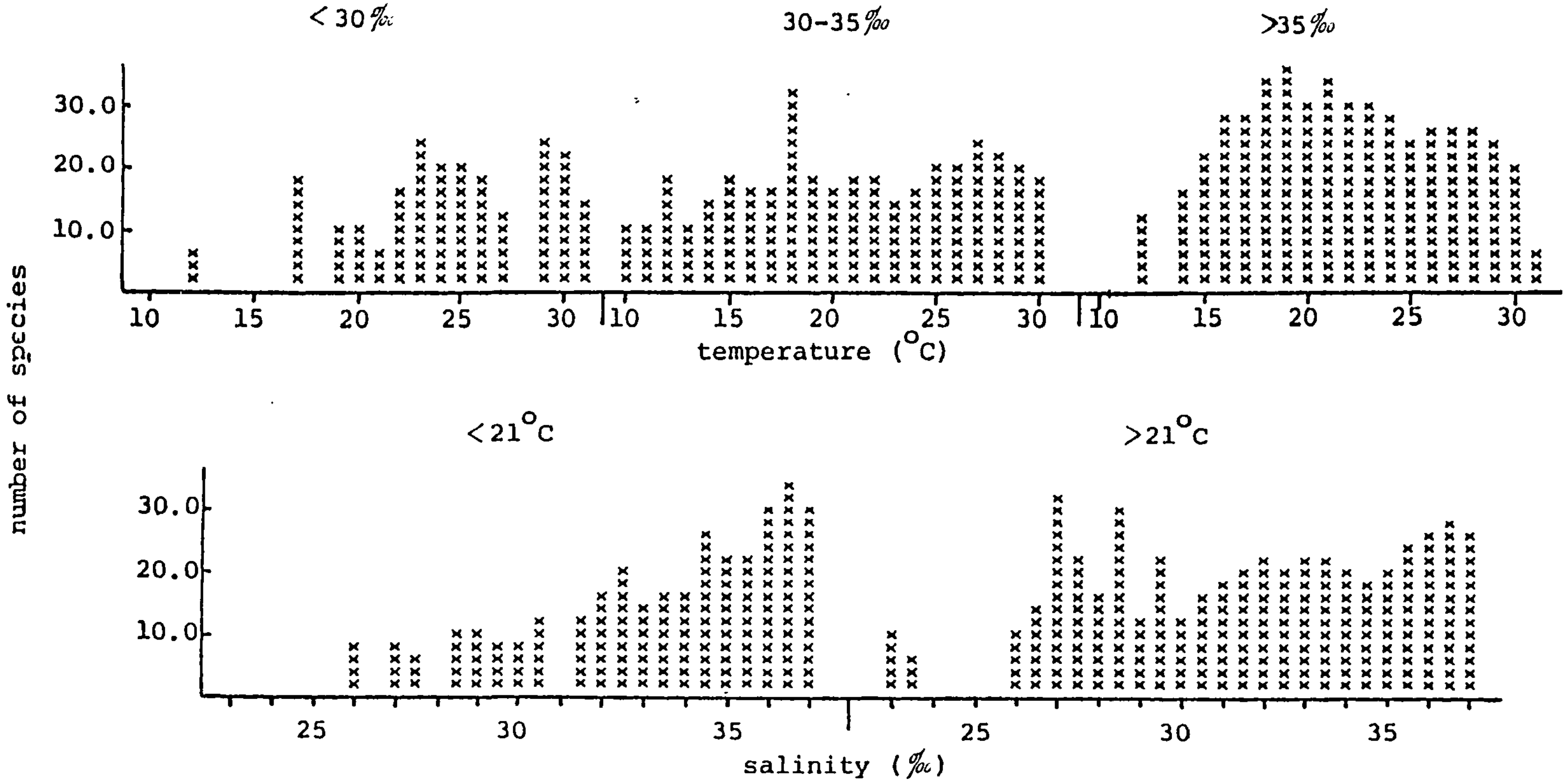


Figure 114. The number of species of adult female copepods found at different surface temperature and surface salinity combinations. See legend of Figure 16 (p. 43).

diversities in the summer and fall. He attributed these high diversities to the intrusion of oceanic waters during these periods.

Correlated Species Groups

Species of adult female copepods were grouped or clustered by first comparing their log transformed densities through product-moment correlation coefficients and constructing a species x species correlation matrix. The species examined along with their identity codes and relative abundances are listed in Table 7. All 513 samples were used in this analysis.

The properties of the correlation coefficient as a similarity index for ecological abundance data have been discussed by Cassie (1961), Clifford and Stephenson (1975), and Boesch (1977). Its use is most appropriate for species grouping or reverse numerical classification. Correlation coefficients have the advantage of a sign which distinguishes between a negative correlation and no correlation and they also incorporate a test of statistical significance. These properties are generally not found in other similarity indices (e.g., Bray-Curtis, Canberra Metric).

The use of the correlation coefficients in normal analyses (entity or site grouping), however, is usually avoided as it often yields small similarity values especially when a large number of zeros are present in the data matrix. This problem is generally due to a few species being abundant and most others relatively rare. Also, correlating entities or sites violates the assumption of independence implicit in the coefficient and causes the statistical significance tests to become unreliable.

Table 7. Codes used to identify species of adult female copepods in the correlated species group analysis. Percent abundance for each species was determined by densities over the entire sampling area.

Code	Species	Percent Abundance
PI	*Paracalanus indicus*	16.0
AT	*Acartia tonsa*	11.9
PQ	*Paracalanus quasimodo*	10.7
PC	*Paracalanus crassirostris*	9.7
CF	*Clausocalanus furcatus*	6.8
OM	*Oncaea media*	6.1
ON	*Oithona nana*	5.6
OP	*Oithona plumifera*	3.9
TT	*Temora turbinata*	3.6
OV	*Oncaea venusta*	3.1
PA	*Paracalanus aculeatus*	3.0
AL	*Acartia lilljeborgi*	2.2
CAZ	*Corycaeus amazonicus*	1.8
FG	*Farranula gracilis*	1.8
CA	*Corycaeus americanus*	1.6
CV	*Centropages velificatus*	1.2
CJ	*Clausocalanus jobei*	1.1
OMD	*Oncaea mediterranea*	1.0
EP	*Eucalanus pileatus*	0.9
CG	*Corycaeus giesbrechti*	0.9
CH	*Centropages hamatus*	0.7
CPS	*Calaocalanus pavoninus*	R
CP	*Calaocalanus pavo*	R
CS	*Calocalanus styliremis*	R
TS	*Temora stylifera*	R
AD	*Acartia danae*	R

R = less than 0.5%

Other measures of species associations found in ecological studies often use presence-absence (binary) data. In particular, various forms of Fager's (1957) "recurrent group analysis" have been used extensively in marine zooplankton work (Fager and McGowan, 1963; Bowman, 1971; Fleminger and Hulsemann, 1974; Livingston, 1974; Shulenberger, 1976). The information loss involved in the use of binary data not only seems unnecessary but also seems undesirable in some instances. Depending on the size of the sampling area, a situation could easily arise where two common species are always found together in ecological samples although their abundances in these samples are inversely related. The tendency for this to occur seems especially likely in zooplankton sampling where relatively long tows tend to homogenize the small scale distributions of species (Cassie, 1961). The use of presence-absence data would cause these species to cluster strongly although their overall distributions would be dissimilar.

In addition to the above problem with very abundant or ubiquitous species, Hurlbert (1969) recognized that there is a very basic difference between correlation coefficients and indices based on binary data; they are not measuring the same thing. The recurrent group type of analysis on presence-absence data is an attempt to establish groups of species which occur together frequently and are possibly members of a community. Group analysis based on correlation coefficients is an attempt to find groups of species which vary in density together either in relation to changes in one another or to extrinsic factors such as food or physical attributes of the environment. The formation of these groups could be related to competition. Species competing with each other for limited resources should have a tendency to appear in different groups. Species which have similar temporal and spatial distributions should be grouped together. In this paper, these groups of species which appear to vary in abundance together will be called correlated species groups.

In the species grouping analysis, I only included the 25 most abundant species of copepods, as determined by their mean densities over the entire sampling area. Data reduction of this type is usually necessary even with an inverse analysis since correlations between rare species found missing together frequently are often high although of no real ecological significance.

After the construction of the correlation matrix a graphical method was used to group species (Wirth et al., 1966; Clifford and Stephenson, 1975). Decreasing levels of r were chosen and species correlated at each level were connected with a line. The length of the line was not significant. As the level of r and subsequently the entry level into a group got lower, the number of members in groups increased and groups often fused. The groups formed at correlation levels from 0.75 to 0.40 are shown in Figures 115 to 117. Members that were completely interconnected within a group were enclosed in a dashed line and the linkages between these species were omitted.

The first group was formed when the correlation level reached 0.78. This group (a.75) included *Clausocalanus furcatus* and *Oncaea venusta*. Both of these species occurred at the deeper stations during the late summer to early winter months and the densities of both species appeared to be positively related to surface temperature and

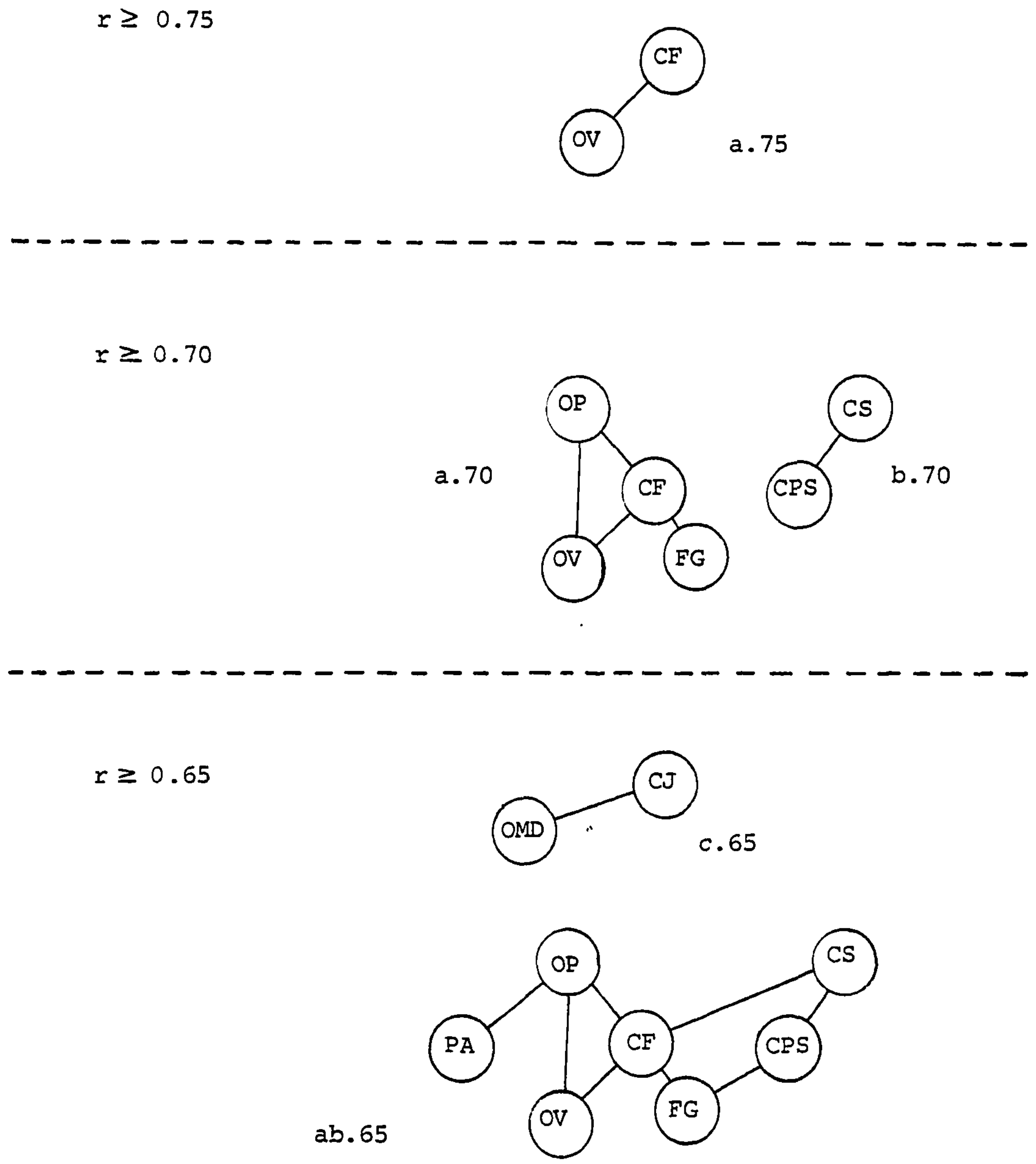


Figure 115. Correlated species groups of adult female copepods formed at correlation coefficient levels between 0.75 and 0.65. Species codes are listed in Table 7 (p. 187). The correlation coefficients were calculated on the natural log of the density for each species. Solid lines connecting species denote correlation at the level indicated.

