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## **A Comparison of Recruitment Strategies Among Brachyuran Crustacean Megalopae of the York River, Lower Chesapeake Bay and Adjacent Shelf Waters**

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A COMPARISON OF  
RECRUITMENT STRATEGIES  
AMONG BRACHYURAN CRUSTACEAN MEGALOPAE  
OF THE YORK RIVER, LOWER CHESAPEAKE BAY AND  
ADJACENT SHELF WATERS

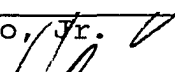
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A Dissertation Submitted to the Faculty of  
Old Dominion University in Partial Fulfillment of the  
Requirement for the Degree of

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Approved by:

Anthony J. Provenzano, Jr.   
(Director)

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## ABSTRACT

### A COMPARISON OF RECRUITMENT STRATEGIES AMONG BRACHYURAN CRUSTACEAN MEGALOPAE OF THE YORK RIVER, LOWER CHESAPEAKE BAY AND ADJACENT SHELF WATERS

David Franklin Johnson  
Old Dominion University, 1982  
Director: Dr. Anthony J. Provenzano, Jr.

Twenty-one stations forming a transect of the Pamunkey River, York River, lower Chesapeake Bay and adjacent coastal waters were sampled from July through September 1980. The megalopa stages of 11 brachyuran species were sampled. Vertical and horizontal distributions are described for each species in relation to salinity and water column stratification. The megalopae are assigned to three apparent recruitment strategies: retained estuarine, expelled estuarine and retained coastal megalopae. The megalopa stages of estuarine adults, such as Hexapanopeus angustifrons, Neopanope sayi, Panopeus herbstii and Pinnotheres ostreum, are retained in estuarine epibenthic waters, while Rhithropanopeus harrisii are retained in slightly shallower estuarine waters. The larvae of some estuarine species such as Callinectes sapidus, Uca spp. and Pinnixa sp., are expelled from the estuary, resulting

in maximum megalopal abundances on the shelf. Differences in vertical distribution, distance from the bay entrance and the proportion of the catch within the estuary suggest the megalopa is important in reinvasion of the estuary for Uca spp. and Pinnixa sp., but facultatively reinvasive for Callinectes sapidus. Two shelf species, Portunus sp. and Cancer irroratus are most abundant in the neuston of shelf waters and thus their dispersal to the estuary is impeded.

Another shelf form Libinia spp., is commonly found as an adult in the lower Chesapeake Bay. Although their megalopae are most common in the epibenthos on the shelf, 9% are found in the bay.

All megalopae displayed a strong tendency to be distributed either above or below a pycnocline, when present. Five species show significant shifts in vertical distribution between stratified and homogeneous water columns. No evidence of decreased dispersal is found for increasingly estuarine species.

## ACKNOWLEDGEMENTS

This project required more than thirty days at sea with an uncompensated scientific crew of more or less 10 people per cruise. Most people helped for one or two days; however, four people provided extraordinary assistance for more than ten days, while one fellow attended every cruise. These people, to whom I express my deepest gratitude, are listed below, in order of the number of days contributed: P. Sadler, J. Clark, H. Winnik, B. Hester, K. Worthington, M. Gallano, E. Deaver, J. Avis, D. Driver, L. Kalenak, G. Kitzig, M. Masters, E. Miller, T. Tomlin, D. Valenski, T. Anderson, P. Anninos, G. August, J. T. Booher, M. Bundy, M. Bushing, M. Cholko, M. Jugan, B. Korniker, M. Paula, K. Ruppe, D. Sadler, R. Smith and J. Winfield.

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I also thank the members of my advisory committee, Dr. Ray Alden, Dr. Ron Johnson, Dr. Phil Mundy, Dr. John McConaugha and my major advisor, Dr. Anthony J. Provenzano, Jr. for their helpful criticisms, teachings and encouragement during the course of this study.

I also wish to thank Dr. L. D. Peterson and Dr. S. P. Hines, Jr. for their discussion and advice on Latin and Greek grammar.

Finally, this research would not have been possible without the partial financial support of Sea Grant Cont. No. NA81AA-D-00025, which not only supplied funds for part of the sampling program, but also provided my salary until President Ronald Reagan took office.

DEDICATION

To my wife Beverly

Ad hoc, Ad loc  
Quid pro quo  
So little time,  
So much to know

Jeremy Hillary, Ph.D.  
"Yellow Submarine"



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CHAPTER I  
LITERATURE REVIEW

On the history of megalopa

The first published description of a larval decapod is ascribed to Linnaeus (Williamson 1915). Linnaeus (1767, p. 1047) gave the form species status, Cancer Germanus (sic.) and apparently described a megalopa (Thorax inaequalis, e cujis medio Spina valida, horizontalis, supra caudam extensa. Cauda teres articulis 5, globosis). Leach (1815) described Megalopa as a genus of supposedly adult forms. In a summary of Leach's work, Williamson (1915) names three genera to which were attributed the form now called a megalopa: Megalopa, Megalops and Megalopus.

Thompson (1828) was close to describing the larval nature of the megalopa, but his animals died in the process of molting. His most monumental observation was the metamorphosis of the zoea, which at that time was also considered a genus of adult forms. Thompson selected the largest living specimen from a collection of zoeae and daily supplied it with fresh seawater for one month, after which it died in the process of molting. Thompson carefully diagramed the zoea before and after the incomplete

process of metamorphosis and very plainly illustrated the pereopods from the right side of a crab-like form. Thompson repeated the experiment, but again the larvae died during molting, causing a frustration which is commonly experienced today. Thompson, not to be defeated, obtained a gravid crab (Cancer pagurus), successfully hatched the eggs and observed the zoeae, thus proving the larval nature and metamorphosis of the zoea. In the same paper Thompson suggested the use of a small gauze towing net to capture plankton and suggested placing the net in the outflow of a seawater pump in rough sea conditions. To my knowledge, this is the first mention of either a net or a pump used to collect plankton.

Amid much dissent over his report of a zoeal metamorphosis Thompson (1835) reported the double metamorphosis of larval crabs. However, the megalopa as a developmental stage of crabs was not fully appreciated for many years thereafter, as several authors still considered the megalopa an adult form (Lucas 1842, 1846; Dana 1852). Since that time, the terms metalopa (e.g. Williamson 1915, Gurney 1942, Chamberlain 1961, Bookhout and Costlow 1977, Lough 1976) and megalops (e.g. Brooks 1882, Hay 1905, Churchill 1919, Costlow and Bookhout 1971, Lough 1976) have been used interchangeably as the developmental stage succeeding the zoea of crabs. Some confusion has existed as to the use of these terms, especially the plural. Megalops

has been used not only as the singular form but also the plural (Costlow and Bookhout 1959, 1962; Knudsen 1960, Costlow 1967; Tagatz 1968; Johnson 1974). Megalopa also has been used as both the singular and plural (Perkins 1973, Epifanio 1979, McConaughy and Costlow 1980). Furthermore megalopa has also been used in the plural as megalopas (Gurney 1942). The terms megalopa and megalops were derived from Greek roots, with Latin endings added to produce genus names. Thus, the plurals should reflect Latin plurals, so that megalopa becomes megalopae, while megalops becomes megalopses.

Some additional confusion exists over the designation of the megalopa as a larval or postlarval form. The use has not been consistent, as many references refer to the megalopa as a larva (Brooks 1882, Sandoz and Rodgers 1948, Costlow and Bookhout 1959, Sheltema 1971, Costlow and Bookhout 1971) while others designate it a postlarva (Williamson 1915, Gurney 1942, Chamberlain 1961, Sandifer 1972, Goy 1976). Chia (1974) reexamined the definition of larva with regard to meroplankton, and defined larva as "a developmental stage, occupying the period from post-embryonic stage to metamorphosis and it differs from the adult in morphology, nutrition or habitat." Chia specifically included the megalopa as a larval form; however, his definition might be further improved if "metamorphosis" is further defined as terminal metamorphosis.



### The Importance of Accurate Larval Descriptions

The field study of larval crabs has often been hampered by the lack of detailed published descriptions of the developmental stages. Many older descriptions of larvae are based on reconstructions of forms found in the plankton (e.g. Birge 1883, Hyman 1925, Churchill 1942). Naturally the accuracy of such descriptions is often in doubt and the literature contains many misrepresentations. Conversely, laboratory rearings reported in the older literature frequently failed to maintain the larvae up to the juvenile crab stages. However by the late 1950's, refinements in laboratory technique ultimately produced the complete larval development of Callinectes sapidus, a species commercially important as well as difficult to rear (Costlow and Bookhout 1959). Since that time the number of publications with detailed larval descriptions has increased dramatically. Yet, less than half of the larval decapods of the Chesapeake Bay are described (Goy 1976), and by my own estimate, only slightly more than half of the brachyuran larvae of the Chesapeake Bay and adjacent waters are described at this time. Without accurate and detailed larval descriptions of the species in a study area, it is difficult to study the field ecology of these forms.

