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CALLINECTES (DECAPODA: PORTUNIDAE) LARVAE IN THE MIDDLE ATLANTIC BIGHT, 1975-77¹

PETER O. SMYTH²

ABSTRACT

Distribution of *Callinectes* larvae in surface (neuston) and subsurface shelf waters in the Middle Atlantic Bight was determined from quarterly zooplankton collections taken during a 2-year study. Observations confirmed the presence in offshore waters of a large larval pool from which recruitment may take place. Larvae were predominantly late zoeae and megalopae, with peak abundances in late summer collections reaching 16,000 per 100 m³ in neuston collections. During summer, crab larvae were distributed across the shelf with the majority at 10-80 km offshore. Abundances were significantly greater in neuston than subsurface zooplankton collections and generally greater in neuston collections taken at night. Water temperature and distance from shore were factors most closely correlated with abundance of larvae in the neuston. Megalopae of *Callinectes* were present at outer shelf stations in winter and spring and together with megalopae of *Portunus* and other forms were of southern origin. Based on experimentally determined temperature-salinity preferences reported in the literature for *Callinectes* larvae, metamorphosis may be delayed in cooler offshore waters, thus increasing chances of long-range transport.

The community of organisms of the surface layer (the neuston³) has received increasing attention in terms of sampling problems and possible ecological significance. Zaitsev (1970) described the neuston as consisting chiefly of early developmental stages of fishes and invertebrates. Berkowitz (1976) and Morris (1975), however, found oceanic neuston faunistically impoverished in comparison with zooplankton of the immediate subsurface. Few studies of the neuston of shelf and shallow waters exist; preliminary indications are that the zooplankton of the surface waters of the continental shelf are at least quantitatively enriched (Grant⁴).

Callinectes, euryhaline members of the predominantly marine Portunidae, spawn along the shore of open oceans and in mouths of inlets and estuaries. Larval development occurs in shelf wa-

ters, with probable return inshore by megalopae and juveniles (Williams 1965, 1971, 1974; Costlow 1967; Tagatz 1968). *Callinectes* megalopae have been reported offshore in shelf waters (Nichols and Keney 1963; Dudley and Judy 1971); retention in shelf waters and subsequent transport of megalopae have been proposed as mechanisms in dispersal, widespread distribution, and maintenance of genetic continuity in the species (Costlow 1967; Williams 1971, 1974; Cole and Morgan 1978).

Callinectes larvae, at least zoeae, have surface affinities (Tagatz 1968; Dudley and Judy 1971; Sandifer 1972), but megalopae have generally been less numerous in collections than zoeae and limited to bottom samples (Tagatz 1968; Sandifer 1972; Goy 1976). Williams (1971), however, reported *Callinectes* megalopae to be active in estuarine surface waters at night.

With the widespread distribution and known abundance of *Callinectes* adults and the accepted migratory sequence of developmental stages (inshore-offshore-inshore), the reported abundance of late stage larvae is surprisingly low. Furthermore, the existence in shelf waters of a *Callinectes* larval pool from which recruitment to estuaries may occur is based on relatively few studies and limited sampling.

This paper reports the identification, distribution, and abundance of *Callinectes* larvae in neus-

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³Neuston has generally been defined operationally as the community of organisms sampled by gear specifically designed to sample the surface layer. The term is used in that sense in this paper. For a review of numerous terms associated with the surface layers, see Banse (1975).

⁴Grant, G. C. 1977. Middle Atlantic Bight zooplankton: seasonal bongo and neuston collections along a transect off southern New Jersey. Spec. Rep. Appl. Mar. Sci. Ocean Eng., Va. Inst. Mar. Sci. 173, 138 p.

ton and subsurface water column collections from shelf waters in the Middle Atlantic Bight. My objectives specifically were to: 1) determine whether a reservoir of *Callinectes* larvae, particularly megalopae, exists in shelf waters; 2) determine abundance relationships between *Callinectes* larvae in neuston and water column samples; 3) examine the role of certain environmental factors (e.g., temperature, salinity, location) in the distribution and abundance of these larvae; 4) assess the role of *Callinectes* megalopae in larval recruitment and dispersal in view of my findings and results of laboratory studies of temperature-salinity tolerances of larvae; and 5) examine interaction of the developmental migratory sequence, biogeography, and evolutionary history of *Callinectes*.

METHODS

Zooplankton collections were made as part of a 2-yr survey (Table 1) conducted by the Virginia Institute of Marine Science (VIMS) for the Bureau of Land Management (1975-77). This study was designed to provide ecological information prior to drilling for oil on the Middle Atlantic Bight continental shelf. In addition to zooplankton studies the survey included studies of benthic and epibenthic communities and the physical, chemical, and geographical oceanography of the shelf and overlying waters.

During the first year, six stations were occupied seasonally (quarterly) on a transect across the shelf off Atlantic City, N.J. (Figure 1; Table 2: C1, D1, N3, E3, F2, J1). Zooplankton in the water column was sampled at night by paired, double oblique tows with 60 cm diameter, opening-closing bongo nets (McGowan and Brown⁵) (505 μ m and 202 μ m mesh). Bongo nets were metered (General Oceanics, Inc. flowmeters⁶) and were closed during passage through the surface layer. Neuston was sampled every 3 h over a 24-h period with a neuston net designed at Woods Hole Oceanographic Institution. This sampler consisted of two hydrodynamically-shaped, foam-filled floats connected by an endless fiber glass band (Grant⁷). The

TABLE 1.—Dates for cruises in the Middle Atlantic Bight, 1975-77, over which *Callinectes* larvae were sampled.

Season	First year		Second year	
	Cruise	Date	Cruise	Date
Fall	01W	23-30 Oct. 1975	05W	5-28 Nov. 1976 ¹
Winter	02W	5-16 Feb. 1976	06W	20 Feb.-6 Mar. 1977
Spring	03W	8-16 June 1976	07W	18-28 May 1977
Summer	04W	1-9 Sept. 1976	08W	19-29 Aug. 1977

¹ Cruise split into two legs.