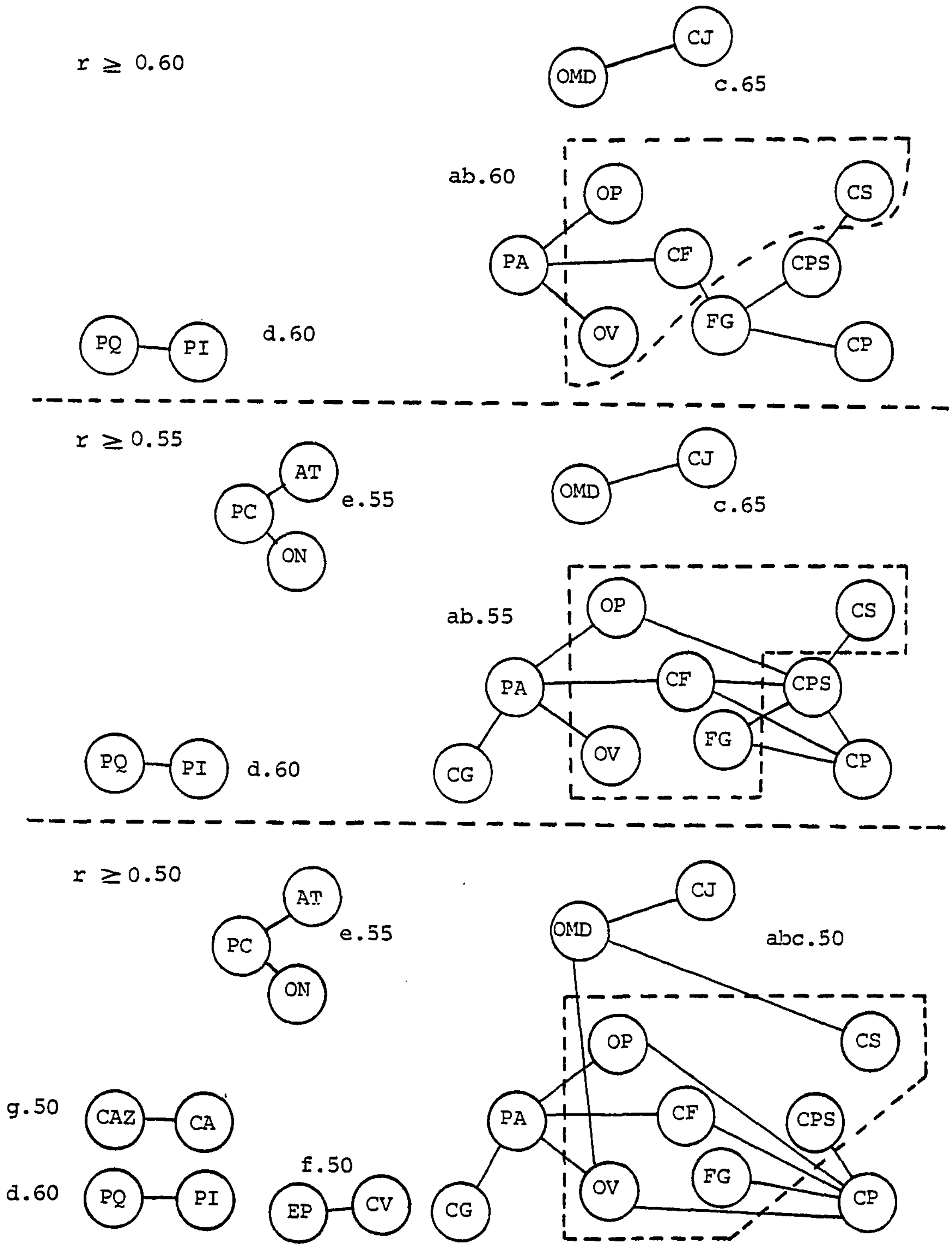


Figure 116. Correlated species groups of adult female copepods formed at correlation coefficient levels between 0.60 and 0.50. Species enclosed within dashed lines are completely interconnected. See legend of Figure 115 (p. 190).

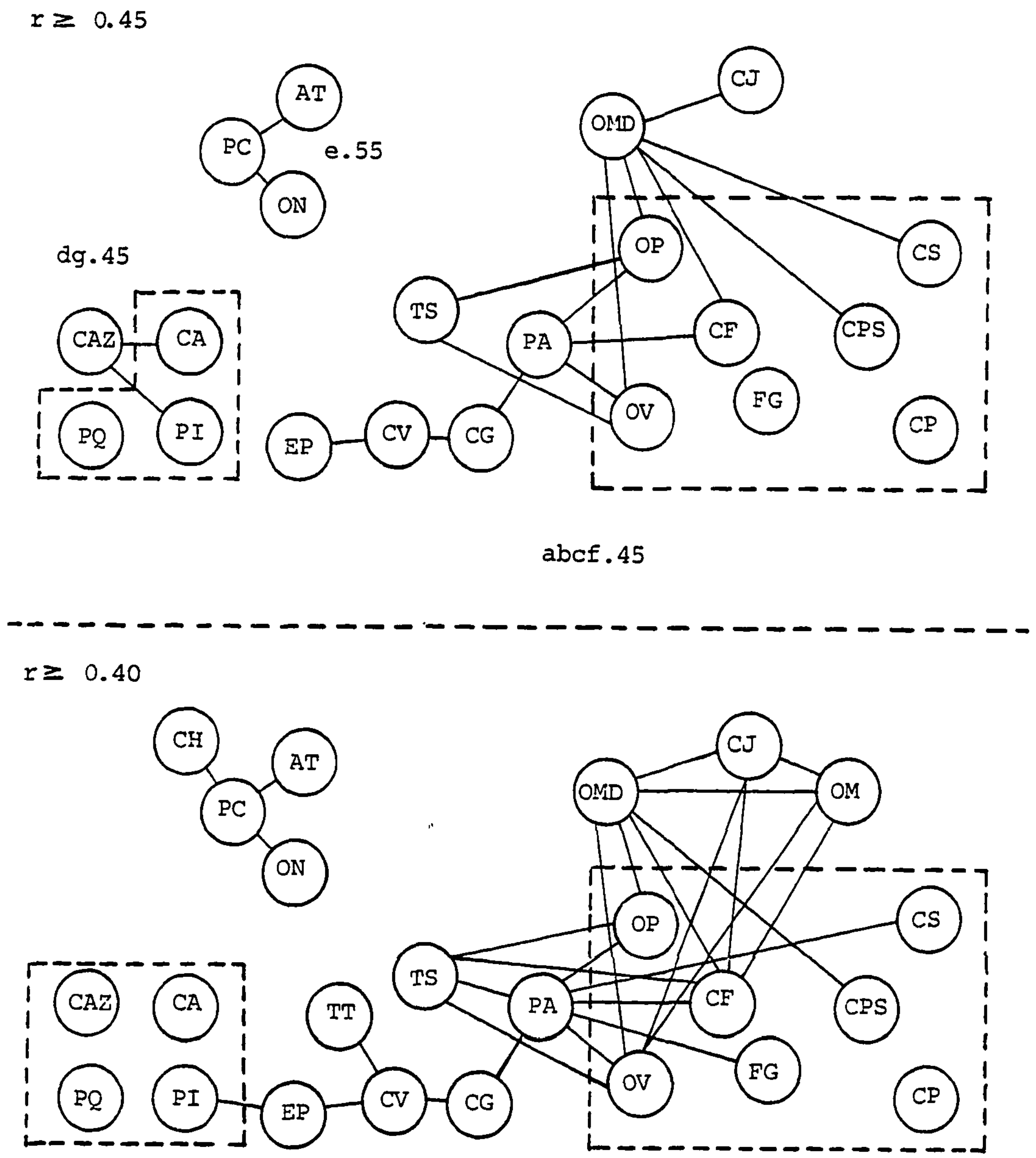


Figure 117. Correlated species groups of adult female copepods formed at correlation coefficient levels between 0.45 and 0.40. Species enclosed within dashed lines are completely interconnected. See legend of Figure 115 (p. 190).

salinity. At r values above 0.70, *Oithona plumifera* and *Farranula gracilis* were added to this offshore group forming group a.70. A new group, b.70, was also formed with a linkage between *Calaocalanus pavoninus* and *Calocalanus styliremis*. Up to this level of the analysis, all of the clustered species were offshore forms. Group a.70 was comprised of relatively abundant species found mostly in summer, fall, and winter. The densities of all of these species were positively related to surface temperature and salinity. Group b.70 was composed of two less abundant species present in samples taken throughout the year.

The inclusion of all species correlated at r values above 0.65 connected groups a.70 and b.70 and added one other species, *Paracalanus aculeatus*, forming the group ab.65. *Paracalanus aculeatus* was relatively abundant in the sampling area and it was found at intermediate depths from June through December. A new group was also formed at this stage of the analysis between *Oncaea mediterranea* and *Clausocalanus jobei*. Both of these fairly abundant species were offshore forms which were found in greatest numbers during the first part of the year (January-August). This group was designated c.65.

At the 0.60 level the only changes included the addition of *Calocalanus pavo* to group ab.65 forming ab.60 and the formation of a new group between two of the most abundant copepods, *Paracalanus indicus* and *Paracalanus quasimodo*. The grouping of these morphologically similar calanoids seemed especially anomalous in relation to competition theory. The distributions of these species are discussed in more detail in the following section on congeneric groups.

When species groups correlated at levels above 0.55 were examined, *Corycaeus giesbrechti* was added to ab.60 and a new group of inshore species was also formed. This inshore group (e.55) included *Oithona nana*, *Paracalanus crassirostris*, and *Acartia tonsa*. Although all of these were inshore species, *O. nana* was found mostly in the fall while *A. tonsa* was found mostly in the spring. They were linked through their relationship with *P. crassirostris* which was very abundant in the spring and appeared to have more representatives in the fall than *A. tonsa*. The densities of *P. crassirostris* and *A. tonsa* were negatively related to both surface temperature and salinity while the densities of *O. nana* only appeared to be negatively related to surface salinity. The correlation between the densities of *A. tonsa* and *O. nana* was low ($r = 0.28$).

The next correlation level, 0.50, linked groups ab.55 and c.65. Two new groups were also formed with linkages between *Eucalanus pileatus* and *Centropages velificatus* (f.50) and between *Corycaeus amazonicus* and *Corycaeus americanus* (g.50). At the next level of r (0.45) the analysis indicated that there were three separate groups:

1. Group abcf.45 was a large offshore group with many marginally linked species. The densities of the core species appeared to be positively related to surface temperature and salinity. Densities of many of the peripheral species also appeared to be positively related to surface salinity.
2. Group dg.45 included four species found at all bottom depths but in highest densities at stations of intermediate depth. The densities of these species did not appear to be related to either temperature or salinity.

3. Group e.55 was an inshore group which included three species. This group persisted unchanged over several levels of the analysis. The densities of these species were all negatively related to salinity.

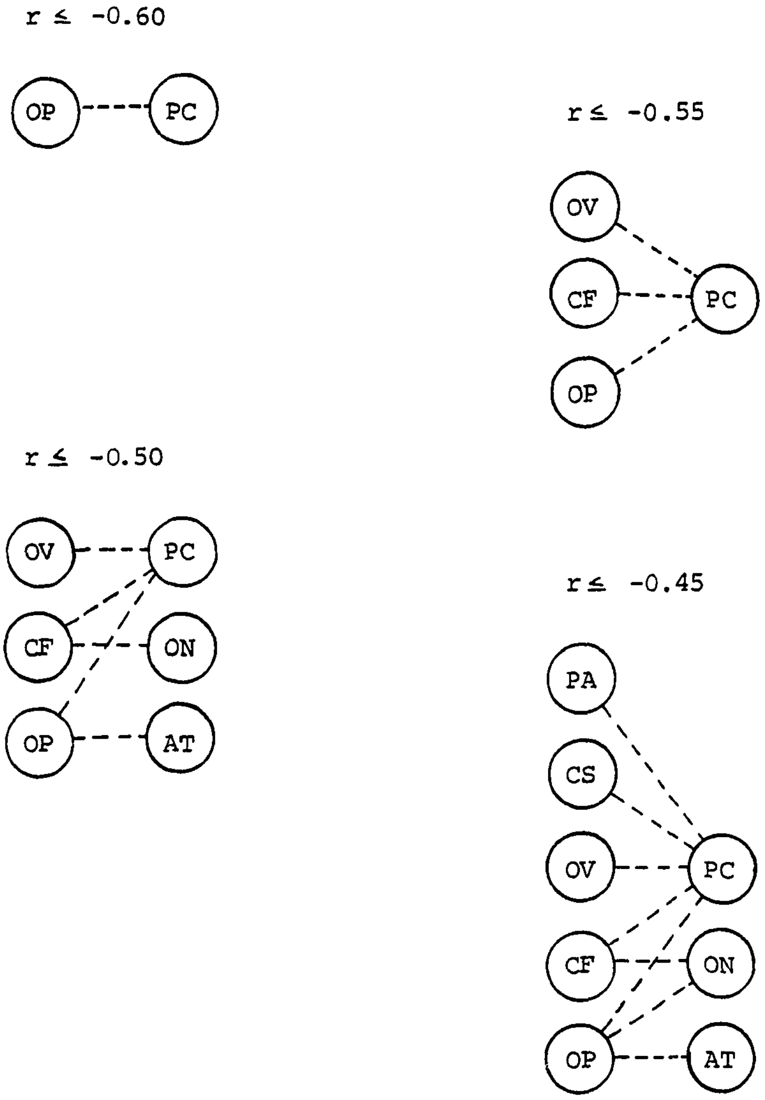
The final level of correlation that was examined (r = 0.40) revealed a single link between the offshore group and the intermediate depth group. These groups were linked through *Eucalanus pileatus* which was present throughout the sampling area in relatively small numbers. Another species, *Centropages hamatus*, was also added to the inshore group. At this level in the analysis, 24 out of the 25 species examined were included in groups.