### Recruitment

Planktonic larval stages are common in the life histories of marine benthic invertebrates. Pelagic larvae

provide several advantages including increasing dispersal capabilities and genetic exchange between populations. Thus animals with pelagic larvae are evolutionarily more flexible and have a greater chance of colonizing new habitats (Thorson 1950, Chia 1974).

The net flow of water in most estuaries is seaward. Thus estuarine species with pelagic larvae face the problem of seaward transport which greatly reduces the chance of recruitment to the estuary (Ketchum 1954). Current evidence suggests that evolutionary pressure on species colonizing estuarine and freshwater habitats has resulted in the reduction or loss of pelagic larval stages. An intermediate or alternative step in this process might be the adoption of recruitment mechanisms to decrease the loss of larvae from the adult population. The data of Sandifer (1972) suggest such retention mechanisms are common in the estuarine decapods of the Chesapeake Bay; however, these data are based on samples which contained few late stage larvae and "postlarvae."

Recruitment mechanisms may be divided among two categories since estuarine larvae tend either to remain within the parental habitat or drift out to sea and return to an estuarine habitat at a later larval stage. Several retention mechanisms have been proposed for estuarine larval forms and at least one reinvasion mechanism has been proposed. Retention mechanisms are defined herein as any

behavior or physical condition which serves to impede the transport of larvae away from the parental habitat. Reinvasion mechanisms are defined as any behavior or physical condition which serves to return late stage larvae or juveniles to the parental habitat, where the early stage larvae are not retained near the parental habitat. The following is a discussion of the various types of retention and reinvasion mechanisms proposed for estuarine larvae.

#### Retention Mechanisms

1. Certain areas of an estuary may have a restricted seaward flow and thereby create havens for planktonic larvae. Chamberlain (1962) described such a nursery area within the Chesapeake Bay. The tidal exchange constituted only 2.3% per tidal cycle and Rhithropanopeus harrisi larvae were retained in this embayment during their development. Lucas (1975) most commonly found the larvae of Halicarcinus in semiencllosed embayments within Australian sounds. Halicarcinus also possesses a short larval development which further minimizes displacement from the parental habitat. Manning and Whaley (1954) indicated that the restricted circulation of water in the St. Mary's River, a tributary of the Chesapeake Bay, precludes a significant water exchange with lower parts of the river. The restricted circulation traps larvae and it is cited as the reason for repeated heavy sets of oysters in that area.

Haskin (1964) suggested that the entrainment of saline bottom water into less saline surface waters at the upper reaches of the estuary near the turbidity maximum also results in a larval trap. Heavy sets of oysters as well as high concentrations of cyprids near the mouths of tributaries of estuaries support this idea (Haskin 1964, Bousfield 1955).

2. Larvae may be transported by tidal currents within an estuary. By remaining on the bottom during ebb phases of the tide and actively swimming at flood phases of the tidal cycle, larvae may be transported landward even though the net estuarine flow is seaward. Christy (in press) caught significantly greater numbers of Uca sp. megalopae on flooding tides than on ebbing tides. Conversely, several studies in the Chesapeake Bay suggest that some decapod crustacean larvae are found in greater concentrations in the water column during the slack before ebb (Sandifer 1973, Goy 1976).

Turgeon (1976) found that larvae of various invertebrates common to the lower estuary swam up into the water column on flooding tides, whereas larvae of species from the upper estuary actively swam during the low water slack. Also, several studies of bivalve molluscs have demonstrated increased numbers of larvae in the water column during flood tides (Carriker 1951, 1961; Haskin 1964; Wood and Hargis 1971) with at least one resulting

in up-estuary transport (Wood and Hargis 1971). Barnacle cypris larvae behave similarly. Their density is greater than water and they tend to sink rapidly, but during periods of maximum current velocities, especially flood tides, these larvae enter the water column (de Wolf 1973, 1974).

3. As larvae molt to later stages, they may be found at different depths in the water column, rather than in close association with the bottom. Many studies of decapod crustacean larvae have found the early larvae stages near the surface, and the later larval stages near the bottom (Bousfield 1955, Dudley and Judy 1971, Sandifer 1975, Goy 1976, and Cronin 1979). This behavior is an effective mechanism for larval retention since many estuaries, including the Chesapeake Bay, predominantly exhibit two-layered flow. Interestingly, Lough (1976) indicated early stage larvae of the coastal crab, Cancer magister, were found near the bottom, while the later stages were found near the surface.

4. Rather than migrations from substrate to water column, cyclic vertical migrations on a diel or tidal basis within a two-layered estuarine water column may effectively limit transport. The adults of the cladoceran, Podon polyphemoides migrate to the surface during the day and return to deeper waters during the night, thereby maintaining this population in a rather narrow area within

the Chesapeake Bay (Bosch and Taylor 1973). Larval Uca spp. have been suggested to make a similar migration, but in phase with the tidal cycle rather than a diel cycle (DeCoursey 1976). Some copepods and mysids also utilize tidal currents, thereby retaining populations within the estuary (Wooldridge and Erasmus 1980). Some brachyuran larvae may behave similarly. Cronin (1979) demonstrated that Rhithropanopeus harrisi larvae undergo rhythmic changes in vertical distribution in the field. Field caught larvae maintained under constant conditions in the laboratory exhibited a tidal rhythm of vertical migration which persisted several days (Cronin 1979).

#### Reinvasion Mechanisms

Reinvasion has been suggested for Callinectes sp. (Tagatz 1968, Smyth 1980, Provenzano et al. in press). If this mechanism is utilized, early stage Callinectes larvae hatch near the mouths of estuaries and remain in the surface layers, predominantly the neuston, on nocturnal ebb tides (Provenzano et al. in press). The larvae are subsequently carried offshore where, barring individual misfortune, they continue to mature. At some point in the life cycle, probably the early crab stages, recruitment to the estuary occurs as a return migration. However, this latter event has not been well-documented through systematic collecting. The timing of larval release in Uca spp. also has been shown in result in

seaward transport of the zoeae and subsequent loss from the estuary (Christy in press, Christy and Stancyk in press). The megalopa was found to be the reinvasive stage and was suggested to be selectively riding nocturnal flood tides (Christy in press).

## CHAPTER II

### FIELD STUDY

#### Introduction

The net flow of water in most estuaries is seaward. Thus estuarine species with pelagic larvae face the problem of seaward transport, which greatly reduces the chance of recruitment to the estuary (Ketchum 1954). Mounting evidence suggests that evolutionary pressure on species colonizing estuarine habitats has resulted in the development of strategies which greatly enhance larval retention in estuaries. These recruitment strategies include retention promoting behaviors such as larval locomotory rhythms (e.g. DeCoursey 1976, Cronin and Forward 1979, Sulkin et al. 1979), movement to surface waters by early stage larvae (Hyman 1925, Russell 1927, Thorson 1946, Carriker 1951, Bousfield 1955, Bayne 1964, Sandifer 1972, Provenzano et al. in press), and movement to bottom waters by late larval stages (e.g. Bousfield 1955, Tagatz 1968, Sandifer 1972). Retention has also been suggested as a consequence of estuarine circulation patterns (e.g. Bousfield 1955; de Wolf 1973, 1981; Wood and Hargis 1971). However, with the multiplicity of species within the range of estuarine and shelf conditions, strategies must be in



use for not only estuarine retention, but estuarine reinvansion for those larvae exported from the estuary, as well as estuarine avoidance for shelf larvae.

Many excellent studies reporting distributions for brachyuran larvae have emphasized the early zoeal stages and have infrequently captured the megalopal stage (Bousfield 1955, Chamberlain 1962, Pinschmidt 1963, Tagatz 1968, Dudley and Judy 1971, Sandifer 1972). This infrequency may be due to the difficulties of collecting the large sample volumes which are needed to quantitatively collect this form, a problem detailed in the discussion. An alternate reason for the lack of emphasis on the megalopa might be the confusion regarding the larval classification of this brachyuran stage. The classification of the megalopa as a postlarval stage has been cited as a reason for its exclusion from larval recruitment studies (Sandifer 1972). The megalopa is often referenced as a postlarva, because former definitions of larva require the form to have distinct larval organs not found in the adult (Gurney 1942). However, Chia (1974) updated the definition of larva to alleviate inconsistencies caused by earlier definitions and specifically included the brachyuran megalopa.

In distribution studies, catch data which are numerically biased towards the early larval stages may obscure important details of larval recruitment for two reasons.