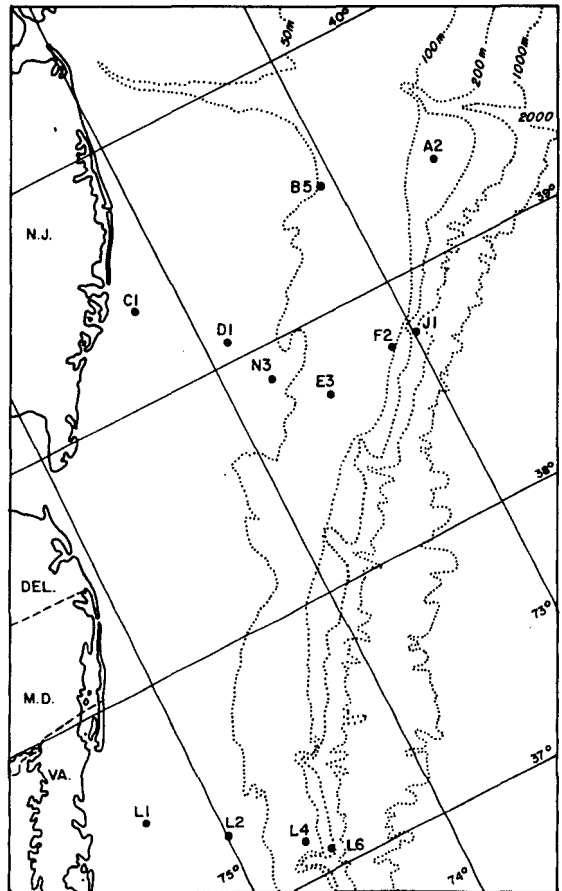


FIGURE 1.—Study area and sampling stations for surface and subsurface zooplankton in the Middle Atlantic Bight, 1975-77. Stations L1, L2, L4, L6, B5, A2 were sampled only during the second year of the study; C1, D1, N3, E3, F2, J1 were sampled both years.

mouth of the net was 1.0 m wide, and in calm water the gear sampled approximately the upper 12 cm of the water column. However, the net appeared to sample, on the average, less than the upper 12 cm due to sea conditions and towing characteristics of the ship and sampler. Calculated volumes were based on a 12 cm sample depth and were thus overestimated, resulting in underestimation of

⁵McGowan, J. A., and D. M. Brown. 1966. A new opening-closing paired zooplankton net. Univ. Calif., Scripps Inst. Oceanogr. Ref. 66-23, 56 p.

⁶Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

⁷Grant, G. C. 1979. Middle Atlantic Bight zooplankton. Spec. Rep. Appl. Mar. Sci. Ocean Eng., Va. Inst. Mar. Sci. 192, 236 p.

TABLE 2.—Station data for zooplankton collections in the Middle Atlantic Bight, 1975-77.

Station	Location		Distance from shore (km)	Bottom depth (m)
	Lat. N	Long. W		
A2	39°21.8'	72°31.8'	149	131
B5	39°28.3'	73°02.1'	93.6	62.6
C1	39°22.2'	74°14.9'	10.2	16.8
D1	39°04.7'	73°53.2'	56.5	37.2
N3	38°51.4'	73°44.8'	83.4	44.7
E3	38°41.2'	73°32.5'	112	59.5
F2	38°44.4'	73°09.2'	132	108
J1	38°44.2'	73°00.7'	141	355
L1	37°31.1'	75°18.3'	31.5	22.3
L2	37°20.1'	74°58.6'	65.8	41.3
L4	37°08.1'	74°36.8'	105	94.6
L6	37°04.4'	74°33.1'	113	322

larval densities. Tows were of 20-min duration except when large abundances of neuston required premature termination of a tow. The net was metered beginning with the June 1976 cruise; before that cruise, sample volumes were estimated on the basis of a standard 20-min tow. Tows were made from an extended boom alongside the ship at speeds of 1.5-2.5 kn.

During the second year two stations to the north and a transect to the south of the original transect were added. On each cruise neuston samples were taken over 24 h at nine stations (Figure 1; Table 2: A2, B5, C1, E3, J1, L1, L2, L4, L6). A single neuston tow was made at stations D1, N3, and F2 as a companion to bongo tows. Bongo tows were made at all 12 stations following the procedure used during the first year. In addition, replicate tows were made at stations A2, B5, and E3 (repeated tows of two bongo nets with paired 202 μ m and 505 μ m mesh nets). Three such replicate tows were made at night at each designated station.

Samples were preserved in a 4% solution of borax-buffered formaldehyde and seawater (Steedman 1976). In the laboratory, major taxonomic groups were quantitatively sorted from whole or split samples (Burrell et al. 1974). Decapods were sorted to species and identified (when possible) on the basis of published descriptions and taxonomic keys.

Megalopae of several taxa, including *Callinectes*, were reared aboard ship to juveniles. Several megalopae were removed from a sample and tentatively identified or identification characters noted. Megalopae were placed in plastic tackle boxes with 505 μ m mesh bottoms and the boxes were floated in an aquarium filled with seawater taken in situ. Megalopae were fed *Artemia salina* nauplii and bits of fresh fish meat. Megalopae with the same characteristics as the megalopae used for rearing were fixed and preserved.

Abundance was expressed as number per 100 m³; for graphical presentation and certain statistical procedures abundance was compressed by the transformation $\log_{10}(X + 1)$. Most statistical procedures were based on station means, with eight neuston collections per station. The distribution of sample means tends to normality as the sample size increases (Snedecor and Cochran 1967), and the logarithmic transformation tends to make variance independent of the mean (Sokal and Rohlf 1969). Based on the *F*-max test (Sokal and Rohlf 1969), untransformed abundances within stations were very heteroscedastic, while log-transformed abundances at stations with *Callinectes* larvae in at least six samples did not have unequal variances at $P < 0.05$. Coefficients of variation for each station were reduced considerably by the log transformation, and abundances appeared better centered about the median based on "box and whisker" diagrams (Tukey 1977). The assumption of a multivariate normal distribution could not be tested for the data set. Significance levels for multivariate data are often difficult to interpret; therefore, significance levels, where indicated for parametric procedures, should be taken as a guide.

A larval stage index (LSI) similar to that of Manzi and Maddox (1976) was calculated for several larval types. The LSI is a point along the continuum of development from hatching (first zoea) to juvenile; the LSI characterizes the stage of an average individual of a given species in a sample. It is calculated as a weighted average, i.e.,

$$LSI = \frac{\sum_{i=1}^n i S_i}{n \sum_{i=1}^n S_i}$$

where i = number of the developmental stage,
 n = number of developmental stages,
 first zoeae through adult,
 S_i = abundance of the i th stage.

The LSI is standardized and constrained in the interval 0.0-1.0 by the assignment of a stage number (1 > the megalopa) to the adult stage. Thus, an LSI = 0.67 characterizes animals that have completed, on the average, about two-thirds of the developmental sequence from hatching to first crab. The LSI is, however, a measure of central tendency and does not indicate statistical dis-

persion. Based on Costlow and Bookhout (1959), n was set at 10 for eight zoeal stages, a megalopa, and an adult.

Comparisons between *Callinectes* abundance in neuston and bongo (surface vs. subsurface) collections at each station were made for: 1) maximum abundance for each gear type; 2) mean abundance of the consecutive pair of tows with the largest collective abundance; and 3) mean abundance for each gear type. Significance of differences for these means was determined by the Wilcoxon signed rank test (Wilcoxon 1945), a distribution-free method (Hollander and Wolfe 1973).

Comparisons between neuston and bongo collections are comparisons between abundances in a single "layer" and abundances integrated over the water column. Therefore, abundances in bongo collections represent mean abundances in the water column (excepting the surface) and do not indicate vertical distribution of the animals.

Diel patterns in neuston abundance during each cruise were represented by total numbers per 100 m³ for each sampling time interval (3 h) summed over the stations in a cruise. To weight frequency as well as abundance during a single cruise, ranks were assigned to abundance during each time interval (lowest to highest) at each station. The rank sum of each time interval was calculated as the sum of the ranks during that time interval over all stations during a single cruise.