This type of graphical clustering has several advantages over the typical dendrograms used in most clustering methods. The species within the dashed lines can be considered core species within a group and the degree of interconnection between core species and peripheral species can be easily seen. The development of the various groups with changing similarity levels also reveals information about the relationships between group members.

When the negative correlation values from the matrix were examined, the greatest negative relationship (r = -0.60) was found between *Oithona plumifera* and *Paracalanus crassirostris*, an offshore and an inshore species. At the -0.50 and the -0.45 levels, the three core species of the inshore group in the original cluster analysis were all negatively correlated with members of the offshore group. *Paracalanus crassirostris* had the greatest number of negative linkages. The species relationships based on negative correlation coefficients are shown in Figure 118.

Although the wide variety of clustering techniques in use makes comparisons with other literature difficult, the results of several studies involving species found in this coastal area agree with the clustering results reported here. Off the southeastern coast of the United States, Bowman (1971) used the affinity index of Fager and McGowan (1963) which is based on presence-absence data to group 13 species of calanoid copepods. He placed seven species in an oceanic association *(Clausocalanus furcatus, Euchaeta marina, Lucicutia flavicornis, Nannocalanus minor, Paracalanus aculeatus, Temora stylifera,* and *Undinula vulgaris),* four species in a shelf association *(Centropages velificatus, Eucalanus pileatus, Paracalanus "parvus",* and *Temora turbinata),* and two species in a coastal or inshore group *(Acartia tonsa* and *Labidocera aestiva).* In the Gulf of Mexico, however, Livingston (1974) used the recurrent group analysis of Fager and McGowan (1963) and found 9 out of the 11 species in Bowman's shelf and oceanic associations to be grouped together. His samples in the coastal and oceanic areas of the Gulf were taken in February and March and he noted that no species assemblage appeared to be indicative of shelf waters.

My results however were very similar to those reported by Bowman (1971). Eight of Bowman's 13 species were included in the analysis of GUS III samples when *Paracalanus indicus* and *P. quasimodo* were combined as *P. "parvus".* The three species identified by Bowman as oceanic species *(Clausocalanus furcatus, Paracalanus aculeatus,* and *Temora stylifera)* were strongly connected to the offshore group (Fig. 117,


r ≤ -0.60

r ≤ -0.55

r ≤ -0.50

r ≤ -0.45

Figure 118. Relationships between adult female copepods in the sampling area based on negative correlation coefficients. These coefficients were calculated on the natural log of the density of each species. Species connected by dashed lines are negatively correlated at the level indicated. Species codes are listed in Table 7 (p. 187).

p. 192). The four species examined in this study which were members of Bowman's shelf association *(Centropages velificatus, Eucalanus pileatus, Paracalanus "parvus",* and *Temora turbinata)* were closely linked to each other and were either marginal members of the offshore group or members of the intermediate depth group. *Acartia tonsa* was an inshore species in both analyses.

It is apparent from these results, however, that attempts to cluster species are potentially misleading. At the final level ($r \geq 0.40$) of my correlated species group analysis, seven-eights of Bowman's species examined in this study were included in one group. An examination of the various linkages, however, readily distinguishes the species relationships. This type of graphical analysis therefore seems valuable as a method of examining species groups in ecological studies.

Park and Turk (1980) also examined groups of copepod species in the neritic waters off the South Texas coast. They grouped 19 species using a cluster analysis based on the Bray-Curtis dissimilarity coefficient. Seventeen of these species were also included in the correlated species group analysis of the GUS III samples. Park and Turk (1980) placed these species into the following four groups.

Inshore

1. *Acartia tonsa*
2. *Corycaeus americanus*
   Corycaeus amazonicus
   Eucalanus pileatus
   Centropages velificatus
   Temora turbinata
   Paracalanus quasimodo
   Paracalanus indicus

Offshore

3. *Oncaea mediterranea*
   Clausocalanus jobei
4. *Farranula gracilis*
   Calocalanus pavo
   Corycaeus giesbrechti
   Paracalanus aculeatus
   Oithona plumifera
   Oncaea venusta
   Clausocalanus furcatus

The offshore groups were very similar to those found at the 0.55 level in my correlated species group analysis (Fig. 116, p. 191). *Oncaea mediterranea* and *Clausocalanus jobei* were separated from most of the other species through their seasonal distributions. The inshore species in group 2 were all connected at the 0.40 level in the correlated group analysis. These were mostly intermediate depth species in the GUS III samples and the strongest linkages were between *Paracalanus indicus, P. quasimodo, Corycaeus americanus* and *C. amazonicus*. Again, *Acartia tonsa* was an inshore species in both analyses.

This comparison between the study done by Park and Turk (1980) and the analysis of the GUS III samples is especially interesting since it involves two independent sampling programs of the copepods off the Texas coast. Although entirely different types of cluster analyses were employed, the results from both studies appear quite similar.

Comparisons of Common Congeneric Copepods

The competitive exclusion principle (Hardin, 1960) has often been used to explain the distributions of closely related species. According to this theory, species that compete for a limited resource cannot co-exist. The relevancy of competition theory in changing environments, however, has occasionally been questioned (Hutchinson, 1961; Wiens, 1977). Variability in the environment may periodically vary the availability of "limiting resources" providing a refuge for species that are poor competitors or it may frequently alter the direction of competition between species. Selective predation may also play an important role in species distribution.

If interspecific competition for food is a major factor affecting the distributions of species within the zooplankton, the effect of this competition should be seen in the temporal and spatial distributions of congeneric copepods. In the classification of calanoid and cyclopoid copepods, most taxonomic differences based on feeding appendages are absent below the family level. The distinction of taxa within families is usually based on reproductive structures and swimming appendages. Almost all morphological differences therefore between feeding structures in congeneric species are due to the size of the organism. This appears to be especially true in particle feeding genera where the size and shape of the setae on the second maxilla determine the efficiency and particle retention capabilities of the filtering mechanism (Marshall and Orr, 1955). Unless food is not limiting or feeding behavioral differences exist, congeners of similar size, found together, probably compete for food particles. This would appear to be especially likely for herbivorous species that feed on a relatively homogeneous food source, the phytoplankton. Competition for food between these species therefore might be related to differences in their temporal and spatial distributions.

The distributions of the common congeneric species from five genera of calanoid copepods (*Paracalanus, Acartia, Clausocalanus, Temora,* and *Centropages*) and three genera of cyclopoid copepods (*Oncaea, Oithona,* and *Corycaeus*) were examined over the study area. Members of these genera made up more than 93% of the adult female copepods examined in this study. The size data on the species reported here came from total length measurements on specimens from samples taken off the South Texas coast in the 1970's by Park (1976b, 1977). These measurements were means or ranges, usually from four to six specimens. They were not intended for this purpose, but should be an adequate estimate of species lengths in the study area.

Since these distributions are based only on data for adult females, any trophic analysis is necessarily incomplete. Ideally, the distributions of the immature forms and the males for each species should be included in an analysis of this type. Problems with identifications of immature forms of congeners along with possible changes in feeding habits with development make the lumping of immature forms with adult females difficult and undesirable. Data on males, although easier to obtain, would be of limited usefulness. The overall abundances of males were generally low. The males of many species also have reduced mouth parts and do not feed as adults. It is important to note however that the lack of data on males could be significant for several groups of copepods. Relatively large numbers of *Acartia* and *Temora* males were present in the samples, and information on cyclopoids may also be lacking due to the abundance of males in the family Corycaeidae.

Paracalanus. Members of this genus dominated this neritic area and comprised more than 39% of the female copepods, based on density. The common species included *P. indicus, P. quasimodo, P. crassirostris,* and *P. aculeatus*. These calanoids are generally considered to be filter feeding herbivores (Wickstead, 1962; Mullin, 1967; Itoh, 1970; Timonin, 1971).

Paracalanus crassirostris, a relatively small species (0.6 mm), and *P. aculeatus* (1.1 mm) had limited distributions in the study area. *Paracalanus crassirostris* was found at inshore stations, mostly in the spring and *P. aculeatus* was abundant at stations of intermediate depth during the fall.

The two most abundant species in this genus, *P. indicus* and *P. quasimodo*, provided an interesting taxonomic and distributional problem. These two species are very similar morphologically and were first separated by Bowman (1971). Originally, both species had been identified as *Paracalanus parvus*. *Paracalanus parvus* however differs in the spinature of the swimming legs and the shape of the forehead and Bowman (1971) reported this species from the northeastern coastal waters of the United States. Past records on the worldwide distribution of *P. parvus* therefore need to be re-examined.

The major distinguishing characters between the females of *P. indicus* and *P. quasimodo* include a dorsal hump and the presence of hairs on the genital segment in *P. quasimodo* (Figs. 119 and 120). The mouth parts and swimming legs appear to be identical. The sizes of both species are approximately 1 mm. Although the dorsal hump character appeared to be intermediate in about 5 to 10% of the specimens examined from this area, *P. quasimodo* could always be distinguished by the generally rounded shape of the forehead. When the specimens were grouped in this manner, the presence of hairs on the genital segment almost always was consistent with the cephalothorax shape attributed to *P. quasimodo*. Although Bowman also considered the shape of the spermatheca to be a valid character separating these species, this character did not appear

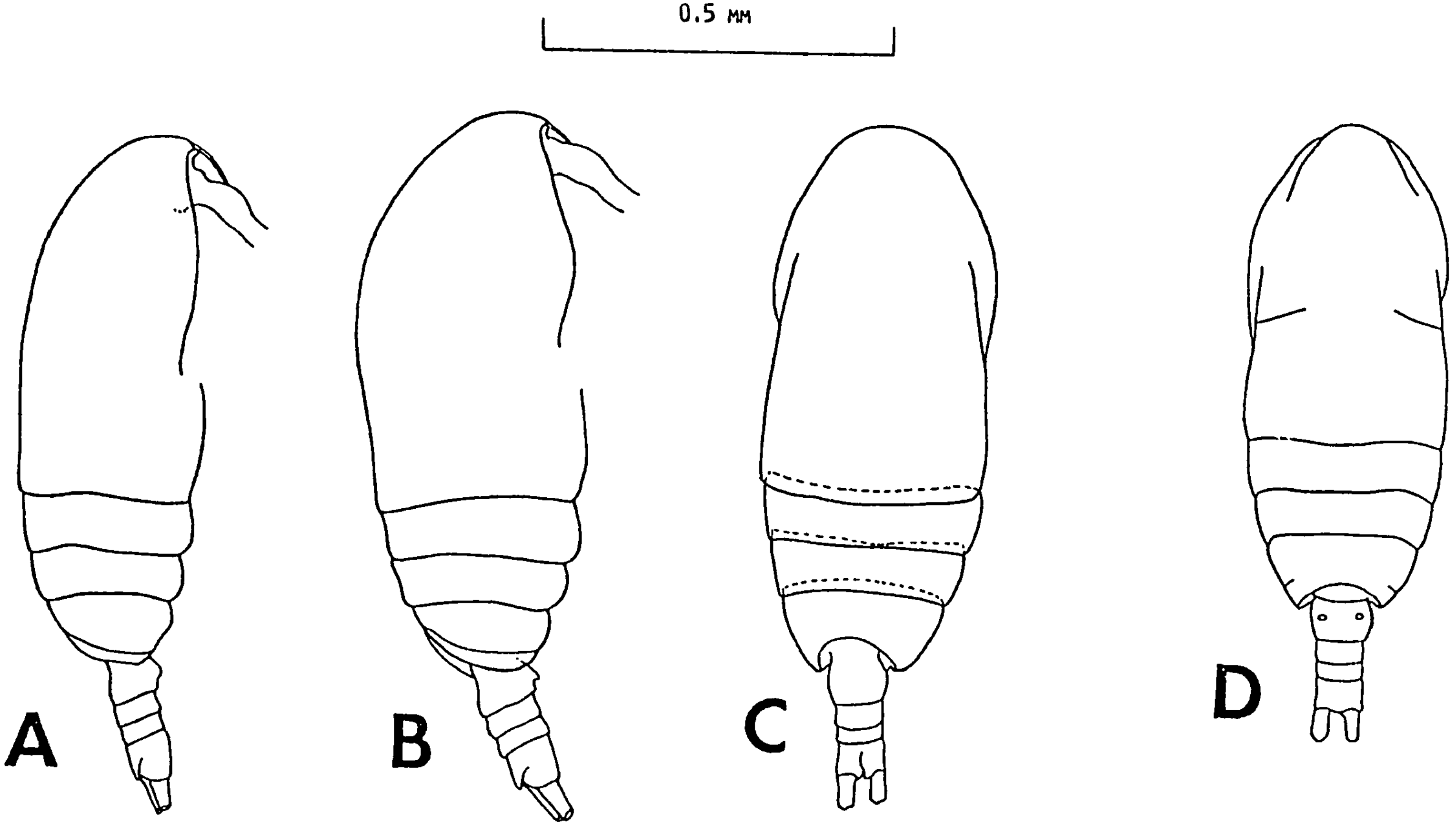


Figure 119. Dorsal and lateral views of female *Paracalanus indicus* (A and C) and *Paracalanus quasimodo* (B and D).