A single hatch of larvae occurs frequently as a point source; thus, a large catch of early larvae may reflect the capture of a hatch near the source, rather than general trends in larval dispersal. Also, the distribution of early larval stages may be a consequence of the parental distribution, since the interval from hatching to capture represents a relatively short part of larval development. To elucidate trends in the horizontal distribution of brachyuran larvae, the megalopa stage must be included, since the megalopa is widely regarded as the stage most important for recruitment to the adult population (Knudsen 1960, Costlow 1967, Tagatz 1968, More 1969, Williams 1971, 1974, Sandifer 1975, Smyth 1980, Sulkin et al. 1980).

#### Objectives

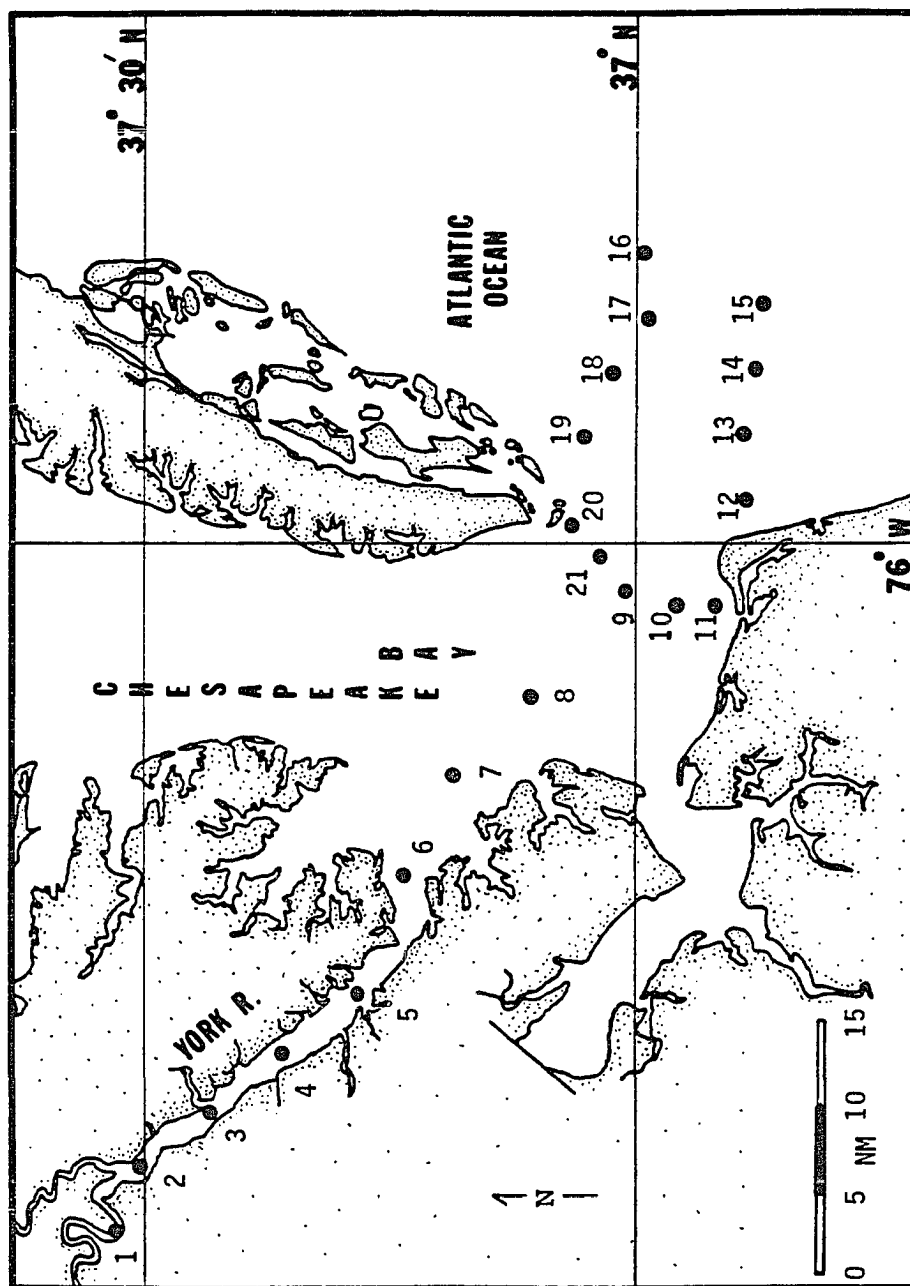
For 11 species of estuarine and shelf brachyurans, horizontal megalopal distributions are described and compared to reported distributions of the zoeae and adults. The distribution and literature records are then used to estimate the success of larval retention for estuarine species. The vertical megalopal distribution is analyzed with respect to stratified and homogeneous water columns. The implications of the vertical and horizontal distributions of megalopae for recruitment strategies are then discussed. Finally, several authors hypothesize that larvae spawned by upper estuarine species have more restricted distributions than those larvae spawned by lower

estuarine species (Carriker 1967, Williams 1971, Sandifer 1975). This hypothesis is examined using retained estuarine megalopae as the model system. As salinity weighting minimizes the bias imposed by variations in mixing conditions throughout the estuary, the variance of salinity weighted distributions is compared between species retained in the estuary for evidence of decreased variance in increasingly estuarine conditions.

#### Description of the Study Area

This study was conducted in the lower Pamunkey River, York River, lower Chesapeake Bay and adjacent continental shelf (Figure 1). The Pamunkey River is the larger of the two major tributaries of the York River, with a drainage basin of 3825 sq km as compared to 2354 sq km for the Mattaponi (Burrell 1972). Tides extend approximately 106 km up the Pamunkey River from its confluence with the Mattaponi (Tide Tables). The mean tidal range is 0.7 m at Lee Marsh (station 1) on the Pamunkey River 3 km from its mouth. The surface ebb excursion persists longer than the bottom ebb, whereas the bottom floods longer than the surface, which produces a net downstream flow on the surface with concomitant upstream flow near the bottom (Brehmer 1970). The depth of the Pamunkey River along the study area varied from 7 m in the channel to 18 m in scour holes at the river bends.

Figure 1. Chart of the York River, lower Chesapeake Bay adjacent continental shelf, showing the location of the 21 stations used in this study.



The York is formed by the confluence of the Pamunkey and Mattaponi Rivers. It is tidal throughout its entire length. The tidal range at the mouth is 0.7 m with surface salinities of 15-24 parts per thousand (ppt) (Haas 1977). Only two towns are located on the York River, West Point and Yorktown located at the upper and lower ends of the York River, respectively. Treated wastewater from a West Point paper mill and effluent cooling water from an electricity generating facility in Yorktown along with agricultural runoff enter the York River. Additionally, an oil refinery at Yorktown is a potential source of oil spills. However, the York is relatively unpolluted and is reported to be the least polluted major tributary of the Chesapeake Bay (Brehmer 1970).

The York River oscillates between conditions of vertical salinity stratification and homogeneity, which is strongly correlated with the spring-neap monthly tidal cycle (Haas 1977). Homogeneity is most developed 1-6 days after spring tides, otherwise stratification is most typical. Variation in river flow appears to be of secondary importance in the hydrographic regulation of this estuary (Haas 1977).

The Chesapeake Bay represents the drowned river valley of the Pleistocene-incised Susquehanna River valley (Ludwick 1972). Its tributaries constitute the largest estuary in the United States and has been classified as

moderately stratified with semidiurnal tides (Pritchard 1967). The York River is considered the southernmost tributary of the ancient Susquehanna, since the James River was probably a separate system during the Pleistocene (Pritchard 1967). The Chesapeake Bay mouth measures 15 km between Cape Henry and Cape Charles. The depth of this region varies from 14 m in the three navigation channels to 4 m in shoal areas. The circulation of the Chesapeake Bay mouth typically consists of a two-layer flow (Pritchard 1955, Boicourt 1981), with a net outflow of low salinity surface waters and a net inflow of shelf water along the bottom (Pritchard 1955, Boicourt 1981). As a refinement of the description of the bilayered flow of this region, the pycnocline has been reported to be slanted, due to the Coriolis effect, such that the pycnocline intersected the surface near the northern side of the bay entrance (Boicourt 1973, Heltzel 1973). This condition indicated a net inflow of shelf water at the northern edge of the bay entrance (Boicourt 1973). However, a recent study indicates a net surface outflow for that region (Boicourt 1981). The source of the inflowing water to the bay is influenced by wind direction and the greatest inflow is in the Chesapeake Channel, just south of the center of the Chesapeake Bay mouth (Boicourt 1973). The outflowing surface water is affected by Coriolis and thus outside of the bay veers toward the south (Boicourt 1973, 1981; Johnson 1976).