For neuston collections the relationship between mean abundance per station and environmental factors (temperature, salinity, station depth, and distance from shore) was examined. Data were analyzed using subprograms (multiple Regression and Partial Corr (partial correlation) of the Statistical Package for the Social Sciences (SPSS, Nie et al. 1975). Relationships between abundance and factors were examined in terms of bivariate as well as multivariate distributions.

RESULTS

Identification

Callinectes zoeae were identified and staged on the basis of Sandifer's (1972) key and descriptions of laboratory-reared zoeae of *C. sapidus* (Costlow and Bookhout 1959) and *C. similis* (Bookhout and Costlow 1977). Key characters include: 1) relative length of the antennal exopodite ($< \frac{1}{3}$ protopodite length) and the presence of two unequal terminal setae on the antennal exopodite; 2) the presence of

lateral projections on abdominal somites 2 and 3; 3) the presence of relatively long, sharply pointed posterolateral spines on abdominal somites 3-5; and 4) the presence of one dorsal and one lateral spine in each telson furca. Structure and setation of mouthparts and appendages were compared with published descriptions for further confirmation. The above characters effectively separated *Callinectes* zoeae from all other zoeal types in my collections. The planktonic material appeared to include seven or eight distinct zoeal stages after allowance for individual variation in certain structures, setal counts, relative lengths, etc. (e.g., the antennal endopodite "bud" denoting stage 5, which varied from little more than a swelling to a definite projection).

Identification of *Portunidae* megalopae was based on Kurata's (1975) list of familial and subfamilial (*Portuninae*) characters, which include the presence of sternal cornua (paired spines projecting posteriorly from the fourth sternal segment beyond the base of the fifth leg) (Figure 2), and the presence of paddlelike dactyls with long, hooked setae on the fifth pereopods.

Callinectes and *Portunus* megalopae were separated on the basis of the characters listed by Bookhout and Costlow (1974), which include the absence in *Callinectes* and the presence in *Portunus* of a ventral spine on the coxa of the second pereopod (Figure 2), and carpal spine(s) on the first pereopod.

My collections included numerous megalopae attributable to *Portunus*; all had a coxal spine on the second pereopod and a carpal spine on the first pereopod. The basischiopodite hook reported for

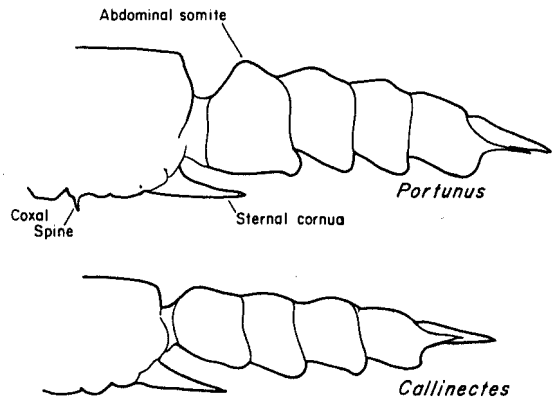


FIGURE 2.—Lateral profile including the abdomen of *Callinectes* and *Portunus* megalopae. Distinguishing characters are indicated. Sizes are not relative.

Portunus (Bookhout and Costlow 1974; Kurata 1975) and *Callinectes* (Costlow and Bookhout 1959; Bookhout and Costlow 1977) was present for all *Callinectes* and most, but not all, *Portunus* specimens.

The profile of abdominal somites was a more subjective, yet reliable, criterion for the separation of *Portunus* and *Callinectes* megalopae. In *Portunus* the dorsal surface of each somite, particularly the first, was noticeably raised, creating a "bumpy" profile; in *Callinectes* the profile was noticeably smoother (Figure 2). (See also Bookhout and Costlow 1974, fig. 11; 1977, fig. 11.) Although identifications were based on numerous characters, this particular criterion was consistent and reliable.

Carapace lengths ($n = 418$, $\bar{X} = 1.56$, $SE = 0.004$ mm) of *Callinectes* megalopae (measured dorsally from the base of the rostrum to the posterior edge of the carapace) were slightly less than carapace lengths reported for *C. sapidus* ($\bar{X} = 1.65$ mm) but considerably greater than lengths reported for laboratory-reared *C. similis* ($\bar{X} = 1.30$ mm) (Bookhout and Costlow 1977).

I recognized no specific differences among *Callinectes* megalopae or zoeae; therefore, larvae referred to as *Callinectes* may represent more than one species. Abundance and known distribution of adults (Williams 1974) indicated that most, if not all, specimens were *C. sapidus*. Several small adult *C. similis*, however, were taken in neuston collections at station C1 in late October 1975.

The above characteristics used to separate *Callinectes* and *Portunus* megalopae were confirmed by specimens reared to the juvenile stage. *Portunus* juveniles were too small (<10 mm carapace width) for specific identification. One *Callinectes* megalopa developed to a juvenile stage tentatively identified as *C. sapidus*.

Distribution

Callinectes larvae were collected on six of eight cruises and were most abundant in late summer (Figure 3).

Mean abundance in neuston collections ($n = 8$) at a single station reached 3,100/100 m³ at L2 in August 1977; at this station abundance in a single neuston collection reached a peak of 16,000/100 m³. Abundance generally decreased offshore of the 50 m isobath during the summer-fall cruises (station J1 in August 1977 was an exception). During the second year, with additional stations, larvae were generally more abundant at stations on the most southern transect than at more northerly stations. Peak abundance often coincided with depressed LSI's inshore, evidence that reproductive activity inshore closely preceded the sampling periods. Except during the summer, larval populations consisted almost exclusively of late zoeae and megalopae, particularly in central and outer shelf waters. Collections of *Callinectes* during the fall of 1975 and winter and spring of 1977 comprised only megalopae.

Mean and maximum abundance (Figure 3; Table 3) was greater in neuston than in bongo collections except at three stations during summer 1977 (Figure 3). During winter 1977, occurrences were too few to be tested at the 0.05 confidence level by the signed rank test. On all other cruises during which *Callinectes* larvae occurred, abundance was significantly greater in surface than subsurface collections (Table 3).

Diel patterns in neuston abundance of *Callinectes* were not consistent over all cruises (Figure 4). A dawn peak in abundance was evident in summer 1976. Dusk peaks appeared in fall 1975 and possibly spring 1977. Total abundance was greatest during darkness (between sunset and

TABLE 3.—Comparison of surface and subsurface (neuston vs. bongo) abundance of *Callinectes* larvae, based on the signed rank test (Wilcoxon 1945). N denotes greater abundance in neuston, significance level indicated by asterisks (* = 0.05, ** = 0.01); P is the probability of a rank sum equal or greater under the null hypothesis of equal surface and subsurface abundance; fraction in parentheses: numerator is the number of occurrences in particular abundance category and denominator is the number of possible occurrences in abundance category.