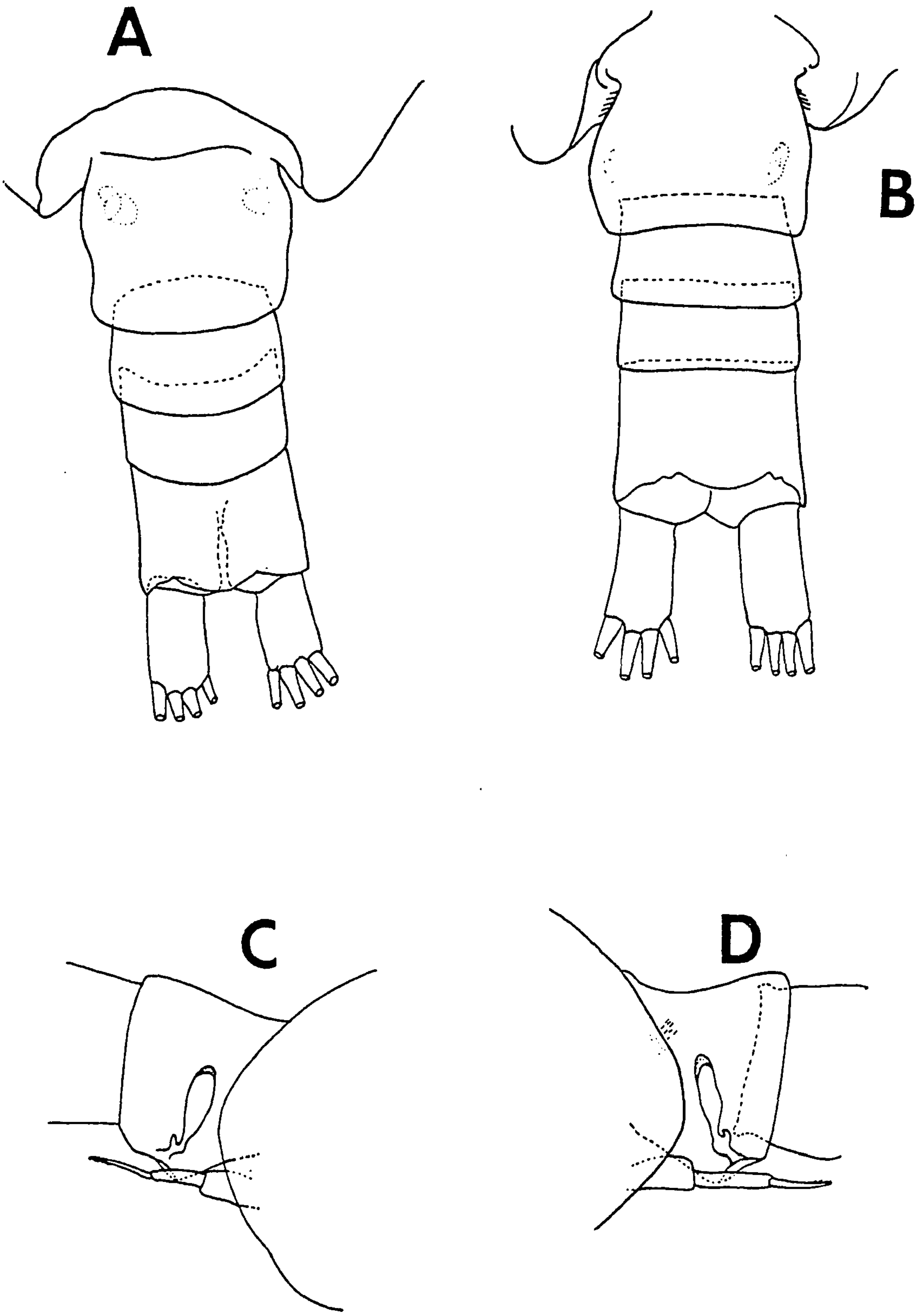


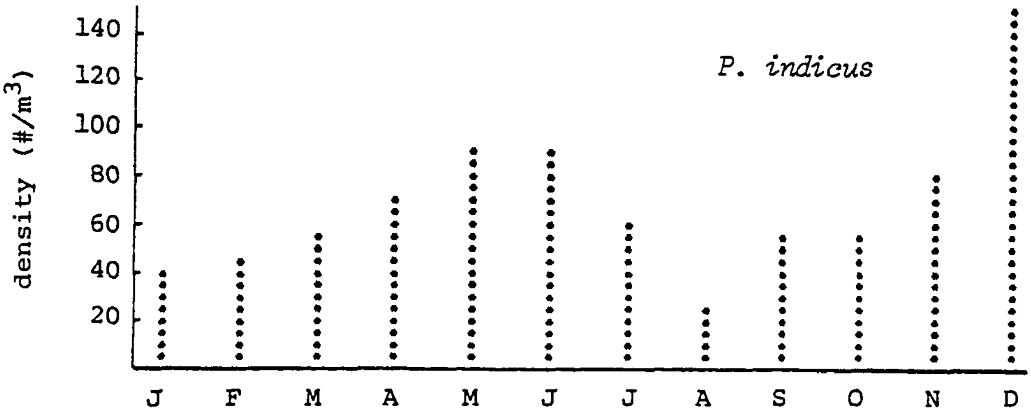
Figure 120. Dorsal and lateral views of the genital segment and urosome of female *Paracalanus indicus* (A and C) and *P. quasimodo* (B and D).

to be dependable in the routine identification of specimens from the GUS III samples. Males were not examined in detail in this study but Bowman reported that the only difference between the males of these species was the presence of hairs on the first urosomal segment in *P. quasimodo*.

Bowman (1971) reported these species from samples taken in October and November off the southeastern coast of the United States. *Paracalanus quasimodo* was approximately three times as abundant as *P. indicus* and *P. indicus* was more frequently found in oceanic samples. In the GUS III samples, *P. indicus* was more abundant than *P. quasimodo*.

The AOV results for these two species indicated that there were several differences in their temporal and spatial distributions. The Depth*Month interaction was highly significant for *P. indicus* while the Transect*Month interaction was significant for *P. quasimodo*. When monthly densities were averaged over the entire sampling area, the overall seasonal distributions also appeared dissimilar (Fig. 121). *Paracalanus quasimodo* had density peaks in April and September while the density of *P. indicus* peaked in May and December. This graphical representation of the main effect of Month in the AOV might give a general picture of the distributional differences between the two species even though several other factors showed significant interaction with Month.

Other results indicated a number of similarities between the two species. Regressions and histograms showed that the densities of both of these species did not appear to be related to physical or chemical factors. The histograms of density versus surface temperature and salinity were especially similar (Fig. 47, p. 100 and Fig. 58, p. 113).



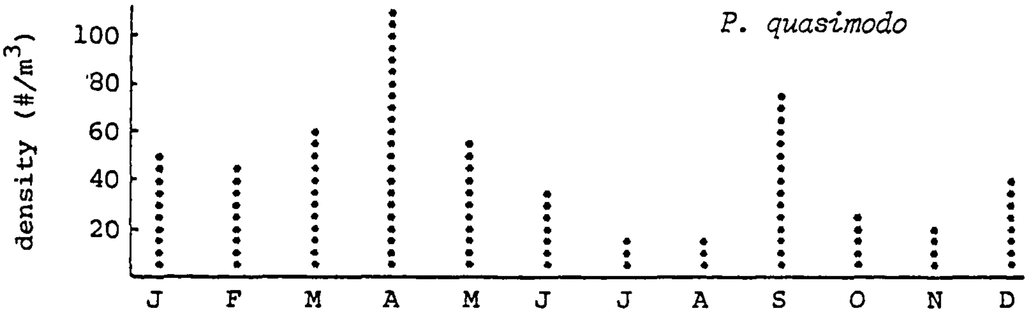


Figure 121. Monthly mean densities of *Paracalanus indicus* and *Paracalanus quasimodo* over the entire sampling area.

Results from the correlated species group analysis showed that the densities of these two species were positively correlated at the 0.60 level. They remained together as a group without interconnections to other species through several levels of the analysis. These correlation data suggest that, especially in relation to other common species, the distributions of *P. indicus* and *P. quasimodo* were quite similar.

The vertical distribution data, however, shown in Figures 122 and 123 indicated that there was a definite vertical separation between these two species during the daylight hours. In daytime surface tows, *P. quasimodo* was almost exclusively found in five out of the six samples. The other daytime surface tow contained almost all *P. indicus*. This indicated that these two species had distinctly separate daytime vertical distributions at the time of sampling. The two species may have been layered in narrow vertical bands and variability in the depth of towing could account for the occurrence of *P. indicus* in the 1200 hr surface tow on July 4. The degree of vertical migration for both species did not appear to be extensive since neither species appeared in large numbers at the 18 m sampling depth. The significance of this behavioral difference in vertical migrations could be related to avoidance of competition or predation.

The ecological separation of the four common congeners of *Paracalanus* in this area appeared to be significant. *Paracalanus crassirostris* is a relatively small species which might indicate some size selective differences in feeding. This species was found in inshore areas and densities were negatively correlated with temperature and salinity. The other congeners, *P. aculeatus, P. indicus,* and

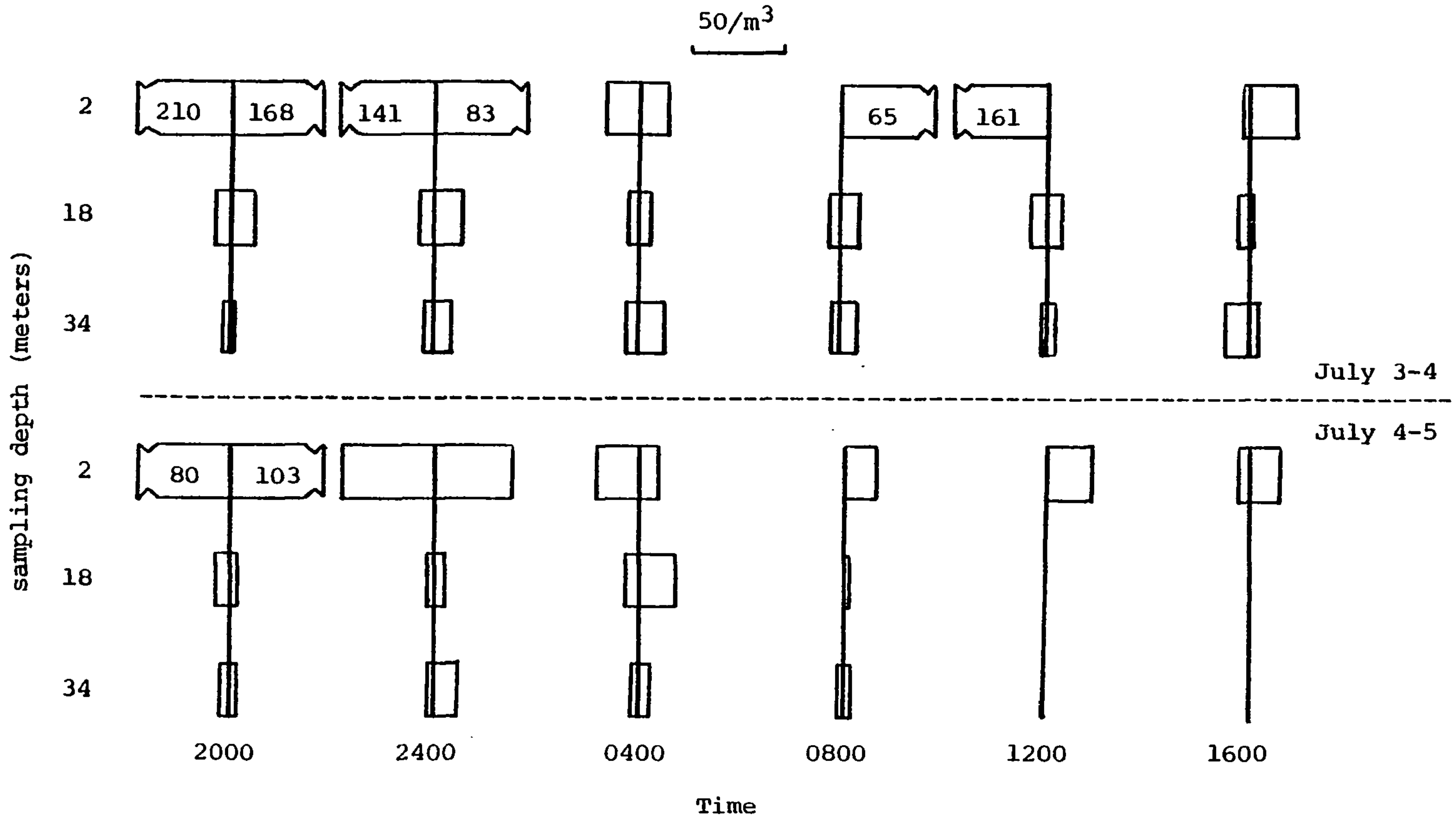


Figure 122. Diel changes in the vertical distribution of *Paracalanus indicus* (left of center line) and *Paracalanus quasimodo* (right of center line) based on density of adult females. Samples were taken at three depths in the water column every four hours at Station B on July 3-5, 1963.