The typical flow of the bay mouth may be disrupted on a short term basis. Boicourt (1973) found that north-west winds could produce an outflow surge which, over 48 hours, could lower the Chesapeake Bay by as much as 10% (Boicourt 1973). Also, the response of the shelf waters to wind forcing affects the nontidal flow through the bay mouth. Strong winds can produce outflow or inflow surges in the bay over a two-day interval but if the winds persist for five to ten days, the original surge can be negated by the wind driven flow on the continental shelf (Wang and Elliot 1978, Wang 1979).

The flow of water on the continental shelf in the region of the Middle Atlantic Bight is typically southward (Bumpus 1973). However, the flow pattern in the region seaward of the Chesapeake Bay is variable (Beardsley and Boicourt 1980, Boicourt 1981). The currents of the inner shelf, away from the influence of estuarine flows, are dominated by wind patterns because the southerly drift, which is at a maximum near the shelf break, gradually decreases towards shore, due to bottom friction (Boicourt 1981). Furthermore, the inner shelf is shallow and easily wind driven (Boicourt and Hacker 1976, Boicourt 1981). Current measurements for a 38 day period beginning 23 June 1980 showed a northward drift of the inner shelf surface waters greater than 20 km east of the Chesapeake Bay mouth, as a result of the prevailing southerly winds



of summer (Boicourt 1981). Bottom waters during this period tended to flow towards the bay (Boicourt 1981).

### Materials and Methods

The field study utilized samples from 21 stations which represent the full range of estuarine and marine conditions (Figure 1 and Table 1). Eight of these stations form a 102 km transect of the lower Pamunkey, York River and lower Chesapeake Bay, while the remaining 13 stations form a U-shaped pattern extending from the Chesapeake Bay Bridge Tunnel an additional 41 km seaward. The intense sampling within the Chesapeake Bay mouth was warranted by the complex circulation characteristics of this area.

Each of the 21 stations was sampled on biweekly cruises from 1 July 1980 through 30 Sept. 1980, using the 20 m R/V Linwood Holton. At each station salinity, temperature and conductivity profiles were recorded with a Beckman inductive salinometer followed by vertically stratified, large volume, plankton tows, one from each of the following strata of the water column: neuston, 3 m, 6 m and epibenthos.

The neuston net was designed and constructed by David Johnson, John Clark, and Kathy Philips, Department of Oceanography, Old Dominion University. The net with a mouth measuring 30 cm by 122 cm is designed to sample the uppermost 15 cm of the sea surface. In operation, the net

Station	Latitude (N)		Longitude (W)		Description
	deg.	min.	deg.	min.	
1	37	31.49	76	50.49	Lee Marsh
2	37	29.31	76	46.31	Goff Pt.
3	37	25.43	76	41.39	Poropotank
4	37	22.17	76	37.90	Capahosic
5	37	18.32	76	34.78	Blundering Pt.
6	37	14.57	76	21.83	Tue Marsh
7	37	11.18	76	15.65	Buoy R14
8	37	08.06	76	11.11	Buoy R6
9	37	00.68	76	03.19	Chesapeake Channel
10	36	58.38	76	03.84	Thimble Shoals Ch.
11	36	56.50	76	03.94	Lynnhaven Roads
12	36	53.59	75	55.95	Cape Henry
13	36	53.87	75	51.14	Atlantic Ocean
14	36	53.37	75	46.61	Atlantic Ocean
15	36	52.78	75	41.83	Atlantic Ocean
16	36	58.37	75	37.63	Atlantic Ocean
17	36	58.37	75	41.24	Atlantic Ocean
18	37	01.67	75	46.34	Atlantic Ocean
19	37	03.02	75	51.86	Cape Charles
20	37	03.80	75	58.03	North Ch.
21	37	02.76	76	00.15	Middle Ground

Table 1. Latitude and Longitude of the stations used in this study.

floats with the net mouth submerged to 15 cm depth in smooth seas without surface chop. In choppy seas, the sampler rides the surface of the larger waves, whereas smaller waves cause the sea surface to oscillate about the mean depth of 15 cm in the net mouth. The neuston sampler is fitted with a flow meter located outside the net mouth, because the 15 cm of water inside the net mouth is too shallow to allow the flow meter to operate freely. An opening-closing device is not necessary since sampling time is easily controlled by raising or lowering the net on the sea surface.

The epibenthic sled was designed and constructed by John Clark, Department of Oceanography, Old Dominion University. The sled is constructed of steel and weighs circa 100 kg. The mouth of the net measures 60 cm by 18 cm and is fitted with a flow meter and a door which remains closed except when in direct contact with the bottom. In operation the net mouth samples approximately 10 cm above the bottom at a speed of 3 knots. At stations 1 through 8, a soft bottom prevented the use of a heavy bottom sled. Therefore, at those stations a large Clarke-Bumpus (30 cm diameter) sampler was towed circa 50 cm above the bottom as determined by placing the sampler on the towing wire 50 cm above a 60 kg wire depressor and skimming the depressor along the bottom during the tow.

The 3 m and 6 m depths were also sampled with large Clarke-Bumpus plankton sampling gear. These samplers have

a 30 cm diameter circular mouth and are equipped with a messenger controlled opening-closing device and flowmeter. In operation these samplers are towed along a straight line course at 3 knots. The depth of the Clarke-Bumpus tows were calculated according to the formula.

$$\text{Depth} = (\text{wire out}) [\cos(\text{wire angle})].$$

The flow rates of all samplers were calibrated against General Oceanic's flow meters which were calibrated in a hydrodynamic test channel at Old Dominion University. All tows lasted 5 minutes. All plankton nets had a mesh of 243  $\mu\text{m}$  and more than a 5 to 1 ratio of net area to mouth area.

In the field each plankton sample was washed into a 1 l collecting jar containing 100 ml of buffered formalin. The remaining volume of the jar was filled with filtered seawater. During several weeks of the summer, ctenophores were caught by the plankton nets. To remove the ctenophores in such cases, the samples were washed through plastic netting (5 mm) prior to washing the sample into the collecting jar. Any residual gelatinous debris was dissolved by soaking the plankton sample in a 0.4% sodium hypochlorite solution up to one hour. Longer soakings were found to produce an undesirable bleaching of the crustaceans in the sample.

Normally the entire plankton sample was enumerated, but if numbers of megalopae of any one species exceeded

200 per sample, the sample was split with a Folsom plankton splitter to a fractional sample which produced approximately 100 counts for that species. All counts were then converted to total number of megalopae per 100 cubic meters for each species.

Eleven brachyuran species were selected for this study. Published descriptions are listed for each species (Table 2). Most of the species identifications were straightforward, but a few require some elaboration. The most important of these is Callinectes sapidus. Megalopae of the genus Callinectes may be differentiated from the genus Portunus by the presence in Portunus of a carpal spine on the first pereopod and a ventral coxal spine on the second pereopod (Bookhout and Costlow 1974). The technique of Smyth (1980), using differences in the profile of the abdominal somites, is also useful. Only two representatives of the genus Callinectes have ever been reported from the Chesapeake Bay and adjacent waters, namely C. sapidus and C. similis (Wass 1972, Williams 1974). Unfortunately, C. sapidus and C. similis megalopae cannot be differentiated practically in field caught samples (Bookhout and Costlow 1977). However, C. sapidus reaches the greatest concentration of its entire range in the Chesapeake Bay, where the annual catch of blue crabs approximates the rest of the United States catch for this genus (Van Engel 1958 and Thompson 1981). Gravid

<u>CLASSIFICATION</u>	<u>DESCRIPTION</u>
Portunidae	
<u>Callinectes</u> <u>sapidus</u>	Costlow and Bookhout 1959
<u>Portunus</u> sp.	Costlow and Bookhout 1974
Cancridae	
<u>Cancer</u> <u>irroratus</u>	Sastry 1977
Majidae	
<u>Libinia</u> spp. ( <u>emarginata</u> )	Johns and Lang 1977
Xanthidae	
<u>Hexapanopeus</u> <u>angustifrons</u>	Costlow and Bookhout 1966
<u>Neopanope</u> <u>sayi</u>	Chamberlain 1957, McMahan 1967
<u>Panopeus</u> <u>herbstii</u>	Costlow and Bookhout 1961
<u>Rhithropanopeus</u> <u>harrisii</u>	Connolly 1925, Hood 1962, Chamberlain 1962
Pinnotheridae	
<u>Pinnixa</u> sp.	Hyman 1924
<u>Pinnotheres</u> <u>ostreum</u>	Sandoz and Hopkins 1947
Ocypodae	
<u>Uca</u> spp.	Hyman 1920

Table 2. Brachyurans selected for this study with published descriptions of larvae.