Comparison	Season and year of collection					
	Fall 1975	Summer 1976	Fall 1976	Winter 1977	Spring 1977	Summer 1977
Maximum neuston vs. maximum bongo	N* P = 0.016 (6/6)	N* P = 0.016 (6/6)	N** P = 0.004 (8/12)	N P = 0.062 (4/12)	N* P = 0.016 (6/12)	N** P = 0.008 (12/12)
Maximum consecutive pair of neuston tows vs. bongos, mean	N* P = 0.016 (6/6)	N* P = 0.016 (6/6)	N** P = 0.008 (7/9)	N P = 0.125 (3/9)	N* P = 0.016 (6/9)	N** P = 0.004 (9/9)
Neuston vs. bongos, mean	N* P = 0.016 (6/6)	N* P = 0.016 (6/6)	N** P = 0.008 (7/9)	N P = 0.125 (3/9)	N* P = 0.016 (6/9)	N** P = 0.010 (9/9)

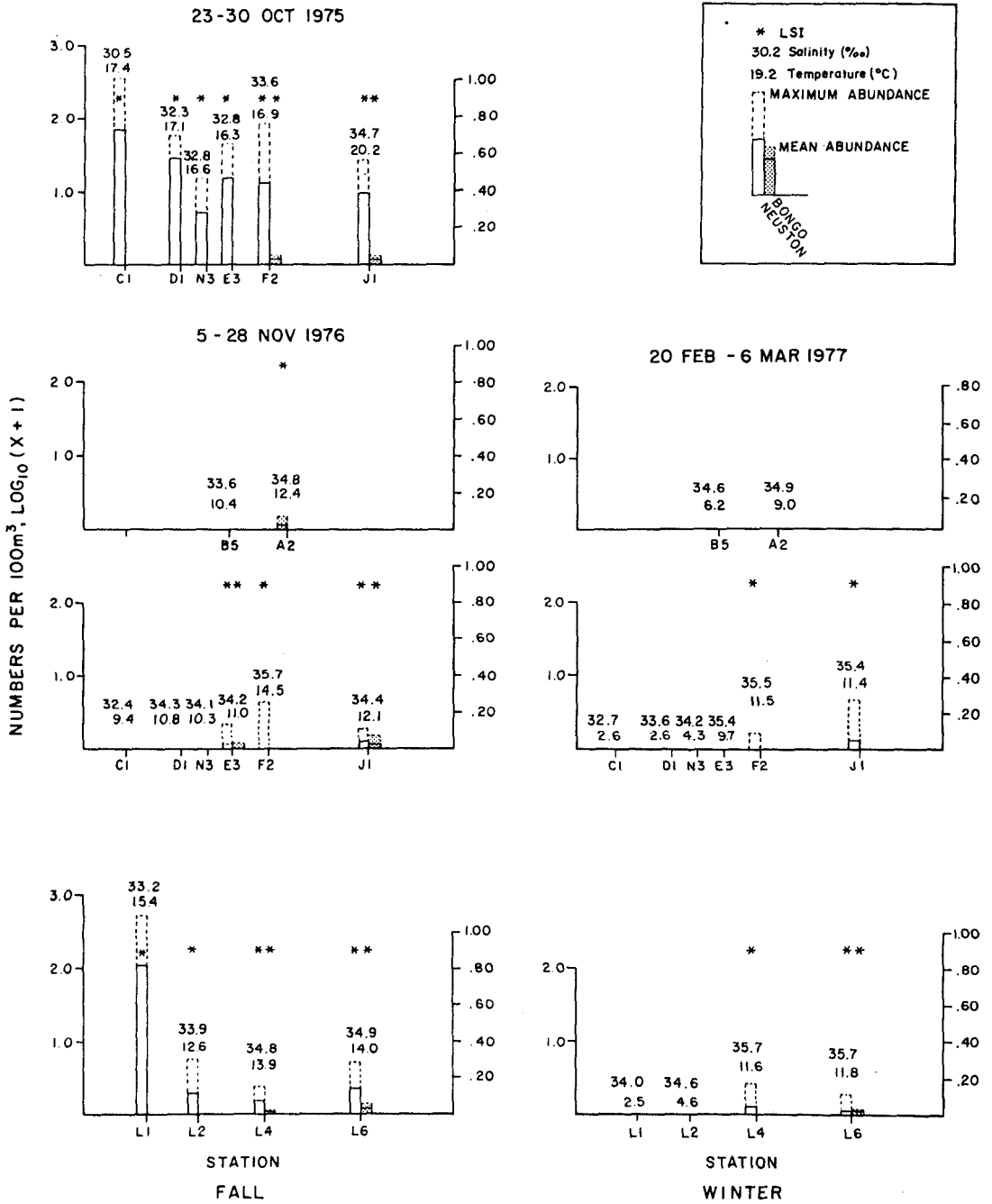
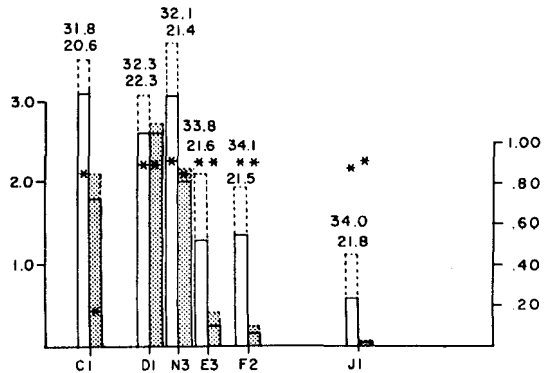
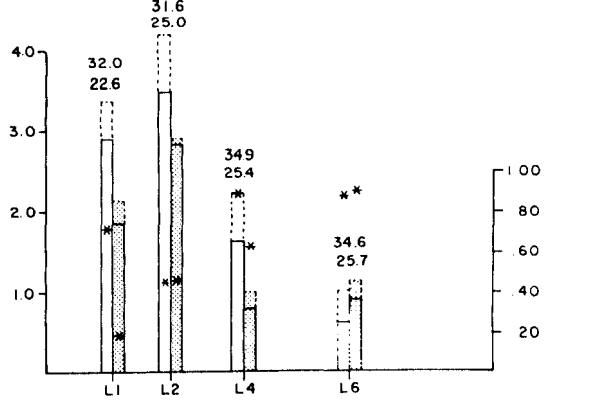
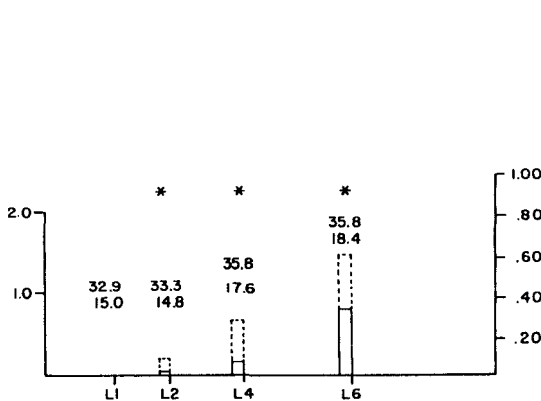
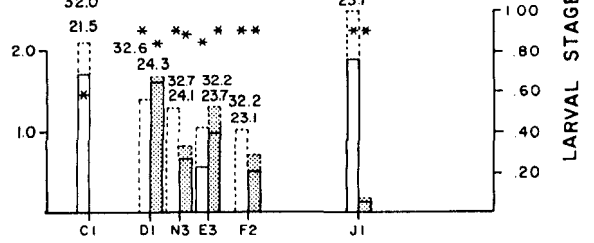
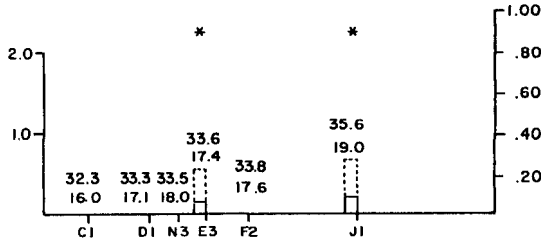
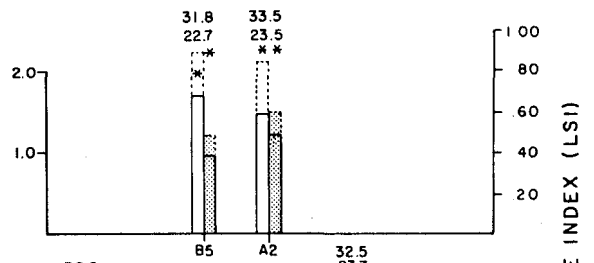
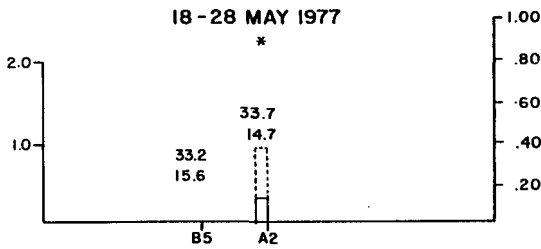