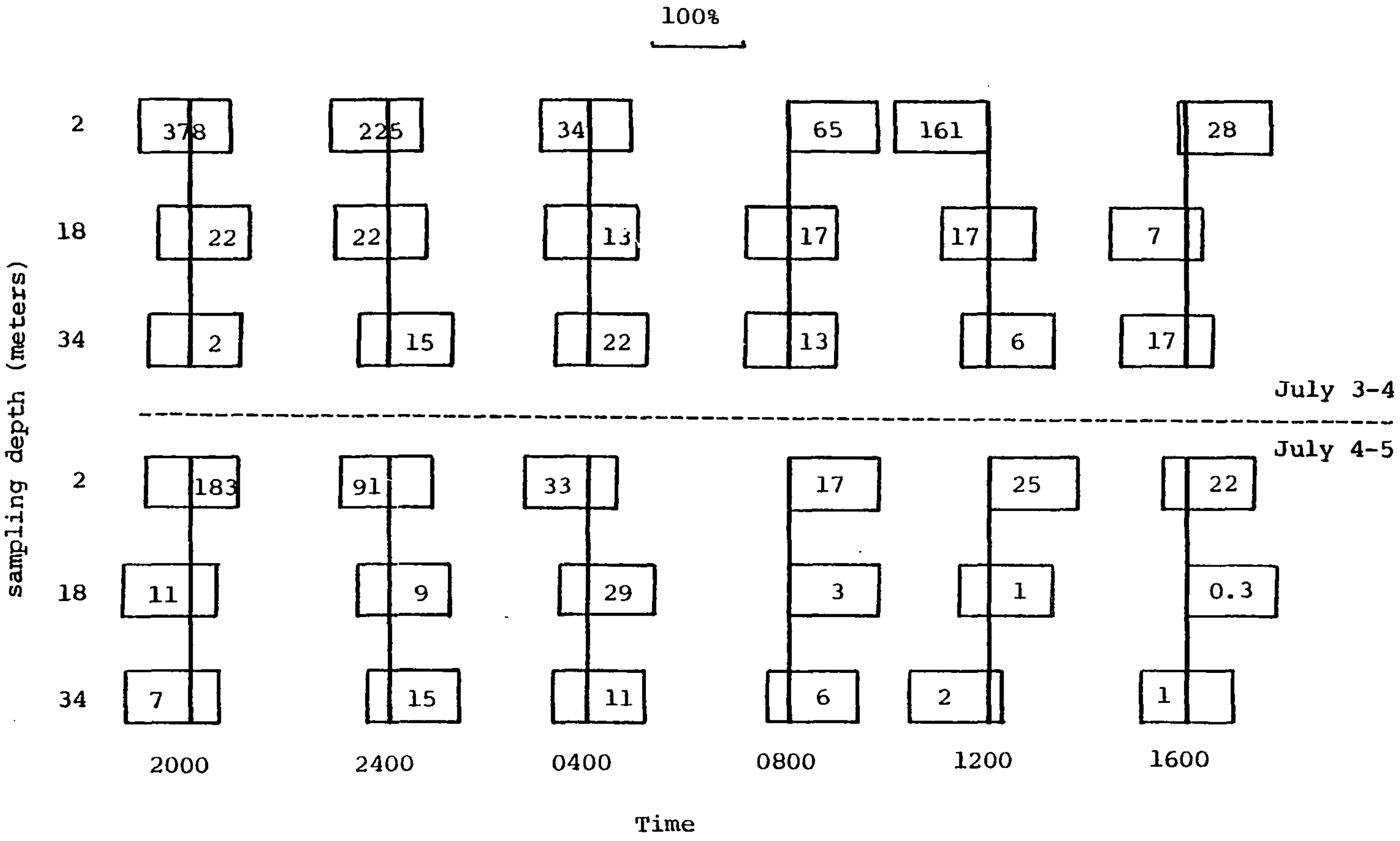


Figure 123. Diel changes in the vertical distribution of *Paracalanus indicus* (left of center line) and *Paracalanus quasimodo* (right of center line) based on the percentage of their combined density. This combined density is indicated in each box. See legend of Figure 122 (p. 208).

P. quasimodo, were all of similar sizes. *Paracalanus aculeatus* had a limited seasonal and spatial distribution and its density was positively related to temperature and salinity. *Paracalanus indicus* and *P. quasimodo* showed little relationship with temperature and salinity and were widely distributed over the sampling area. Some evidence for a temporal separation existed but the vertical distribution data indicated a definite vertical separation in the water column during daytime hours.

These four species of *Paracalanus (P. indicus* and *P. quasimodo* reported as *P. parvus)* have been recorded in the Gulf of Mexico as common inshore and neritic forms by Davis (1950), King (1950), Fleminger (1956), and Grice (1957, 1960). Gonzalez (1957) also reported *P. parvus* as a coastal species found near the mouth of the Mississippi River. I have been unable to find distribution records of *P. indicus* and *P. quasimodo* other than those by Park (1977, 1979).

Fleminger (1956) reported that *P. parvus* was concentrated in neritic waters throughout the Gulf of Mexico and that *P. aculeatus* was an oceanic species which was also abundant in shelf waters. He recorded *P. crassirostris* as a neritic form found to be most abundant in the coastal waters over the northern continental shelf. Grice (1957, 1960) and Park (1977, 1979) reported spatial distributions for these common *Paracalanus* species which were similar to those found in the GUS III samples.

Acartia. Members of the genus *Acartia* made up 14% of the adult female copepods examined. This genus is generally considered to be omnivorous (Anraku and Omori, 1963; Itoh, 1970; Timonin, 1971; Richman, Heinle, and Huff, 1977; Lonsdale, Heinle, and Siegfried, 1979). Most of the specimens were *Acartia tonsa*, a typical estuarine form which was abundant in the nearshore areas. Other congeners included *A. danae*, an oceanic form which occurred in small numbers at offshore stations in the summer, and *A. lilljeborgi*, a slightly larger species (approximately 1.8 mm) which occurred sporadically. The density of *A. lilljeborgi* did not appear to be strongly related to physical or chemical factors, although it was seldom found in samples with high salinity and low temperature combinations. *Acartia tonsa* was found mostly on Transects III and IV during the spring and it exhibited a strong negative relationship with both surface temperature and surface salinity.

Although *A. tonsa* is a typical estuarine copepod, it has been reported frequently as a common and very abundant coastal species in the Gulf of Mexico (Davis, 1950; King, 1950; Gonzalez, 1957; Fleminger, 1956; Grice, 1957, 1960; Park, 1977, 1979). Most of these reports indicate that this species is restricted to nearshore areas. *Acartia lilljeborgi* and *A. danae* have been reported as less common species in the coastal waters of the Gulf by Fleminger (1956) and Park, 1977, 1979). *Acartia danae* has also been reported as rare in neritic waters by Grice (1957), although it is a relatively common oceanic species (Park, 1970; Livingston, 1974; Minello, 1974).

Clausocalanus. Members of the genus *Clausocalanus* made up 7.9% of the adult female copepods examined. Of the seven species found in this genus (Table 5, p. 87), only two, *C. furcatus* and *C. jobei*, were found in any great number. The other five species occurred infrequently and had low overall mean densities. Members of this genus are generally considered to be herbivorous filter feeders (Itoh, 1970; Timonin, 1971).

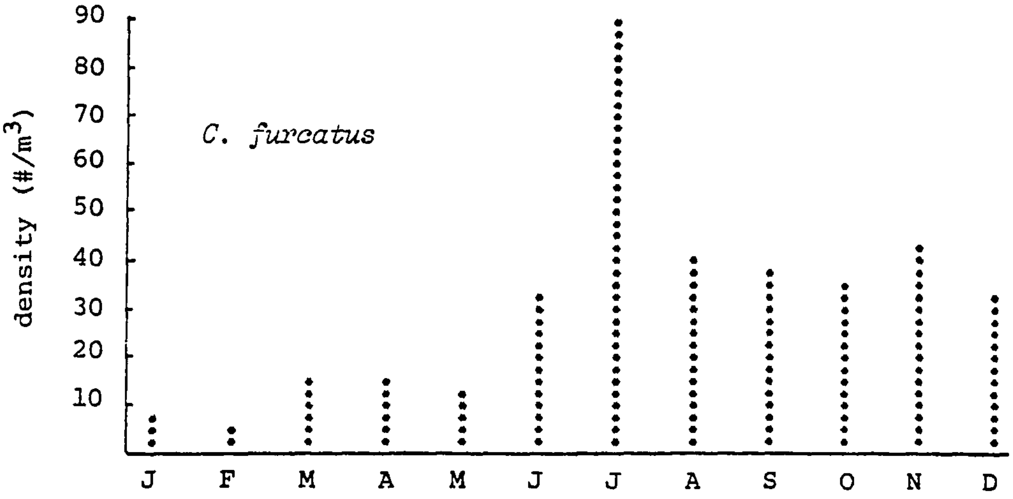
Clausocalanus furcatus ranked fifth in abundance and comprised 6.8% of all adult female copepods. It was found in greatest numbers at the deepest stations during the summer and fall (Fig. 124). The density of this species also exhibited a strong positive relationship with temperature and salinity.

Clausocalanus jobei which was similar in size to *C. furcatus* and was also found at the deeper stations, had the greatest densities in the late winter, spring, and summer. Few specimens were captured during the fall. The density of *C. jobei* did not appear to be strongly related to surface temperature and salinity.

Clausocalanus furcatus has been reported in the coastal waters of the Gulf of Mexico by Davis (1950), Fleminger (1956), Grice (1957, 1960), and Park (1977, 1979). Fleminger (1956) described this species as common in oceanic and neritic waters although Grice (1957) reported it as relatively rare off the west coast of Florida. Park (1977, 1979) has reported *C. furcatus* as a common species at offshore stations in the fall although it was present in low densities throughout the year.

Clausocalanus jobei was not described until 1968 (Frost and Fleminger, 1968). This species has been reported in the coastal waters off Texas during the spring and summer by Park (1977, 1979). Previous studies in the Gulf of Mexico may have reported this species as *C. arcuicornis*.

<u>*Temora*</u>. The two species of *Temora* found in this area, *T. turbinata* and *T. stylifera*, appeared to be distinctly separated through size differences and differences in their spatial distributions. Although both species occurred in greatest numbers during the summer and fall,



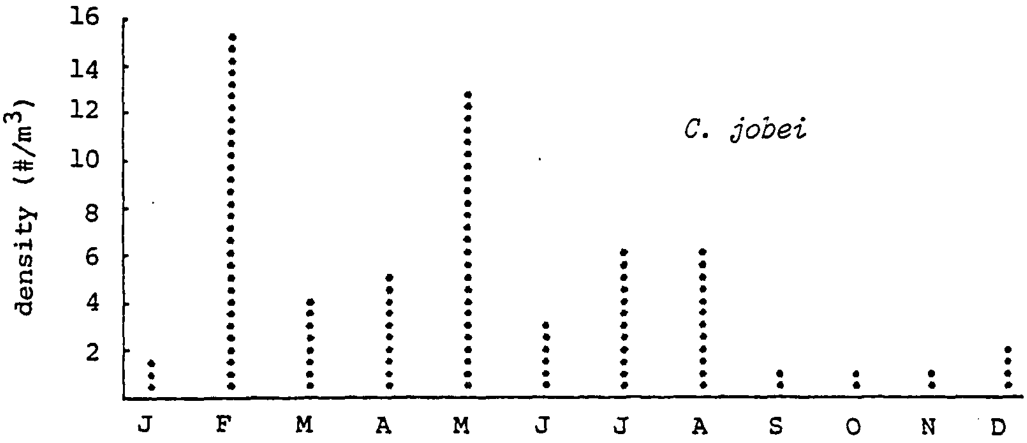


Figure 124. Monthly mean densities of *Clausocalanus furcatus* and *Clausocalanus jobei* over the entire sampling area.

T. turbinata (1.36 mm) was found mostly at inshore stations and *T. stylifera* (2.02 mm) was found at the deepest stations (Fig. 125). Harris and Paffenhoffer (1976) and Paffenhoffer and Knowles (1978) have reported that both of these species eat phytoplankton in the laboratory. They have been considered omnivorous, however, on the basis of the structure of their mouthparts (Anraku and Omori, 1963; Itoh, 1970) and the presence of crustacean remains in gut contents (Marshall and Orr, 1962).

These species of *Temora* have been recorded as common neritic forms in the Gulf by Davis (1950), King (1950), Fleminger (1956), Grice (1957, 1960), and Park (1977, 1979). Grice (1957) and Park (1979) reported *T. turbinata* to be abundant at inshore stations. *Temora stylifera* was relatively rare and most frequently found at offshore stations. Although Fleminger (1956) commonly found both species in coastal and oceanic waters they were seldom found together in large numbers. He suggested that this inverse relationship could indicate competition.