Callinectes sapidus females migrate from the extreme reaches of the Chesapeake Bay to concentrate at the bay mouth, where their larval hatch and congregate at the surface (Churchill 1919, Van Engel 1958, Provenzano et al. in press). On the other hand, C. similis is relatively uncommon in this area (Wass 1972). Williams (1974) reports that the northern limit of the range of C. similis is the Delaware Bay, where only juveniles of this species are found. Hence, the overwhelming majority of Callinectes larvae in the Chesapeake Bay and adjacent waters are C. sapidus. All Callinectes megalopae were designated as C. sapidus for the purposes of this study.

A similar situation exists for Libinia, where the megalopae of the only Chesapeake Bay species, L. dubia and L. emarginata, are indistinguishable (Johns and Lang 1977). Again one species predominates, L. emarginata, but not as overwhelmingly as in the case of C. sapidus (Wass 1972). Thus, these megalopae were classified only as Libinia spp.

The genus Uca has three representatives in the Chesapeake Bay all of which have indistinguishable megalopae: U. pugilator, U. pugnax and U. minax (Hyman 1920). These megalopae were also classified only to genus.

The megalopal stage of one of the representatives of the genus Pinnixa was also commonly caught, but could not be positively identified. The early zoeae of three



representatives of this genus have been described and captured in the Chesapeake Bay plankton: P. chaetoptera, P. cylindrica and P. sayana (Sandifer 1972). Of these zoeae P. chaetoptera were common, P. sayana were less common and P. cylindrica were rare (Sandifer 1972).

Published descriptions of the larvae are sketchy. The last zoea of P. sayana is reported to molt directly to the crab stage, bypassing the megalopa stage (Hyman 1924). P. chaetoptera is reported to have a megalopal stage; however, no description or figure is given (Hyman 1924). P. cylindrica remains undescribed. All attempts in the present study to capture gravid females or live megalopae for the purposes of rearing the larvae to the crab stages failed. Based on the relative abundance of the zoeae and the reported lack of a megalopa in P. sayana, the Pinnixa megalopae reported herein are probably P. chaetoptera; however, these megalopae were classified only to genus.

The Kolmogorov-Smirnov two sample test was used to determine the significance of differences in megalopal distributions (Siegel 1956). To apply the test, a cumulative frequency distribution was constructed for each sample set. The test focuses on the largest of the differences (D) in the intervals of the step function. The method for determining the significance of D depends on the size of the sample sets (N), which was the number of field samples which contained the desired megalopa. If

N of each of the sample sets was equal or the minimum N was above 40, tables were consulted for the critical values of D (Siegel 1956). If the minimum sample sizes were both less than 40 and unequal, D was approximated by the chi square distribution as calculated by the formula:

$$x^2 = 4D^2 \left[ \frac{(N1)(N2)}{(N1 + N2)} \right] \quad \begin{array}{l} \text{where, } N1 \text{ and } N2 \\ \text{are the sizes of} \\ \text{sample sets 1} \\ \text{and 2} \end{array}$$

Reference to a table of critical values of chi square, with two degrees of freedom, revealed the probability associated with the calculated value (Siegel 1956).

It is hypothesized that the horizontal distributions of estuarine larvae should be narrow for larvae originating from parents in the middle and upper reaches of the estuary as compared to those spawned from species common to the lower estuary (Carriker 1967, Williams 1971, Sandifer 1975). In order to test this hypothesis, the mixing effects of the physical circulation must be removed, since mixing increases towards the mouth of the estuary. To that end, the mean salinity weighted by abundance was calculated according to the general equation for weighted means (Sokal and Rohlf 1969).

$$\bar{S}_a = \frac{\sum S_i \cdot A_i}{\sum A_i} \quad \begin{array}{l} \text{where, } S \text{ is salinity and} \\ A \text{ is abundance} \end{array}$$

Standard deviations (SD) were then calculated for these weighted values according to the following formula.

$$(SD)^2 = \frac{\sum (\bar{S}_a - S_i A_i)}{(\sum A_i) - 1}$$

## Results

The local distribution of the adults of the brachyuran species used in this study is adapted from Wass (1972), Ryan (1956) and Williams (1965) (Table 3). Based on this information, the typical habitats of these species will be classified as follows. Portunus, Cancer and Libinia are referenced as shelf species, although Libinia is often found in the lower Chesapeake Bay. All other species are classified as estuarine species.

Table 3 also indicates the percent catch of each species of megalopa captured within the estuary. Ninety-one percent or more of the megalopae of shelf species were captured outside the bay, even though these species were often collected at stations within a few kilometers of the bay mouth. This was true even for Libinia, which as an adult is common in the lower Chesapeake Bay. Of the estuarine species, Callinectes, Uca and Pinnixa were most abundant at stations outside of the estuary, which indicates the larvae of these species were not retained in the estuary. Of the Callinectes megalopae within the bay, only 2.2% of the total catch were found west of the Chesapeake Bay Bridge Tunnel (Stations 1-8). Conversely, Uca and Pinnixa had much higher percentages of megalopal catch

Table 3. The species used in this study, their adult habitat as reported in the literature (see text), and the percent of the total catch of megalopae found within the Chesapeake Bay. x = abundant, oc = occasional

	ADULT HABITAT				MEGALOPA
	upper	estuary	middle	lower shelf	%TOTAL
					IN ESTUARY
<b>Portunidae</b>					
<u>Callinectes sapidus</u>	x	x	x	oc	17
<u>Portunus</u> sp.			oc	x	2
<b>Cancridae</b>					
<u>Cancer irroratus</u>			oc	x	6
<b>Majidae</b>					
<u>Libinia</u> spp.( <u>emarginata</u> )			x	x	9
<b>Xanthidae</b>					
<u>Hexapanopeus angustifrons</u>		x	x	oc	75
<u>Neopanope sayi</u>		x	x		97
<u>Panopeus herbstii</u>		x	x		92
<u>Rhithropanopeus harrisi</u>	x	x			100
<b>Pinnotheridae</b>					
<u>Pinnixa</u> sp.		x	oc		40
<u>Pinnotheres ostreum</u>		x	x		97
<b>Ocypodidae</b>					
<u>Uca</u> spp.	x	x	x		42

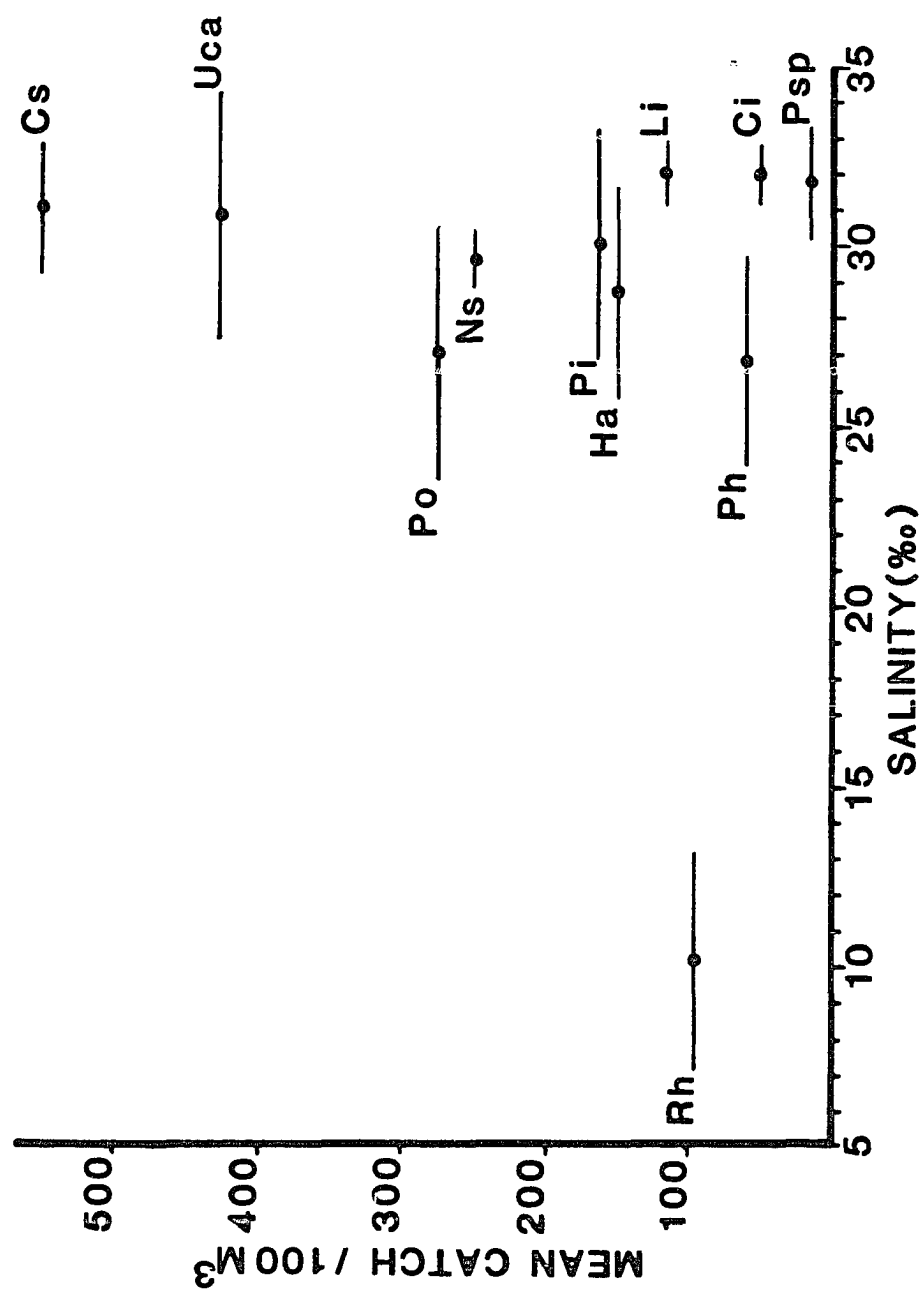
within the bay with 42% and 40%, respectively. With the exception of Hexapanopeus, at least 92% of the megalopae of the remaining estuarine species were retained in the estuary. Seventy-five percent of the Hexapanopeus megalopae were retained, but the adults of this species, while most common in the lower estuary, were also found on the inner shelf adjacent to the Chesapeake Bay. Neopanope megalopae reached peak concentrations at stations 9 and 10, yet only 3% of these megalopae were captured outside of the estuary. This genus also had the most restricted distribution of all estuarine species, even though it is most abundant in the bay mouth.