FIGURE 3.—Abundance and larval stage indices (LSI) of *Callinectes* larvae in surface and subsurface collections in

1 - 9 SEPT 1976



19-29 AUG 1977



STATION
SPRING

STATION
SUMMER

LARVAL STAGE INDEX (LSI)

the Middle Atlantic Bight, 1975-77. Stations are ordered by increasing depth on a logarithmic scale within each graph.

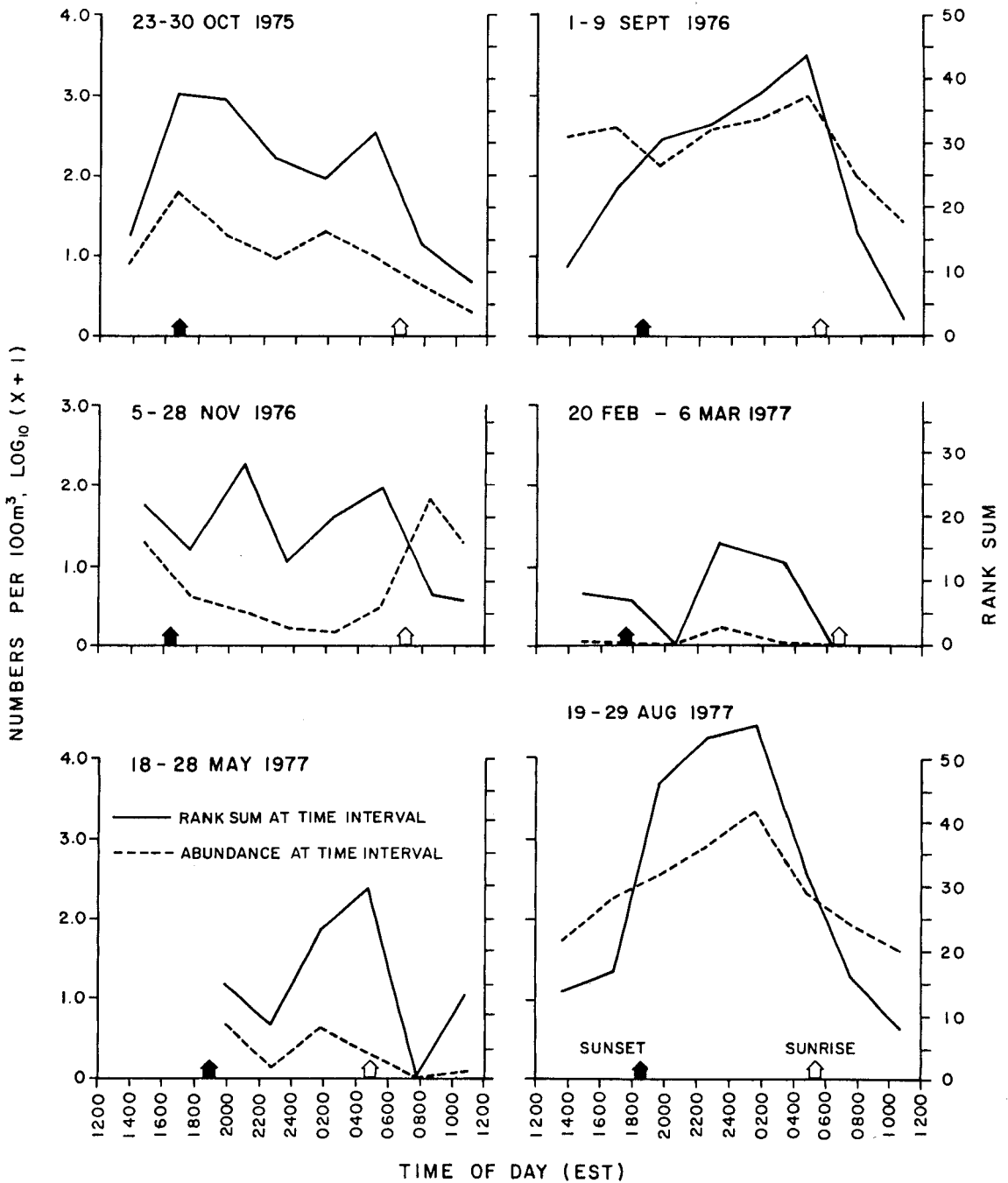


FIGURE 4.—Diel changes in abundance of *Callinectes* larvae in neuston collections in the Middle Atlantic Bight, 1975-77. Abundance (dashed line) for each time interval was averaged over the stations of a cruise. The rank sum for each cruise (solid line) was calculated by summing over all stations the ranks (lowest to highest) of the abundances at each time interval. (The rank sum weights the frequency of occurrence at each time interval.)

sunrise) on all cruises except fall 1976, when abundance was greatest during daylight hours.

The rank sum, which weights both abundance and frequency of occurrence, indicated patterns of

diel change similar to diel patterns of total abundance—except during fall 1976. As distance from shore increased and abundance decreased, however, *Callinectes* larvae (late zoeae and megalopae) were generally collected at the surface only at night. Ten of 15, and 10 of 12 occurrences (megalopae) during winter and spring 1977 were at night.