Centropages. Three species in the genus *Centropages* have been reported from the Gulf of Mexico. These species are similar in size and specimens of all three were collected in the sampling area. Data from feeding studies have indicated that this genus is omnivorous (Marshall and Orr, 1962; Wickstead, 1962; Mullin, 1967), a conclusion supported by the morphology of feeding structures (Anraku and Omori, 1963; Itoh, 1970). *Centropages caribbeanensis* was present only at offshore stations and was found in less than 2% of the samples examined in this study. *Centropages hamatus* and *C. velificatus* were both relatively abundant at the inshore stations but they showed a striking

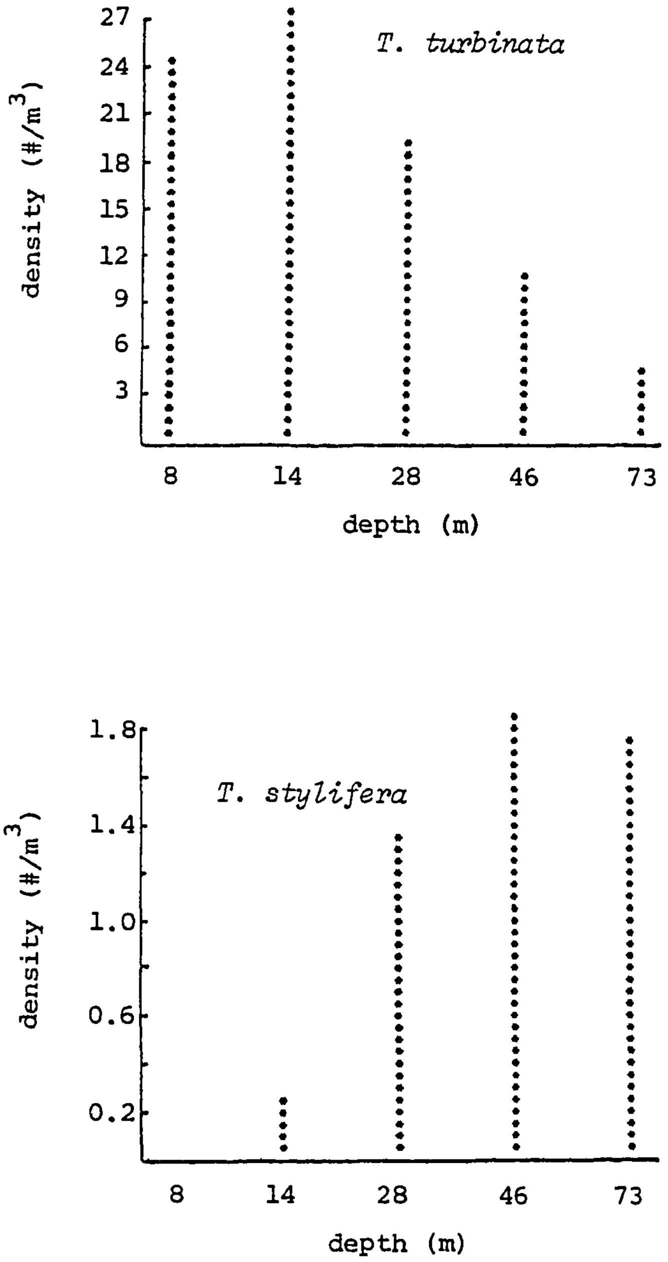
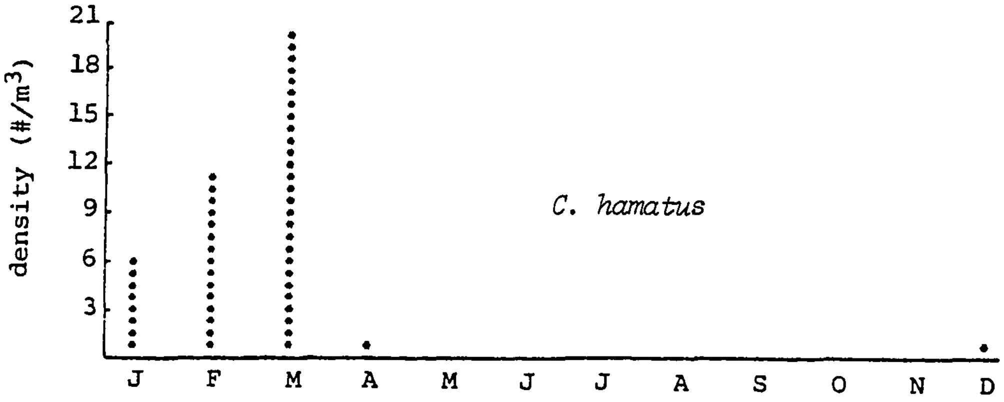


Figure 125. Mean densities of *Temora turbinata* and *Temora stylifera* at each bottom depth.

separation in their seasonal distributions. When monthly means over the entire sampling area were examined (Fig. 126), *C. hamatus* was found almost exclusively from January through March and *C. velificatus* was found in significant numbers only from April through December with a density peak in September.

Centropages velificatus (recorded as *C. furcatus*) has been reported in the coastal waters of the Gulf of Mexico by Davis (1950), King (1950), Gonzalez (1957), and Caldwell and Maturo (1976). Both *C. velificatus* and *C. hamatus* have been reported as coastal species by Fleminger (1956), Grice (1957, 1960), and Park (1977, 1979). In samples analyzed by Grice (1957), *C. velificatus* was common at inshore stations in the summer months and present year-round at the offshore stations. Fleminger (1956) classified *C. velificatus* and *C. hamatus* as coastal and shelf species and described *C. caribbeanensis* (reported as *C. violaceous*) as an oceanic species. *Centropages caribbeanensis* has also been reported from the oceanic waters of the Gulf by Park (1970), Livingston (1974), and Minello (1974, 1976). The distributions for *C. velificatus* and *C. hamatus* described by Park (1979) were very similar to those seen in the GUS III samples. Both species were abundant at inshore stations. *Centropages hamatus* was found only in January, February, and March and *C. velificatus* was collected during the rest of the year.

<u>*Oncaea*</u>. Three common species of *Oncaea* were found in the sampling area, *O. media, O. mediterranea,* and *O. venusta.* Members of this genus made up approximately 4.2% of the female copepods examined and are generally considered to be carnivorous (Wickstead, 1962; Mullin, 1967; Timonin, 1971). *Oncaea mediterranea* was most abundant at the 73 m



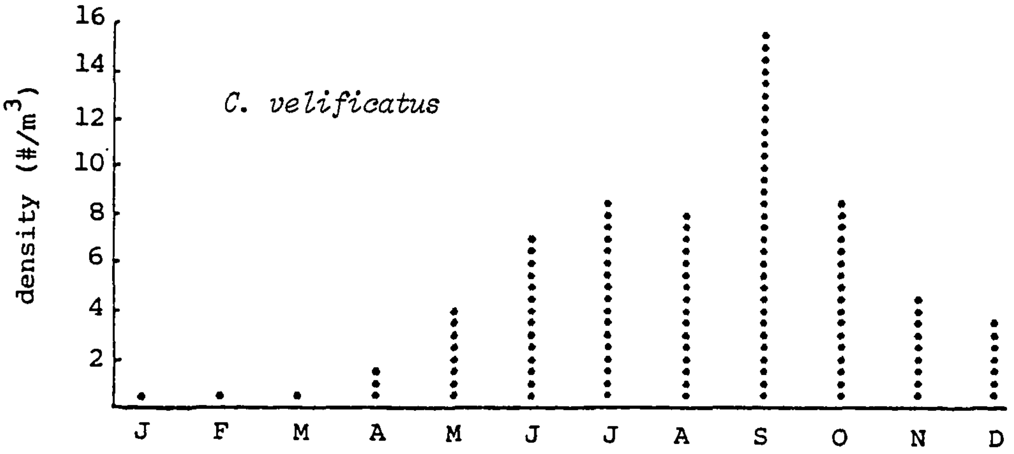


Figure 126. Monthly mean densities of *Centropages hamatus* and *Centropages velificatus* over the entire sampling area.

stations during the spring and summer. *Oncaea venusta* which was similar in size (0.92 to 1.20 mm) and also found at the deeper stations appeared to be most abundant in the late summer, the fall, and the early winter. The third species, *O. media*, was smaller in size (0.58 to 0.82 mm) and appeared to be most abundant at the intermediate and deep water stations. Its seasonal distribution was sporadic although densities were generally low in the fall.

The densities of all three of these species were positively related to surface salinity. *Oncaea venusta* however was the only species with densities related to surface temperature. The overall distributions of these species did not appear to be as distinctly separate as those of the herbivorous congeners. This may reflect a reduced necessity for temporal and spatial distributional differences due to the complexity of their predatory feeding habit.

These three common species of *Oncaea* have also been reported in the coastal waters off of Texas by Park (1977, 1979). Their spatial distributions were similar although the seasonal data (Park, 1979) was highly variable and difficult to compare with the seasonal data from the GUS III cruises. *Oncaea venusta* has also been recorded in the Gulf by King (1950) and Grice (1957, 1960), and Ferrari (1973, 1975) has reported all three species as common open ocean forms in the Gulf of Mexico and Caribbean Sea.

Oithona. Members of the genus *Oithona* made up approximately 9.5% of the female copepods examined from the study area. Timonin (1971) considered the species in this genus to be piercing and sucking carnivores. These organisms however do not have the heavy cuticle and the robustness normally associated with predatory copepods and Marshall and Orr (1962) found that *Oithona* would eat phytoplankton. These species should probably be considered omnivores.

A large number of species of *Oithona* were found in the sampling area (Table 5, p. 87). Most of these were rare and found at offshore stations. The two dominant species, *O. nana* and *O. plumifera*, exhibited distinct differences in their distributions (Fig. 127), sizes, and relationships with temperature and salinity. *Oithona nana*, a relatively small species (0.58 to 0.64 mm) was found at inshore stations from June through December. The density of this species was negatively related to surface salinity. The density of *O. plumifera* (1.15 to 1.50 mm in total length) was also greatest during the summer, fall, and early winter but spatially this species was found at the mid-depth and offshore stations. Regression analyses indicated that *O. plumifera* was most abundant at high surface temperatures and salinities.

Although these two dominant members of the genus *Oithona* appear to be ecologically separated in these coastal waters, it is difficult to explain the occurrence of such a high number of other congeners. Some size differences existed, and most of the species were found at offshore stations where they could have been temporarily displaced from more oceanic areas. The rarity of these species along with normal sampling error would make a more detailed analysis of their distributions from these data unwarranted. There have been other reports of some of these species in the coastal waters of the Gulf of Mexico and the Caribbean Sea. Grice (1960b) reported *O. similis, O. brevirornis (colcarva?),* and *O. simplex* from the West Florida coast and reviewed distributional

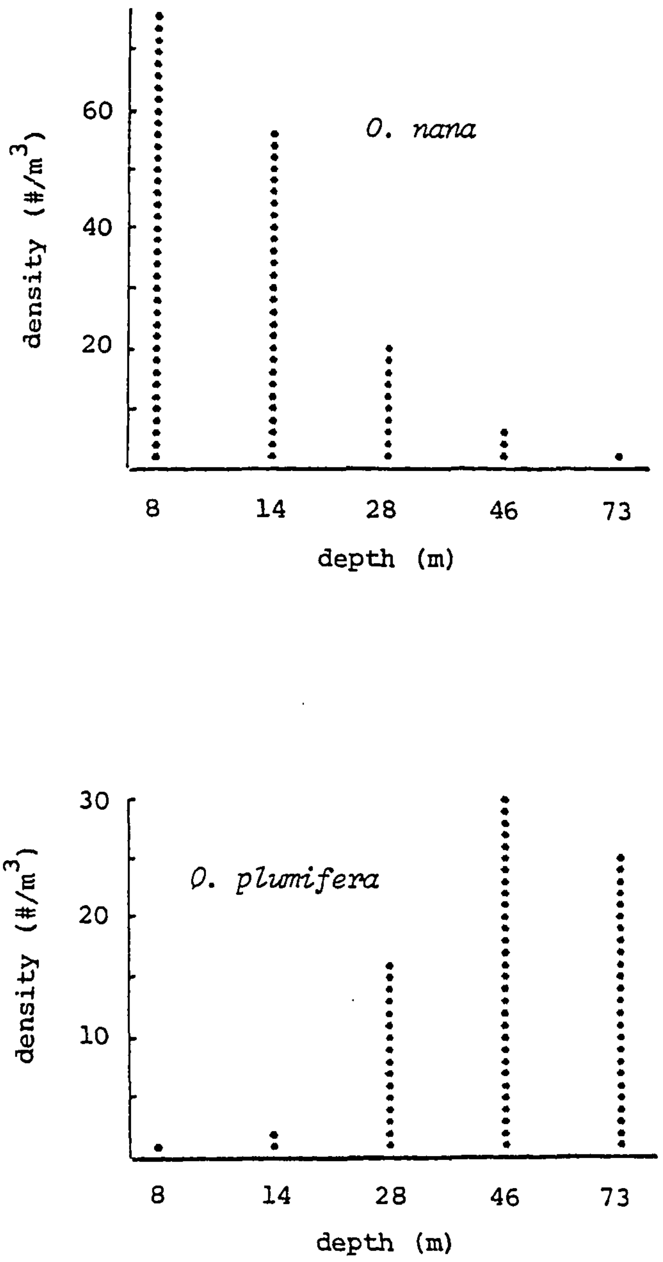


Figure 127. Mean densities of *Oithona nana* and *Oithona plumifera* at each bottom depth.

reports on these species. Owre and Foyo (1967) recorded *O. robusta* and *O. setigera* from the Florida Current and the Caribbean Sea and Gonzalez and Bowman (1965) identified *O. hebes* and *O. simplex* from the coastal waters of Puerto Rico.