Based on the adult classification and the percent retention of the megalopae (Table 3), the species may be divided among three apparent recruitment strategies. First, the shelf species of this study are retained on the shelf, with respect to the estuary. Secondly, the megalopae of most estuarine species are overwhelmingly retained within the estuary. Thirdly, some estuarine megalopae, Callinectes, Uca and Pinnixa, are not retained and, in fact, are most abundant on the inner shelf.

Figure 2 shows the weighted mean salinity and standard deviations of the megalopal distributions for each of the selected species (see methods). The shelf species have markedly more narrow salinity weighted distributions than the estuarine brachyurans. Likewise, the shelf

Figure 2. Mean abundance versus abundance weighted mean salinity of the species used in this study. Range bars represent  $\pm 1$  S.D. Cs = Callinectes sapidus, Po = Pinnotheres ostreum, Ns = Neopanope sayi, Pi = Pinnixa sp., Ha = Hexapanopeus angustifrons, Li = Libinia spp., Ph = Panopeus herbstii, Ci = Cancer irroratus, Psp = Portunus sp., Rh = Rhithropanopeus harrisii





species have higher mean salinities and lower abundances than the estuarine species.

The megalopae of the non-retained estuarine species, which are most abundant on the shelf, are characterized by wide distributions, high mean abundances and high mean salinity, relative to the other species (Figure 2). When ranked in order of mean abundance Callinectes, Uca and Pinnixa ranked first, second, and fifth, respectively.

The megalopal distributions of the related estuarine species are characterized by low mean salinities and mean abundances intermediate to shelf species and non-retained estuarine species. These estuarine species, with the exception of Neopanope, have quite similar standard deviations. Thus, no evidence of decreased dispersal is found for megalopae originating from parents in middle and upper reaches of the estuary as compared to those spawned from species common to the lower estuary. On the contrary, an estuarine species common in the Chesapeake Bay mouth, Neopanope sayi, exhibited the most restricted distribution of all estuarine species. Note that Hexapanopeus was the most abundant xanthid megalopa. The mean abundance presented for Neopanope reflects fewer catches, with larger numbers per catch, relative to the catch of Hexapanopeus (Figure 2).

Figure 2 suggests the distribution of the three previously mentioned recruitment strategies physically

overlap, yet Table 3 indicates the three strategies are quite distinct. The reason for this dichotomy is illustrated by the following graphs of the megalopal distributions relative to the pycnocline and depth.

#### Retained Shelf Megalopae

The shelf species with one exception were found high in the water column. Portunus megalopae were distributed in the surface layers, with 31% in the neuston and 69% at 3 m depth (Figure 3a,b). If a pycnocline was present, all megalopae were found either above or within the pycnocline (Figure 3a). Cancer megalopae were found almost exclusively above the pycnocline when present, even though the distribution of the Cancer megalopae versus depth indicates 40% of the total megalopae were captured at 6 m (Figure 4a,b). The vertical distribution of Libinia differs from the other shelf species of this study (Figure 5a,b). Whereas both Portunus and Cancer were found in the surface waters, Libinia was found below the pycnocline (77%) and in the epibenthos (81%). Libinia also differs from the other shelf species because the adults are often found in the lower estuary.

Figure 3a. Percent total catch of Portunus sp. versus depth, where N = neuston, 3M = 3 meters, 6M = 6 meters, and E = epibenthos.

Figure 3b. Percent total catch of Portunus sp. relative to the pycnocline.

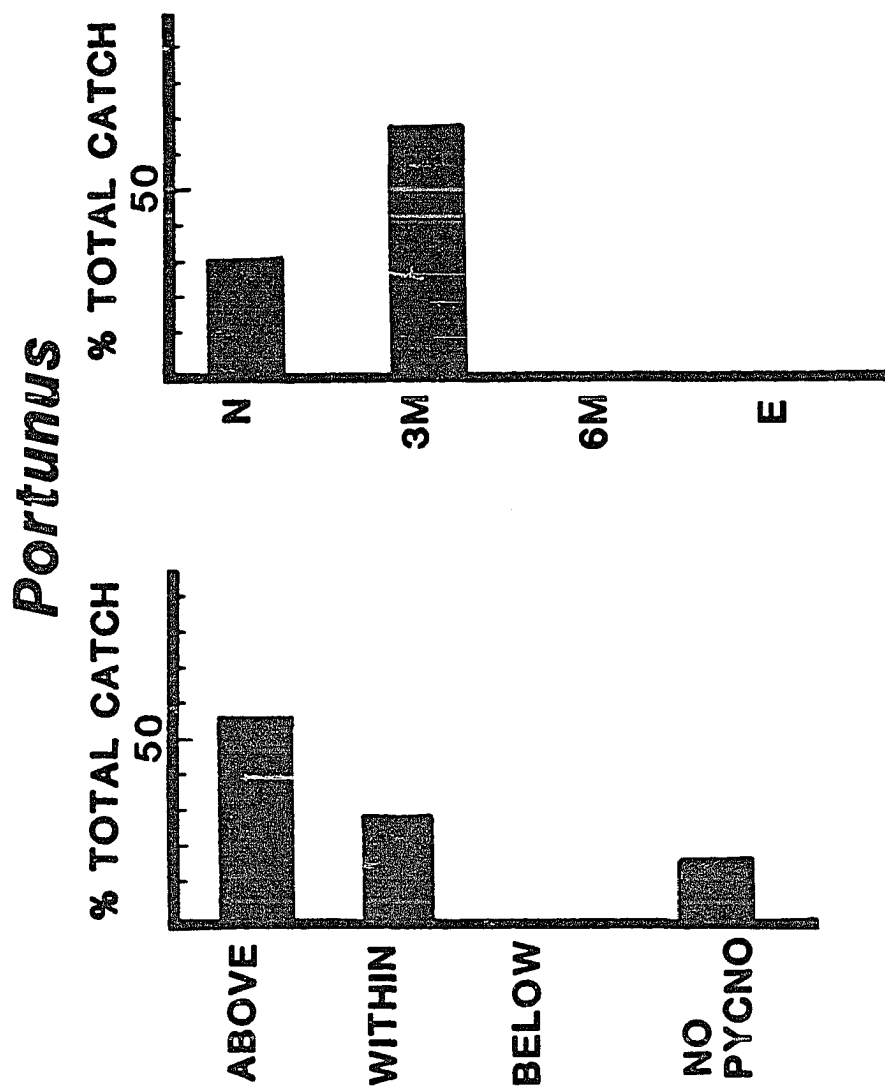


Figure 4a. Percent total catch of Cancer irroratus versus depth, where N = neuston, 3M = 3 meters, 6M = 6 meters, and E = epibenthos.

Figure 4b. Percent total catch of Cancer irroratus relative to the pycnocline.