Larvae were taken at salinities ranging from 30.5 to 35.8‰ and temperatures from 11.0° to 25.7° C (surface temperature and salinity); peak abundance occurred in the ranges 31.6–34.9‰ and 20.6°–25.7° C. Mean temperature, salinity, and distance from shore, weighted for abundance, for all neuston collections of *Callinectes* larvae were 22.9° C, 31.9‰, and 55.9 km. Plots of temperature and salinity vs. abundance indicated no clear relationships among these variables.

For the independent variables—temperature, salinity, distance from shore, and depth—simple (bivariate) correlation analysis indicated strongest correlation between mean neuston abundance per station and salinity and weakest correlation of abundance with bottom depth (Table 4).

TABLE 4.—Simple correlation matrix for surface abundance of *Callinectes* larvae and selected environmental variables.

Variable	Abundance ($\log_{10}[X+1]$)	Temperature (°C)	Salinity (‰)	Distance from shore (km)
Temperature	0.6260***			
Salinity	-0.7086***	-0.5133**		
Distance from shore	-0.5812***	-0.1695	0.6259***	
Bottom depth	-0.4024**	-0.1218	0.5621**	0.6261***

** $P < 0.01$, *** $P < 0.001$.

When considered together, the variables form a multivariate population. Partial correlation analysis (Table 5) indicated a very weak relationship between bottom depth and larval abundance for all second and third, and most first order correlations. Depth was, therefore, deleted from further analysis. Second order correlations among temperature, salinity, and distance from shore revealed strongest correlation of abundance with temperature, followed by distance from shore and salinity.

Based on partial correlation analysis, independent variables were entered into a multiple regression equation in the order temperature, distance from shore, salinity, and depth. These variables explained 66.0% of the variation in abundance (Table 6), the maximum possible for

TABLE 5.—Partial correlation coefficients for surface abundance $\log_{10}[X+1]$ of *Callinectes* larvae with selected environmental variables.

Temperature (°C)	Salinity (‰)	Distance from shore (km)	Bottom depth (m)
First order correlations:			
c ¹	-0.5787	-0.6182	-0.4214
0.4331	c	-0.2502	-0.0069
0.6577	-0.5434	c	-0.0606
0.6350	-0.6372	-0.4613	c
Second order correlations:			
c	c	-0.3969	-0.1240
c	-0.3051	c	-0.0627
c	-0.4514	-0.5017	c
0.5194	c	c	0.1135
0.4472	c	-0.2732	c
0.6578	-0.5493	c	c
Third order correlations:			
c	c	c	0.0378
c	c	-0.3815	c
c	-0.3013	c	c
0.5112	c	c	c

¹c indicates variable which is controlled (effects removed).

any linear combination of these variables. Depth contributed negligibly to explained variance, and salinity very little (Table 6). The regression equation containing only the variables temperature and distance from shore, explaining 62.4% of the variation in abundance, is

$$A = 0.1393 + 0.1124T - 0.0115D$$

where A = abundance ($\log_{10}[X+1]$),
 T = temperature in degrees Celsius,
 D = distance from shore in kilometers.

The regression of abundance on temperature and distance from shore was highly significant (Table 7).

The temperature-distance from shore-abundance relationship for all cruises is summarized in Figure 5. Summer collections formed a unique group, distributed across the shelf. Abundance appeared relatively uniform at least to a distance of 100 km from shore, with a slight increase at the outermost stations. Temperature did not appear to be a limiting factor for these summer collections. Relationships are less clear for other seasons. Fall collections generally decreased in abundance with decreasing temperature and increasing distance from shore. Winter and spring collections formed groups which were limited to the outer shelf.

Cooccurring Decapods

Collections made during periods of peak abundance of *Callinectes* (in the summer) included

TABLE 6.—Variation explained by multiple regression of surface abundance ($\log_{10}[X + 1]$) of *Callinectes* larvae on temperature, distance from shore, salinity, and depth as estimated by the coefficient of determination (r^2). Data were entered in the order indicated in the Statistical Package for the Social Sciences (Nie et al. 1975) stepwise multiple regression procedure.

Temperature, distance from shore, salinity, depth			Salinity, temperature, distance from shore, depth		
Variable	r^2	Δr^2	Variable	r^2	Δr^2
Temperature (°C)	0.3919	0.3919	Salinity	0.5021	0.5021
Distance from shore (km)	0.6243	0.2324	Temperature	0.5955	0.0934
Salinity (‰)	0.6592	0.0350	Distance from shore	0.6592	0.0637
Bottom depth (m)	0.6597	0.0005	Bottom depth	0.6597	0.00049

TABLE 7.—ANOVA table for regression of surface abundance ($\log_{10}[X + 1]$) of *Callinectes* larvae on temperature and distance from shore.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	41	37.23161	0.908088	
Regression	2	23.24224	11.62112	32.39773***
Residual	39	13.98937		

*** $P \leq 0.001$.

peak abundances of inshore and estuarine genera such as *Uca* (zoeae and megalopae), *Emerita* (zoeae), *Palaemonetes* (zoeae), *Upogebia* (zoeae), *Libinia* (zoeae and megalopae), and *Ovalipes* (zoeae and megalopae). Few of the above were found beyond the inner shelf (Figure 1: C1, D1, L1). At offshore stations *Callinectes* larvae frequently occurred with larvae of shelf forms such as *Cancer*, which dominated neuston collections made in the spring. Megalopae and a few zoeae of *Portunus* usually occurred with *Callinectes*. Megalopae of *Ocypode quadrata* were ubiquitous across the shelf during summer 1977. Megalopae of *Dromidia antillensis* and other forms of southern origin often occurred at central and outer shelf stations.

DISCUSSION

Temperature-salinity tolerances of *Callinectes* larvae are available from several laboratory and field studies. Optimum temperature-salinity ranges, experimentally determined, for survival during zoeal development of laboratory-reared *C. sapidus* were 21-28‰, 19°-29° C (Sandoz and Rogers 1944) and 20-32‰ at 25° C (Costlow and Bookhout 1959). Sandifer (1972) collected *C. sapidus* zoeae in Chesapeake Bay in the range 15.7-32.3‰ (most at 20-30‰) and 14°-27.9° C (75% at 25°-26° C). Nichols and Keney (1963) found larvae (zoeae and megalopae) to be most abundant offshore (Florida-North Carolina) at 27.3°-29.1° C and least abundant at 14.3°-16.4° C.

Costlow (1967) reported survival of megalopae to first crab in temperature-salinity combinations

of 15°-30° C, 5-40‰. Survival was similar at 20°, 25°, and 30° C, 10-40‰ (75% survival) and occurred at salinities as low as 5‰ at 25°-30° C. Survival in the lower salinity ranges (5-10‰) increased with increasing temperature to 95% at 30° C, 10‰. Survival in the upper salinity ranges (30-35‰) decreased from 95-100% at 25° C to 42-50% at 15° C. At 15° C larvae did not survive below 20‰, and at 15° C survival was highest at 35‰ (50%).