Oithona nana and *O. plumifera* have been reported in the coastal waters of the Gulf by Davis (1950), King (1950), Gonzalez (1957), Grice (1957, 1960a,b) and Park (1977, 1979). Grice (1957) and Park (1979) recorded *O. nana* as a common inshore species and *O. plumifera* as a common offshore species.

Corycaeus. Members of this genus were considered by Timonin (1971) to be piercing and sucking carnivores and other evidence also exists indicating that these species are predaceous (Wickstead, 1962; Mullin, 1967). Three species of *Corycaeus*, all of similar size (0.90 to 1.16 mm), were abundant in the sampling area. Spatially these species had similar distributions and were common at all bottom depths except at the 73 m stations. Some evidence was present for a seasonal separation in density with *C. amazonicus* peaking in the spring and fall, *C. americanus* in the early winter, and *C. giesbrechti* in the summer and fall. The seasonal distributions of these species, however, were not distinct. Allison (1967) did report some vertical separation in the water column between *C. amazonicus* and *C. americanus (subulatus)* at Station B during June.

King (1950) has recorded *C. americanus* and *C. giesbrechti* (as *C. venustus*) from the west coast of Florida and Ferrari (1973) has reported all three of these species of *Corycaeus* as common open ocean forms in the Gulf of Mexico. Grice (1957, 1960) and Park (1977, 1979) have reported the three species as being widely distributed in coastal Gulf waters. The spatial distributions described by Park (1979) for these species were similar to those found from the GUS III samples. At the three stations that he sampled monthly off the South Texas coast, *C. amazonicus* and *C. americanus* appeared to be abundant in May and June and *C. giesbrechti* was abundant in September.

The similarities between this genus and *Oncaea* were striking. Both genera are considered to be carnivorous and both are widely distributed in this neritic area. Seasonal distributions generally did not appear to distinctly separate their populations. Perhaps the heterogeneity in the size and shape of the prey along with the presence of various behavioral escape mechanisms allow the predators to separate their feeding niches and coexist. This could explain the relative lack of temporal and spatial separation in the common carnivorous species when compared to the distributions of the common herbivore and omnivore congeners.

CONCLUSIONS AND SUMMARY

Zooplankton densities examined from the GUS III samples taken in the coastal waters of the northwestern Gulf of Mexico exhibited a number of general trends. Densities decreased with increasing bottom depths and mean values indicated a threefold decrease from the 8 m stations to the 73 m stations. Peak densities occurred in the spring and in the fall and the lowest densities were found in January and February. The effect of latitude (as determined from the Transect effect) did not appear to be significant, even though the sampling area extended from the Mexican border (Transect I) to Atchafalaya Bay, Louisiana (Transect V).

The major groups of zooplankton included copepods (averaging 61% of the zooplankton in the sampling area), larvaceans, bivalve larvae, ostracods *(Euconchoecia)*, gastropod larvae, cladocerans *(Penilia)*, and medusae. These groups are listed in the order of their relative densities in the sampling area. Seasonal distributions and zones of peak abundance varied with each individual group. The general distribution of the chaetognaths, however, appeared relatively similar to that of the copepods. This may reflect a predator-prey interaction.

Copepods dominated the zooplankton at all depths and times of the year. This group exhibited a distribution pattern which was similar to that described for the zooplankton as a whole. Adult female copepods were found in similar densities as copepodids (immature forms). The percentage of copepodids generally peaked when copepod densities were highest indicating the relationship between immature forms and increasing populations. The density of adult males was relatively stable and remained at about 15-20% of the population. Calanoid and cyclopoid copepods were abundant while the harpacticoids were relatively rare. The mean percentage of calanoids in the copepods decreased from the inshore stations to the offshore areas but always remained above 50%. Cyclopoids were most abundant at the offshore stations.

A total of 134 species of adult female calanoid and cyclopoid copepods were identified from this coastal area. The five most abundant species in the sampling area were *Paracalanus indicus, Acartia tonsa, Paracalanus quasimodo, Paracalanus crassirostris,* and *Clausocalanus furcatus.* These five species combined made up over 55% of the adult females examined. Other common species in the order of their abundance were *Oncaea media, Oithona nana, Oithona plumifera, Temora turbinata,* and *Oncaea venusta.* These ten most abundant species in the area made up over 77% of the adult female copepods.

The temporal and spatial distributions of the 18 most abundant copepods and the major groups of zooplankton were examined graphically and through the use of an analysis of variance. The analysis of variance results indicated the significance of the effects of Month, Depth, Transect, and Year on the densities of these groups. The Depth*Month interaction appeared to be the most frequently significant factor indicating changes in the seasonal distributions of these groups with changes in bottom depth. The main effects of Bottom Depth and Month appeared to be more important than Transect and Year in describing the distributions of these organisms. The effect of the sampling time during the day was examined through the use of correlations and an analysis of covariance. In most cases this effect, which was probably due to the vertical migrations of the animals, did not appear to affect the significance of the analysis of variance results.

Regression analyses were used to examine the relationships between the natural log of the density of each group or species and the physical and chemical factors examined. Densities of the major groups of zooplankton generally appeared to be poorly correlated with these factors. Densities of individual species of copepods appeared to be most frequently related to surface salinity and surface temperature. In most cases these relationships could also be seen in the temporal and spatial distributions of the species. The other factors such as local runoff, previous month's Mississippi runoff, stability, upwelling and the cross shelf current were seldom highly significant in the regressions and did not appear to explain a large part of the variability in the densities of the species examined. Most of these variables were only rough estimates of the parameter and this could be the reason for their poor fit in the regression models.

The lack of an apparent relationship between the densities of some of the typical estuarine copepods and the local river runoff values was especially puzzling. *Acartia tonsa* is an estuarine species which appeared to be strongly associated with low salinities in the sampling area. The density of *A. tonsa* was examined with respect to local runoff over the entire area, on each transect, and at each station through the use of regressions and histograms. Changes in the mean monthly local runoff did not appear to affect the density of this species. Therefore, although it is generally assumed that large blooms of species such as *A. tonsa* in coastal waters are caused by flushing from the local estuaries, the data from the GUS III cruises did not seem to support this conclusion. Estuarine flushing, however, may lag behind peak river flows delaying the movement of estuarine populations into coastal areas.

There are three basic possibilities for finding no significant relationship between the density of a species and a possible causal variable in linear regression models.

1. There is no significant relationship.
2. The variables are not accurately measuring the phenomena involved.
3. The relationship is not linear.

All three of these reasons have probably contributed to the regression results reported in this paper. The variables used in this study to describe upwelling, stability, and the cross shelf current probably only crudely approximate the real phenomena. Although any error in their measurement theoretically violates linear regression assumptions, they were used strictly as exploratory variables in this analysis. The presence of a non-linear relationship between population densities and the chemical and physical variables is also a possible explanation for the poor fit of many of the regression models. A relationship of this type could be frequently seen in the histograms of density versus surface temperature. In many cases an optimum temperature occurred around 20 to 22°C. Mean densities decreased in both directions from this temperature.

Species diversity, measured as the number of species of adult female copepods present, increased markedly with the bottom depth in the sampling area. This trend has also been reported in many of the coastal zooplankton studies reviewed in this paper. Sanders (1968, 1969) felt that in the marine environment stable areas generally supported a larger number of species than unstable areas. The seasonal temperature and salinity charts indicate that both of these factors vary less throughout the year at the deepest stations. Open ocean areas which generally display moderate seasonal changes in temperature and salinity generally have high diversities and estuaries which are very unstable generally have very low diversities.

The analysis of correlated species groups revealed several clusters of copepod species that appeared to vary in density together. Most of these species grouped together showed similar relationships with temperature and salinity. A distinct offshore group with many marginally linked members, an intermediate depth group, and an inshore group of species were present. Other studies on these same species from the southeastern coast of the U.S. and off the South Texas Coast, using different clustering techniques, have reported similar results. The graphical method used to cluster species in the GUS III samples was found to be preferable to the use of dendrograms. Although the inherent complexity of the graphical clustering technique makes it more difficult to interpret in some ways as opposed to dendrograms, this complexity is informative and in many cases may be essential in order to avoid misinterpreting results.

Although the significance of competition in plankton systems is a matter of controversy, competition for food might be expected between similar sized congeneric copepods. The temporal and spatial distributions of eight copepod genera were examined in this analysis. Most congeners appeared to be distinctly separated by their sizes, distributions over the shelf, or their temporal distributions. The major exceptions occurred between two herbivorous calanoid species, *Paracalanus indicus* and *P. quasimodo*, and between species in the predaceous genera of cyclopoids, *Corycaeus* and *Oncaea*. Vertical distribution data from a 2-day period in July at a station off Galveston, Texas appeared to show a distinct vertical separation in the water column for the *Paracalanus* species. The vertical distribution data reported by Allison (1967) for the species of *Corycaeus* and *Oncaea* were incomplete, however, and inconclusive. A possible explanation for the apparent lack of temporal and spatial separation in these species of cyclopoids could be related to their predatory feeding habit. The diversity of food available to a predator in marine plankton systems would appear to be greater than that available to a herbivore. Selective feeding in the species of *Corycaeus* and *Oncaea* could result in niche separation.

Although most of the work done in the Gulf of Mexico has provided only a limited amount of information on zooplankton populations, the study that is perhaps most comparable to the work presented here was done by Park (1979) and Park and Turk (1980) in the coastal waters off South Texas. They examined seasonal samples taken at nine stations and monthly data were reported from three stations. Their data on zooplankton and copepod densities, species distributions, species diversity, and species groups were generally similar to the data reported here from the GUS III samples.

The analysis of the GUS III samples presented in this study provides essential information on temporal and spatial distributional patterns and relationships with physical and chemical factors for the neritic zooplankton populations of the northwestern Gulf of Mexico. In order to determine the environmental conditions affecting population densities and potential rates of increase for populations in the area, however, field work on food availability and predator densities is necessary. Laboratory studies on feeding, predation, reproductive, and developmental rates are also needed. Although some of this information is available in the literature, many zooplankton species are not readily adaptable to laboratory conditions. This general lack of basic information on zooplankton populations also makes it difficult to interpret information on interspecific competition and community structure in plankton systems.

LITERATURE CITED

Adelman, H. C. 1967. The taxonomy and summer and fall vertical distribution of the Chaetognaths off Galveston, Texas. Ph.D. Dissert., Texas A&M Univ., College Station. 54 pp.

Allison, T. C. 1967. The diel vertical distribution of copepods off Galveston, Texas. Ph.D. Dissert., Texas A&M Univ., College Station. 77 pp.

Anraku, M. and M. Omori. 1963. Preliminary survey of the relationship between the feeding habit and the structure of the mouth-parts of marine copepods. Limnol. Oceanogr. 8: 116-126.

Armstrong, R. 1976. Circulation patterns. Pages 47-54 *in* Environmental studies of the South Texas Outer Continental Shelf, 1975, Vol. II. Physical oceanography. Report, Bur. Land Mgmt., Interagency Agreement 08550-1A5-19. 290 pp.

Arnold, E. L., Jr. 1958. Gulf of Mexico plankton investigations: 1951-53. U.S. Fish Wildl. Serv., SSR-269, 53 pp.

Austin, H. M. and J. I. Jones. 1974. Seasonal variation of physical oceanographic parameters on the Florida Middle Ground and their relation to zooplankton biomass on the West Florida shelf. Fla. Scient. 371: 16-32.

Barnes, R. D. 1974. Invertebrate zoology. W. B. Saunders Co., Philadelphia. 870 pp.

Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. Environmental Protection Agency, Rept. No. EPA-600/3-77-033.

Bowman, T. E. 1971. The distribution of calanoid copepods off the southeastern United States between Cape Hatteras and southern Florida. Smithsonian Contr. Zool. No. 96. 58 pp.

Caldwell, J. and F. Maturo. 1976. Analysis of zooplankton from the MAFLA OCS area, Vol. 4. MAFLA monitoring study, 1976. Final Report, Bur. Land Mgmt., Contract 08550-CT5-30.

Cassie, R. M. 1961. The correlation coefficient as an index of ecological affinities in plankton populations. Mem. 1st Ital. Idrobiol. de Marchi 13: 151-177.

Clifford, H. T. and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, New York. 229 pp.

Davis, C. C. 1950. Observations of plankton taken in marine waters of Florida in 1947 and 1948. Quart. J. Fla. Acad. Sci. 12(2): 67-103.

Dragovich, A. 1961. Relative abundance of plankton off Naples, Florida, and associated hydrographic data, 1956-57. U.S. Fish Wildl. Serv., SSRF-372. 41 pp.