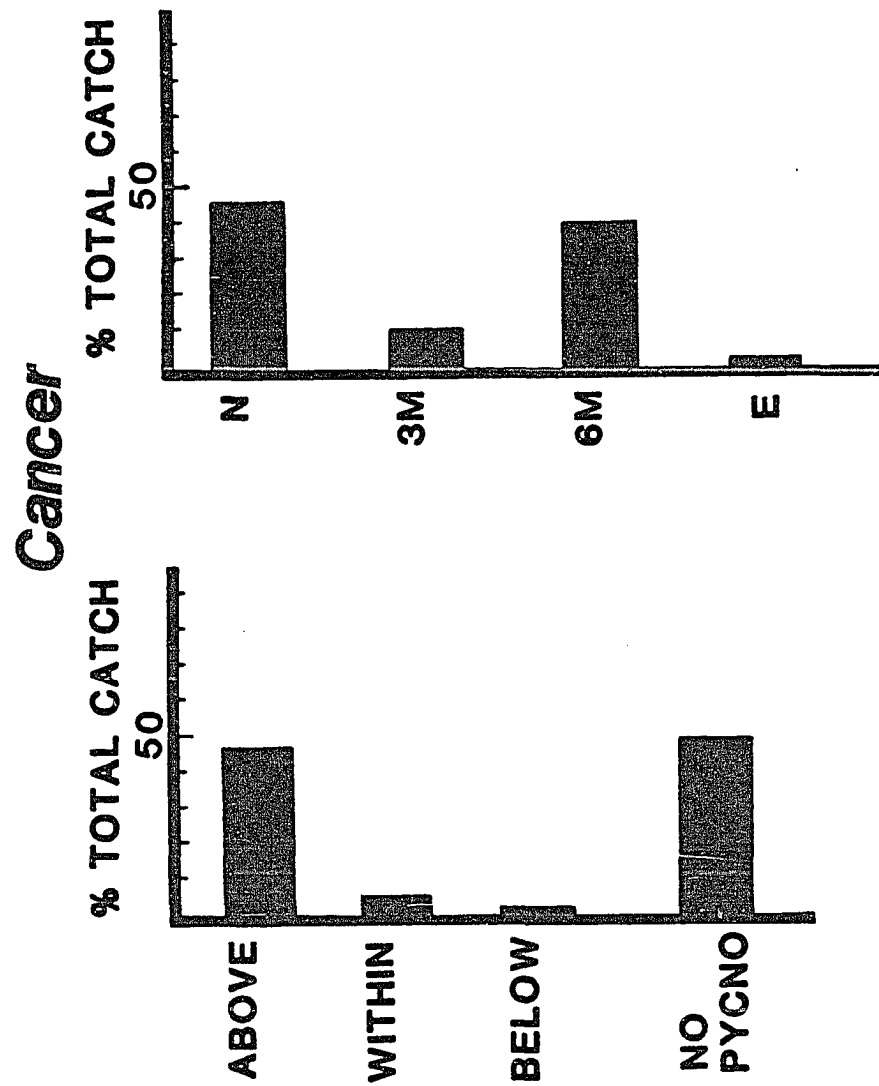
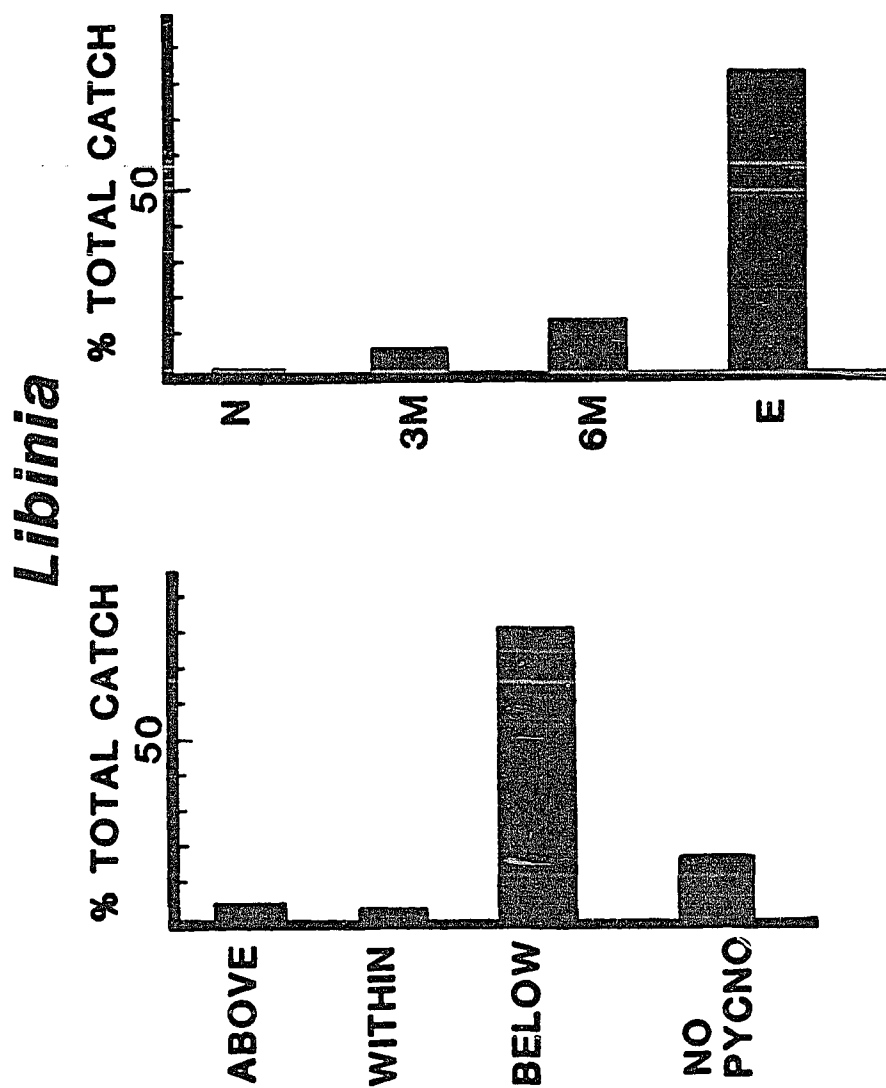


Figure 5a. Percent total catch of Libinia spp. versus depth, where N = neuston, 3M = 3 meters, 6M = 6 meters, and E = epibenthos.

Figure 5b. Percent total catch of Libinia spp. relative to the pycnocline.





### Expelled Estuarine Megalopae

Also found on the shelf were the non-retained estuarine megalopae. The overwhelming majority of Callinectes megalopae were caught in the neuston (74%) and above the pycnocline (67%) (Figure 6a,b). Conversely, Uca were netted below the pycnocline (64%) and almost exclusively in the epibenthos (93%) (Figure 7a,b). Pinnixa megalopae were also captured below the pycnocline (56%) and in the epibenthos (94%) (Figure 8a,b).

### Retained Estuarine Megalopae

The retained estuarine megalopae were found below the pycnocline and, with the exception of Rhithropanopeus, near bottom. Sixty-six percent of the Pinnotheres megalopae were collected in the epibenthos (Figure 9a,b), whereas the megalopae of Hexapanopeus, Panopeus and Neopanope were collected almost exclusively in the epibenthos (Figures 10a,b; 11a,b; 12a,b). Rhithropanopeus megalopae were most abundant at 3 m, and most of the megalopae were collected under conditions of a well-mixed water column (Figure 13a,b).

Figure 6a. Percent total catch of Callinectes sapidus versus depth, where N = neuston, 3M = 3 meters, 6M = 6 meters, and E = epibenthos.

Figure 6b. Percent total catch of Callinectes sapidus relative to the pycnocline.