Costlow and Bookhout (1959) found zoeal development to require 31-49 days, with no significant difference in larval duration at salinities from 20.1 to 31.1‰ (at 25° C). Duration of the megalopal stage ranged from 5-11 days at 30° C (5-40‰) to 30-67 days at 15° C (20-40‰) (Costlow 1967). Costlow (1967) reported significant interaction between temperature and salinity only at 15° C. Larval duration at 35‰, 15° C was 37-56 days. Costlow (1967) did not rear larvae at temperatures <15° C and did not include a regression equation for extrapolation to lower temperatures.

Based on experimentally determined tolerances noted above, summer temperatures in the estuaries and inshore waters along most of the middle Atlantic and southeastern U.S. coast are sufficiently warm for completion of larval development. Metamorphosis of megalopae may occur during the warmer months at salinities found from offshore to upper estuaries. Greatest survival, however, is at higher salinities (30-40‰), and at 15° C occurs only in the range of oceanic salinities. Furthermore, at these oceanic salinities the duration of the megalopal stage increases as temperature decreases. Thus, megalopal life may be extended in the cooler, offshore water of the Middle Atlantic Bight, a conclusion supported by the presence of *Callinectes* megalopae at outer shelf stations (11°-12° C, 35-36‰).

Results of multivariate analysis of data were predictable (Figure 5; Tables 5-7). The importance of temperature (positive correlation) reflected the seasonal nature of spawning and development (in

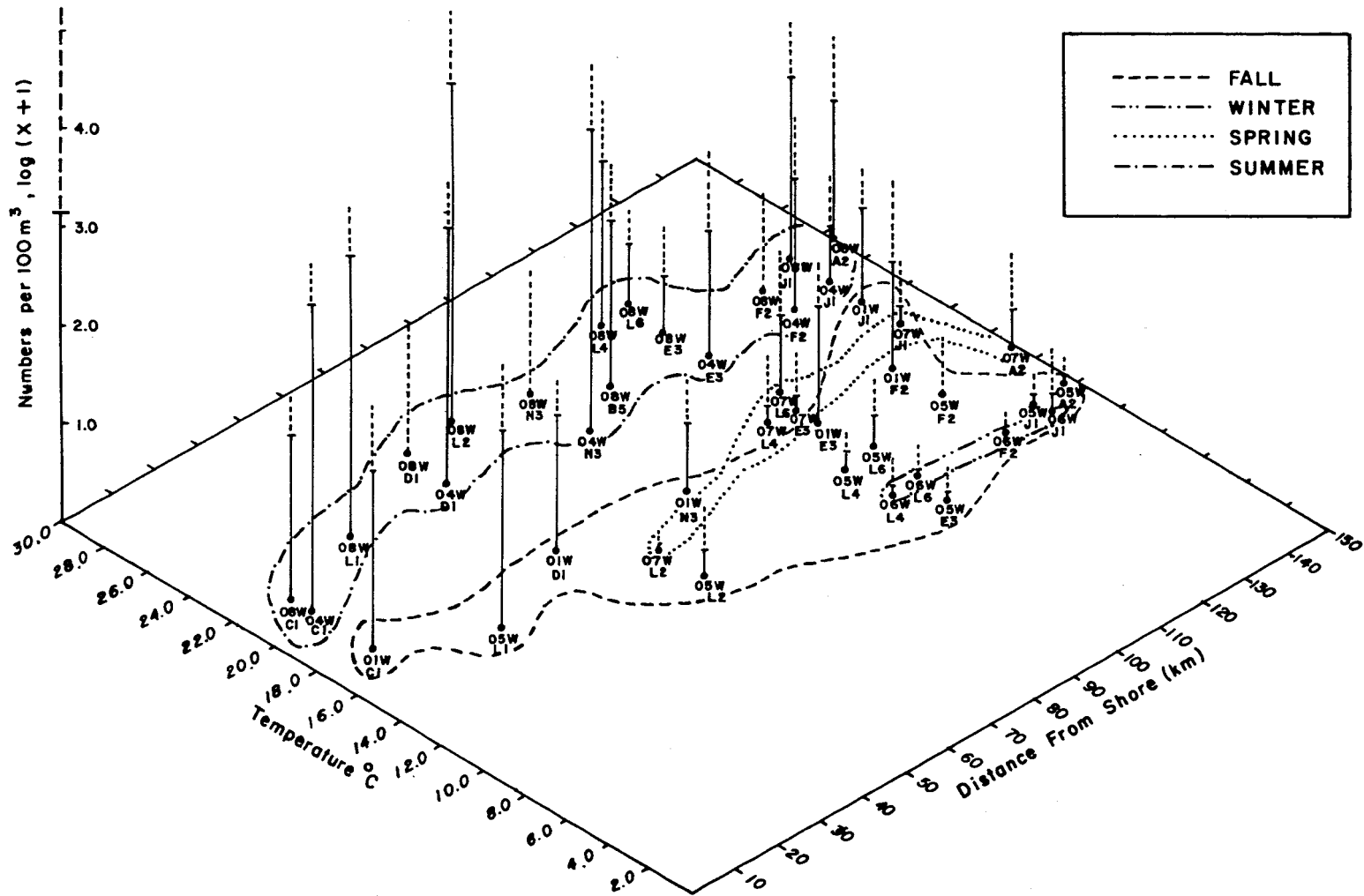


FIGURE 5.—Temperature-distance from shore-abundance diagram for *Callinectes* larvae in neuston collections in the Middle Atlantic Bight, 1975-77. Abundance is indicated on the vertical scale by a solid line for mean abundance and dashed line for maximum abundance. Stations (under cruise numbers) are grouped by season within broken lines.

summer). The secondary importance of distance from shore (negative correlation) was reflected in decreasing abundances with increasing distance from shore. Because all collections were made well within the range of optimum salinities for development, salinity could have been expected to contribute little to explained variation in abundance.

Results of multivariate analysis of data emphasize that a bivariate approach to multivariate data can be misleading. Salinity had the highest simple correlation (-0.7086 ; Table 4) with abundance. Consequently, in the usual SPSS stepwise multiple regression procedure (Nie et al. 1975) salinity would be entered as the first variable in the analysis. The proportion of variation (r^2 , Δr^2) in abundance explained by temperature, distance from shore, salinity, and depth was quite in contrast to proportions of explained variance when salinity, rather than temperature, was entered first in the multiple regression equation (Table 6).

The relative importance of temperature, distance from shore, and salinity was best illustrated by partial correlation coefficients (Table 5). This procedure examines correlation between two variables when the effect of other variables is controlled. I recommend partial correlation as a preliminary step to multiple regression procedures and as more appropriate than bivariate procedures.

This paper reports for the first time the existence of a large population of *Callinectes* larvae in offshore shelf waters of the Middle Atlantic Bight. The presence of an offshore population, necessary to the accepted model of larval distribution, has had relatively little documentation. Nichols and Keney (1963) found advanced stages of *Callinectes* as far as 64-97 km offshore, with greatest abundance at stations 32 km offshore. Dudley and Judy (1971) reported zoeae, chiefly stage III and earlier, and a few megalopae at stations 10-13 km offshore. Tagatz (1968) reported a few megalopae as far upstream as 40 km in the St. Johns River, Fla., and Williams (1971) collected megalopae "... almost the entire length of the [North Carolina] estuary."