________. 1963. Hydrography and plankton of coastal waters at Naples, Florida. Quart. J. Fla. Acad. Sci. 26: 22-47.

Eldred, B., J. Williams, G. T. Martin and E. A. Joyce, Jr. 1965. Seasonal distribution of penaeid and postlarvae of the Tampa Bay area, Florida. Fla. St. Bd. Conserv., Tech. Ser. 44. 47 pp.

Fager, E. W. 1957. Determination and analysis of recurrent groups. Ecology 38: 586-595.

________ and J. A. McGowan. 1963. Zooplankton species groups in the North Pacific. Science 140: 453-460.

Ferrari, F. D. 1973. Some Corycaeidae and Oncaeidae (Copepoda: Cyclopoida) from the epipelagic waters of the Gulf of Mexico. Ph.D. Dissert., Texas A&M Univ., College Station, 215 pp.

________. 1975. Taxonomic notes of the genus *Oncaea* (Copepoda: Cyclopoida) from the Gulf of Mexico and northern Caribbean Sea. Proc. Biol. Soc. Wash. 88(21): 217-232.

Finucane, J. H. 1976. Baseline survey of ichthyoplankton. Pages 20-30 *in* W. B. Jackson, ed. Environmental studies of the South Texas Outer Continental Shelf, 1975, Vol. 1. Plankton and fisheries. Report, Bur. Land Mgmt., Interagency Agreement 08550-125-19. 425 pp.

Fleminger, A. 1956. Taxonomic and distributional studies of the epiplanktonic calanoids (Crustacea) of the Gulf of Mexico. Ph.D. Dissert., Harvard College, Cambridge, Mass. 317 pp.

________ and K. Hulseman. 1974. Systematics and distribution of the four sibling species comprising the genus *Pontellina* Dana (Copepoda, Calanoida). U.S. Fish Wildl. Serv., Fish. Bull. 72: 63-120.

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. Oceanogr. 12: 1-235.

Gillespie, M. 1971. Analysis and treatment of zooplankton in estuarine waters off Louisiana. Pages 109-175 *in* Cooperative Gulf of Mexico inventory and study, Phase I-Area description and Phase IV-Biology. La. Wildl. Fish. Comm., New Orleans. 175 pp.

Gonzalez, J. G. 1957. The copepods of the Mississippi Delta region. M.S. Thesis, Texas A&M Univ., College Station. 111 pp.

________ and T. Bowman. 1965. Planktonic copepods from Bahia Fosforescente, Puerto Rico, and adjacent waters. Proc. U.S. Nat. Mus. 117(3513): 241-304.

Grice, G. D. 1957. The copepods of the Florida West coast. Ph.D. Dissert., Fla. State Univ., Tallahassee. 196 pp.

________. 1960a. Calanoid and cyclopoid copepods collected from the Florida Gulf Coast and Florida Keys in 1954 and 1955. Bull. Mar. Sci. Gulf Carib. 10(2): 217-226.

________. 1960b. Copepods of the genus *Oithona* from the Gulf of Mexico. Bull. Mar. Sci. Gulf Carib. 10(4): 485-490.

Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292-1298.

Harper, D. E., Jr. 1968. Distribution of *Lucifer faxoni* (Crustacea; Decapoda; Sergestidae) in neritic waters off the Texas coast, with a note on the occurrence of *Lucifer typus*. Contr. Mar. Sci. 13: 1-16.

Harrington, D. L. 1966. Oceanographic observations on the continental shelf of the northwestern Gulf of Mexico. U.S. Bur. Comm. Fish., Circ. 246, pp. 7-10.

Harris, R. P. and G. A. Paffenhoffer. 1976. The effect of food concentration on cumulative ingestion and growth efficiency of two small marine planktonic copepods. J. Mar. Biol. Ass. U.K. 56: 875-888.

Hedgpeth, J. W. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Publ. Inst. Mar. Sci. 3(1): 107-204.

Hurlbert, S. H. 1969. A coefficient of interspecific association. Ecology 50: 1-9.

Hutchinson, G. E. 1961. The paradox of the plankton. Amer. Nat. 95: 137-145.

Itoh, K. 1970. A consideration on feeding habits of planktonic copepods in relation to the structure of their oral parts. Bull. Plankton Soc. Japan, No. 7, pp. 1-10.

Jones, A. C., D. E. Dimitriou, J. J. Ewald and J. H. Tweedy. 1970. Distribution of early developmental stages of the pink shrimp, *Penaeus duorarum*, in Florida waters. Bull. Mar. Sci. 20(3): 634-661.

Kelly, J. A., Jr. and A. Dragovich. 1967. Occurrence of macrozooplankton in Tampa Bay, Florida and the adjacent Gulf of Mexico. U.S. Fish Wildl. Serv., Fish. Bull. 66: 209-221.

Kimsey, J. B. and R. F. Temple. 1964. Currents on the continental shelf of the northwestern Gulf of Mexico. U.S. Bur. Comm. Fish., Circ. 183, pp. 25-27.

King, J. E. 1950. A preliminary report on the plankton of the west coast of Florida. Quart. J. Fla. Acad. Sci. 12(2): 109-137.

Kutkuhn, J. H. 1963. Expanded research on Gulf of Mexico shrimp resources. Proc. Gulf Caribb. Fish. Inst., 15th Ann. Sess., 1962, pp. 65-76.

Livingston, G. P. 1974. Examination of the recurrent species groups and abundances of the calanoid Copepoda in the epipelagic waters of the Gulf of Mexico. M.S. Thesis, Texas A&M Univ., College Station. 100 pp.

Lonsdale, D. J., D. R. Heinle and C. Siegfried. 1979. Carnivorous feeding behavior of the adult calanoid copepod *Acartia tonsa* Dana. J. Exp. Mar. Biol. Ecol. 36(3): 235-249.

Lynch, S. A. 1954. Geology of the Gulf of Mexico. Pages 67-86 *in* P. S. Galtsoff, ed. Gulf of Mexico, its origins, waters, and marine life. U.S. Fish Wildl. Serv., Fish. Bull. 89, Vol. 55, 604 pp.

Malone, T. C. 1977. Plankton systematics and distribution. MESA New York Bight Atlas Monograph 13, New York Sea Grant Inst., Albany. 45 pp.

Marshall, S. M. and A. P. Orr. 1955. The biology of a marine copepod. Oliver and Boyd, Edinburgh, England. 195 pp.

________ and ________. 1962. Food and feeding in copepods. Rapp. Cons. Explor. Mer. 153: 92-98.

McEwen, G. F., M. W. Johnson and T. R. Folsom. 1954. A statistical analysis of the performance of the Folsom Plankton Splitter, based upon test observations. Archiv fur Meterologie, Geophysik and Bioklimatologie, Series A, 6: 502-527.

Minello, T. J. 1974. The day and night vertical distributions of calanoid copepods in the western Gulf of Mexico, with reference to feeding relationships. M.S. Thesis, Texas A&M Univ., College Station. 125 pp.

________. 1976. A description of the male of *Centropages caribbeanensis* Park (Copepoda, Calanoida). Crustaceana 31(1): 42-44.

Mullin, M. M. 1967. On the feeding behavior of planktonic marine copepods and the separation of their ecological niches. Biol. Ass. India Symp. on Crustacea, Part III, pp. 955-964.

Munro, J. L., A. C. Jones and D. E. Dimitriou. 1968. Abundance and distribution of the larvae of the pink shrimp *(Penaeus duorarum)* on the Tortugas Shelf of Florida, August 1962-October 1964. U.S. Fish Wildl. Serv., Fish. Bull. 67: 165-181.

Owre, H. B. and M. Foyo. 1967. Copepods of the Florida Current. Fauna Caribaea. No. 1. 137 pp.

Paffenhoffer, G. A. and S. C. Knowles. 1978. Feeding of marine planktonic copepods in mixed phytoplankton. Mar. Biol. 48(2): 143-153.

Park, T. S. 1970. Calanoid copepods from the Caribbean Sea and Gulf of Mexico. 2. New species and new records from plankton samples. Bull. Mar. Sci. 20(2): 472-546.

Park, E. T. 1976a. Historical zooplankton. Pages 4-10 *in* W. Jackson, ed. Environmental studies of the South Texas Outer Continental Shelf, 1975, Vol. I. Plankton and fisheries. Report, Bur. Land Mgmt., Interagency Agreement 08550-1A5-19. 425 pp.

________. 1976b. Zooplankton project. Pages 154-164 *in* P. L. Parker, ed. Environmental assessment of the South Texas Outer Continental Shelf, chemical and biological survey component, 1975. Final Report, Bur. Land Mgmt., Contract 08550-CT5-17. 598 pp.

________. 1977. Zooplankton, Chapter 6, Pages 6-1 to 6-42 *in* R. D. Grover, ed. Environmental studies, South Texas Outer Continental Shelf, biology and chemistry, 1976. Final Report, Bur. Land Mgmt., Contract AA550-CT6-17.

________. 1978. Historical zooplankton. Pages 1-61 *in* W. Jackson, ed. Environmental studies of the South Texas Outer Continental Shelf. Report, Bur. Land Mgmt., Interagency Agreements AA500-1A7-3 and AA500-1A7-21. 492 pp.

________. 1979. Zooplankton project, Chapter 14, Pages 14-1 to 14-58 *in* R. W. Flint and C. W. Griffin, eds. Environmental studies, South Texas Outer Continental Shelf, biology and chemistry, 1977. Final Report, Bur. Land Mgmt., Contract AA550-CT7-11.

________ and P. Turk. 1980. Zooplankton project, Chapter 9 *in* R. W. Flint and N. Rabalais, eds. Environmental studies, South Texas Outer Continental Shelf, 1975-1977, Vol. III. Study element reports. Report, Bur. Land Mgmt., Contract AA551-CT8-51.

Pierce, E. L. 1951. The chaetognatha of the west coast of Florida. Biol. Bull. 100(3): 206-228.

Raymont, J. E. 1963. Plankton and productivity in the oceans. Pergamon Press, New York. 660 pp.

Richman, S., D. Heinle and R. Huff. 1977. Grazing by adult estuarine calanoid copepods of the Chesapeake Bay. Mar. Biol. 42: 69-84.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. Amer. Nat. 102: 243-282.

________. 1969. Benthic marine diversity and the stability-time hypothesis. Brookhaven Symp. Biol. 22: 71-81.

Schulenberger, E. 1976. Recurrent group analysis of hyperiid amphipods from the North Pacific Central Gyre. CalCOFI Reports 19: 73-77.

SEADOCK, Inc. 1975. Environmental report: Texas offshore oil unloading facility. Texas A&M Res. Fdn. Proj. 945 Report.

Snider, J. E. 1975. Quantitative distribution of shelled pteropods in the Gulf of Mexico including related sampling studies. Ph.D. Dissert., Texas A&M Univ., College Station.

Temple, R. F. 1976. Relative seasonal abundance and areal distribution of larval shrimp (*Penaeus* spp.). Pages 11-19 *in* W. Jackson, ed. Environmental studies of the South Texas Outer Continental Shelf, 1975, Vol. I. Plankton and fisheries. Report, Bur. Land Mgmt., Interagency Agreement 08550-125-19. 425 pp.

________ and C. C. Fischer. 1965. Vertical distribution of the planktonic stages of penaeid shrimp. Publ. Inst. Mar. Sci. Univ. Texas 10: 59-67.

________ and ________. 1967. Seasonal distribution and relative abundance of planktonic-stage shrimp (*Penaeus* spp.) in the northwestern Gulf of Mexico, 1961. U.S. Fish Wildl. Serv., Fish. Bull. 66(2): 323-334.

________, D. L. Harrington and J. A. Martin. 1977. Monthly temperature and salinity measurements of continental shelf waters of the northwestern Gulf of Mexico, 1963-1965. NOAA Tech. Rept., SSRF-707. 26 pp.

________ and J. A. Martin. 1976. Currents. Pages 30-35 *in* Environmental studies of the South Texas Outer Continental Shelf, 1975, Vol. II. Physical oceanography. Report, Bur. Land Mgmt., Interagency Agreement 08550-1A5-19. 290 pp.

________ and ________. 1979. Surface circulation in the northwestern Gulf of Mexico as deduced from drift bottles. NOAA Tech. Rept., SSRF-730. 13 pp.

Timonin, A. G. 1971. The structure of plankton communities of the Indian Ocean. Mar. Biol. 9(4): 281-289.

U. S. Geological Survey. 1969. Surface water supply of the United States 1961-1965. Part 7. Lower Mississippi River Basin, Vol. 1. Lower Mississippi River Basin except Arkansas River Basin. Geological Survey Water-Supply Paper 1920. U.S. Dept. Interior, U.S. GPO, Washington, D.C.

Uchupi, E. 1975. Physiography of the Gulf of Mexico and the Caribbean Sea. Pages 1-53 *in* A. E. M. Nairn and F. G. Stehli, eds. The ocean basins and margins, Vol. 3. The Gulf of Mexico and the Caribbean. Plenum Press, N. Y. 706 pp.

Wickstead, S. H. 1962. Food and feeding in pelagic copepods. Proc. Zool. Soc. London 139: 545-555.

Wiens, J. A. 1977. On competition and variable environments. Am. Sci. 65(5): 590-597.

Wirth, M. G. F. Eastbrook and D. J. Rogers. 1966. A graph theory model for systematic biology, with an example for the Oncidiinae (Orchidaceae). Syst. Zool. 15: 59-69.

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