Abundance reported here (Figure 3) is somewhat less than that previously reported. Sandifer (1972) and Tagatz (1968) reported maximum larval abundance of 42,000 and 46,100/100 m³, respectively, and Dudley and Judy (1971) reported maximum abundance of 105,000/100 m³. These data, however, included few megalopae. Williams

(1971) found considerably greater numbers of megalopae than did previous workers but reported abundance as numbers per sample (10's-1,000's).

My results confirm the reported affinity of *Callinectes* larvae, particularly megalopae, for surface layers. Previously Sandifer (1972) reported that 89.4% of the *Callinectes* larvae that he collected were from surface samples but reported only three occurrences of megalopae, all in bottom samples. Dudley and Judy (1971) found, overall, more *Callinectes* larvae in surface (1.0 m) than in subsurface (8.0 m) collections except at offshore (10-13 km) stations. They collected advanced zoeae (their last three stages) only at offshore stations. Tagatz (1968) collected more zoeae at the surface than at the bottom, and Williams (1971) reported *Callinectes* megalopae to be active at night in surface waters. The results of these studies, however, reflect differences in gear types, mesh sizes, and sampling design; gear specifically designed to sample surface layers was in no case employed.

Reasons for the affinity of *Callinectes* and other megalopae for the neuston are not readily apparent. Diel increases in abundance in night collections of neuston may indicate a negative phototropic response or possibly net avoidance in the daytime. Numerous holoplankters (copepods, etc.) exhibit the same diel pattern, and the upward movement of megalopae may be related to feeding strategies. It is not surprising that of the megalopae collected in this study, the Portunidae (swimming crabs) showed the strongest affinity for the neuston. Megalopae of other crabs, however, such as *Cancer*, *Ocypode*, and *Dromidia* also showed strong surface affinities.

Spatial distribution of plankton in shelf waters is largely determined by circulation patterns. With cross-shelf flow in the Middle Atlantic Bight offshore at the surface and onshore at depth (Bumpus 1973), coastal organisms in the surface layers would be transported offshore, with the possibility of return at depth. A coastal boundary layer, a band of trapped nearshore flow some 10 km wide, has been reported off New Jersey (Csanady 1976). Coastal boundary layers are associated with the upwelling of cold water as a consequence of the offshore movement of surface waters and subsequent thermocline tilt (Csanady 1976). Most coastal and estuarine larvae in my collections (species of *Uca*, *Palaemonetes*, *Libinia*, etc.) were infrequent seaward of station C1 and are evidently retained within this zone. Late stage

Callinectes larvae were most abundant outside the coastal boundary layer in my collections as well as in those of Nichols and Keney (1963). *Callinectes* juveniles or adults were not collected during this study in extensive benthic sampling (otter and small biological trawls, dredge and grab samplers), and small adults were collected only once in plankton samples (*C. similis*, $n = 5$, station C1, neuston, October 1975). Thus, this study presents no evidence for recruitment to inshore and estuarine populations, either by juveniles or megalopae; the evidence, however, does not preclude recruitment from the offshore larval population.

General longshore drift in the Middle Atlantic Bight is southwestward (Iselin 1955; Harrison et al. 1967; Bumpus 1973; and others) and may occur as sporadic events rather than in a continuous sweep (Ruzecki et al. 1976). Reversals of the longshore flow, usually confined to a narrow belt close inshore, may occur from April to September (Bumpus 1969, 1973). A general constraint, however, seems to be placed on larval origins, viz. adult populations are more likely to be replenished by recruitment from larval populations spawned to the north. Given a mean longshore drift of 5 cm/s (Bumpus 1973) and a megalopal duration of 5-67 days (Costlow 1967), a megalopa has a range of 22-290 km; at inshore temperature-salinity ranges (20°-25° C, 30-35‰) a megalopa might be transported 26-56 km.

Callinectes megalopae collected on the outer shelf in the winter and spring, as well as some megalopae found there in the summer and fall, probably have southern origins. Water masses of Gulf Stream origin, as meanders and warm-core eddies, have frequently been observed in the slope-outer shelf regions (Saunders 1971; see Wright 1976 for a review). Although large-scale, long-range transport is not evident, the presence of *Callinectes* and *Portunus* megalopae at station J1 in the winter indicates either transport from the south or, less plausibly, delayed metamorphosis of megalopae from Middle Atlantic Bight populations as a result of low winter temperatures. Based on Costlow's (1967) response surfaces, a megalopa in Gulf Stream waters would have a duration of 7-26 days and a range, at 2 km, of 600-2,300 km. Thus, some megalopae in the Middle Atlantic Bight may originate from late spawning populations to the south. Metamorphosis would be further delayed by depressed temperatures of shelf and slope waters. The presence of

definite southern larval forms (e.g., *Dromidia*) in outer shelf collections supports the hypothesis that at least some of the *Callinectes* and other megalopae were produced by southern crab populations.

The developmental model of *Callinectes*, i.e., larval development in shelf waters and subsequent recruitment to inshore and estuarine adult populations, reflects the evolutionary history of the group. Portunids are "reproductively conservative," migrating to waters of oceanic, or near oceanic, salinities to release larvae (Norse 1977). Williams (1974) described *Callinectes* as "a portunid group evolving at the geographic limits of the family, specializing in occupation of estuaries, . . ." In this light, the migratory sequence of larval stages is a response to the problems of an essentially marine group invading the estuaries. Spawning areas (marine) may represent a primitive condition, and the spatial sequence of stages returns larvae to habitats in which the adults are successful. It is, as Williams (1974) described it, a "homeostatic developmental feature in the life histories of the species" that has not been carried to an evolutionary conclusion, that is, retention within the estuary for the entire life history.

It can be argued that such a model of development may in part account for the success and widespread distribution of *Callinectes*. If, as Norse (1977) and others have indicated, recruitment occurs through metamorphosis of megalopae rather than immigration of adults, then such a sequence would allow dispersal into numerous estuaries yet assure genetic continuity over broad areas. Such a role has been suggested by Cole and Morgan (1978). Furthermore, it would seem more likely that this is a primitive mechanism retained, rather than developed, through selection pressures.

The essential features of *Callinectes* development appear to be spawning and hatching in or near the primitive habitat (along the shore) during most of the warmer months, maintenance of a large larval population in the shelf waters (chiefly in the surface layers), recruitment from the larval pool, and exploitation of the estuarine habitat as adults.

There is, however, a paradox in the biogeography of *Callinectes* and the spatial sequence of developmental stages. Given the southern affinities of the genus and general southerly longshore movement of waters along most of the

U.S. Atlantic shelf, the distribution of *Callinectes* is counter to the direction of immediate larval transport. Recruitment to adult populations at the northern limits of *Callinectes* is problematical. Not all larvae can originate from parental stocks to the north. This may indicate that recruitment takes place from megalopal populations closer inshore than those reported in this study and by Nichols and Keney (1963), with the coastal boundary layer possibly retaining larvae. The megalopae collected farther offshore may represent larval wastage to parental populations (but not necessarily to the species).

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