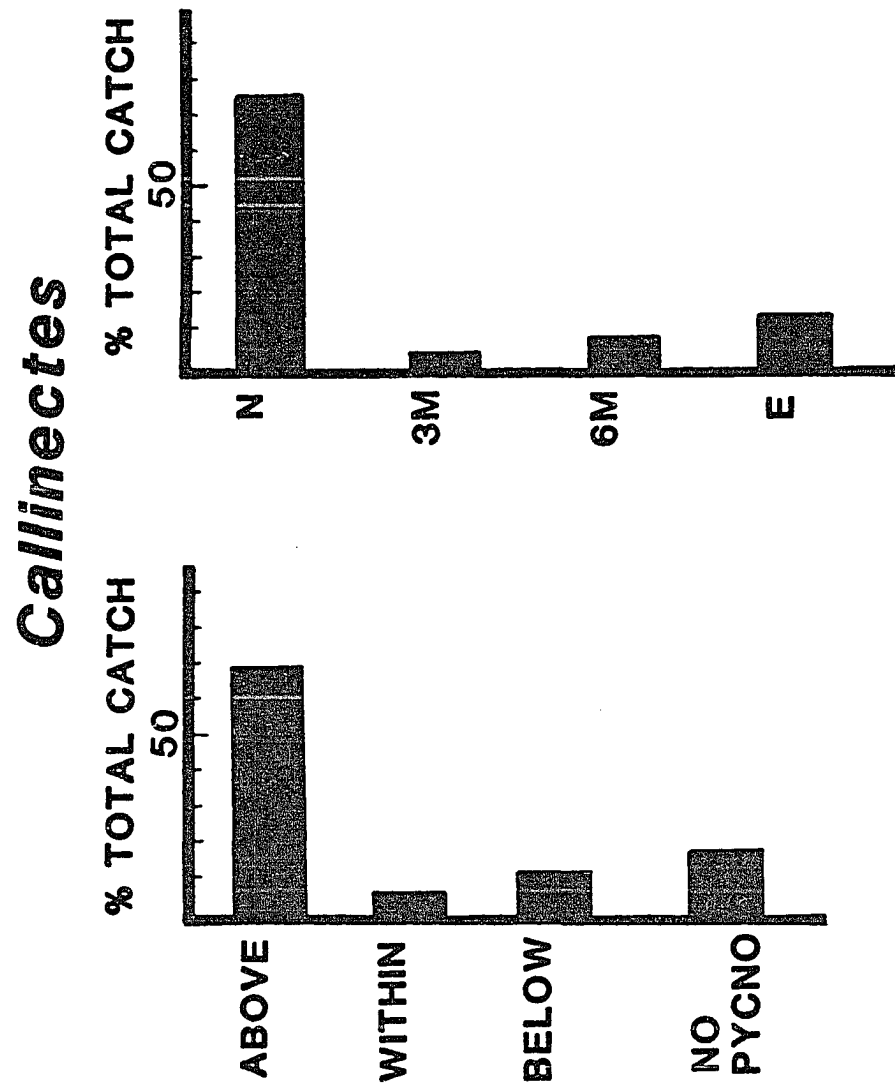


Figure 7a. Percent total catch of Uca spp. versus depth  
where N = neuston, 3M = 3 meters, 6M = 6 meters, and  
E = epibenthos.

Figure 7b. Percent total catch of Uca spp. relative to  
the pycnocline.

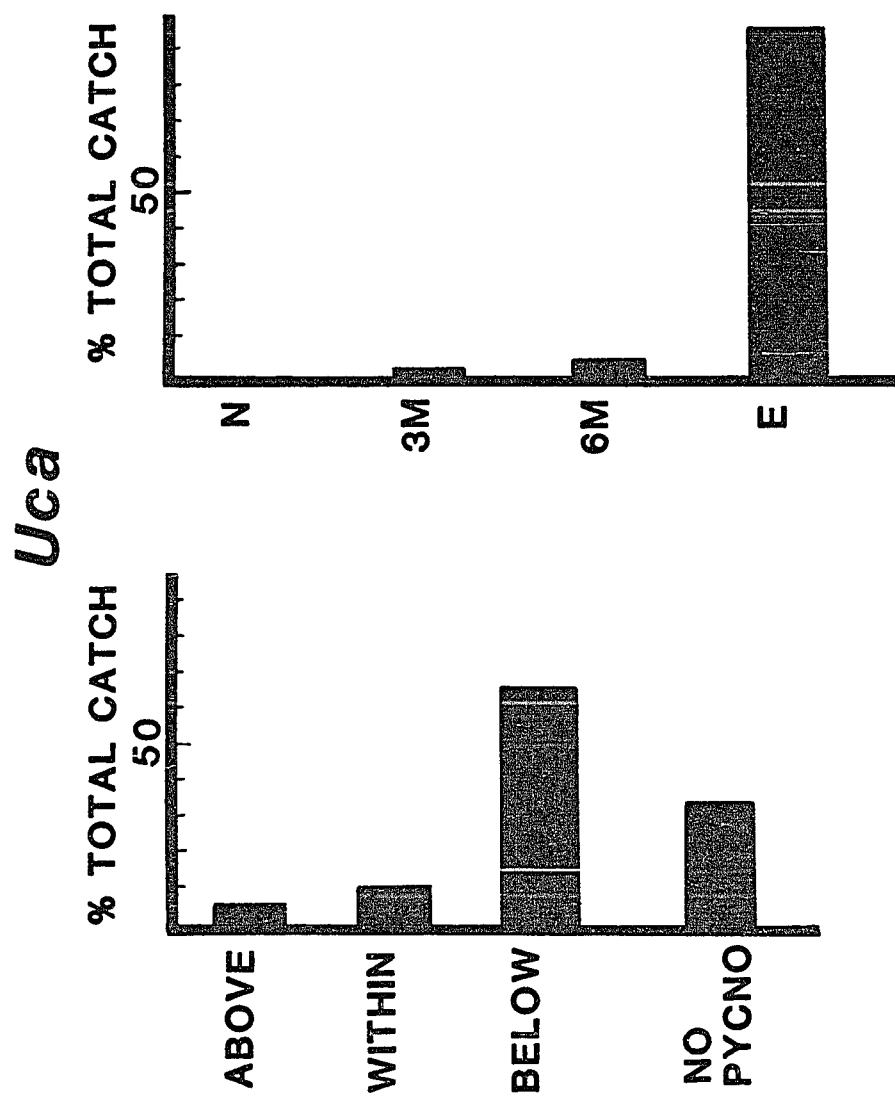


Figure 8a. Percent total catch of Pinnixa sp. versus depth, where N = neuston, 3M = 3 meters, 6M = 6 meters, and E = epibenthos.

Figure 8b. Percent total catch of Pinnixa sp. relative to the pycnocline.

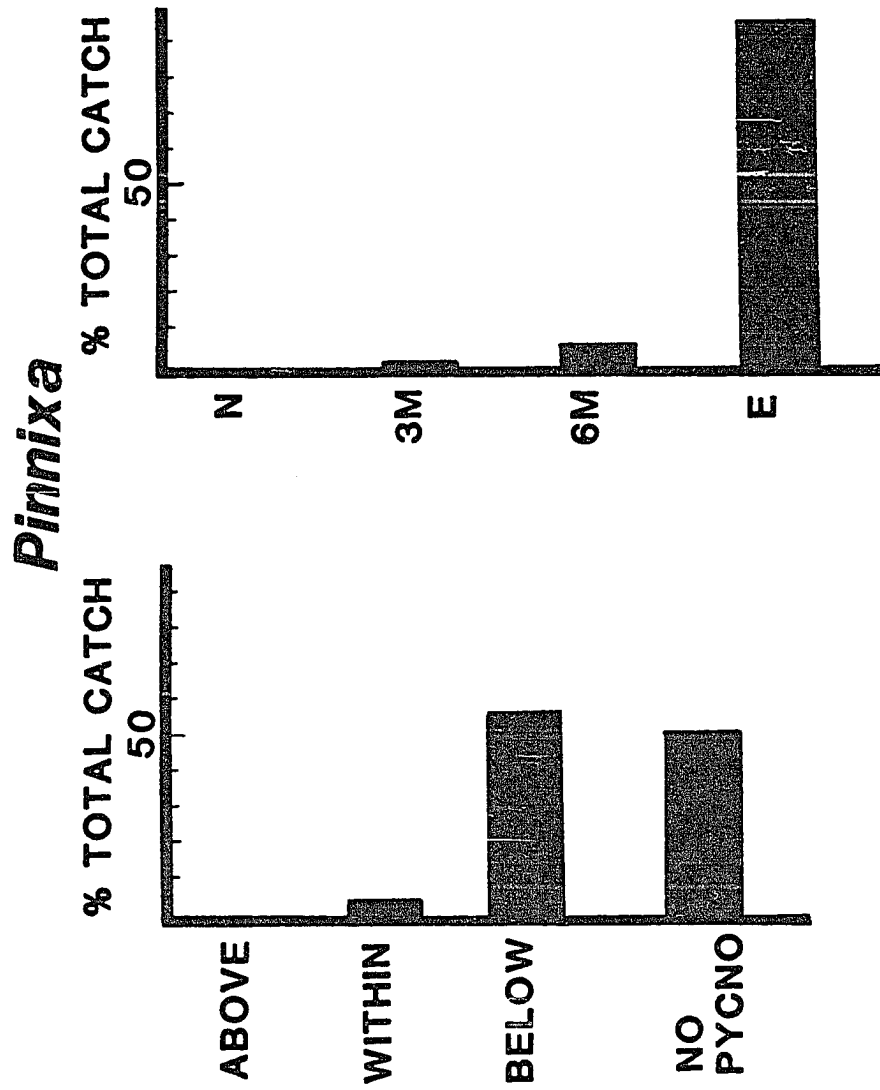




Figure 9a. Percent total catch of Pinnotheres ostreum  
versus depth, where N = neuston, 3M = 3 meters,  
6M = 6 meters, and E = epibenthos.

Figure 9b. Percent total catch of Pinnotheres ostreum  
relative to the pycnocline.

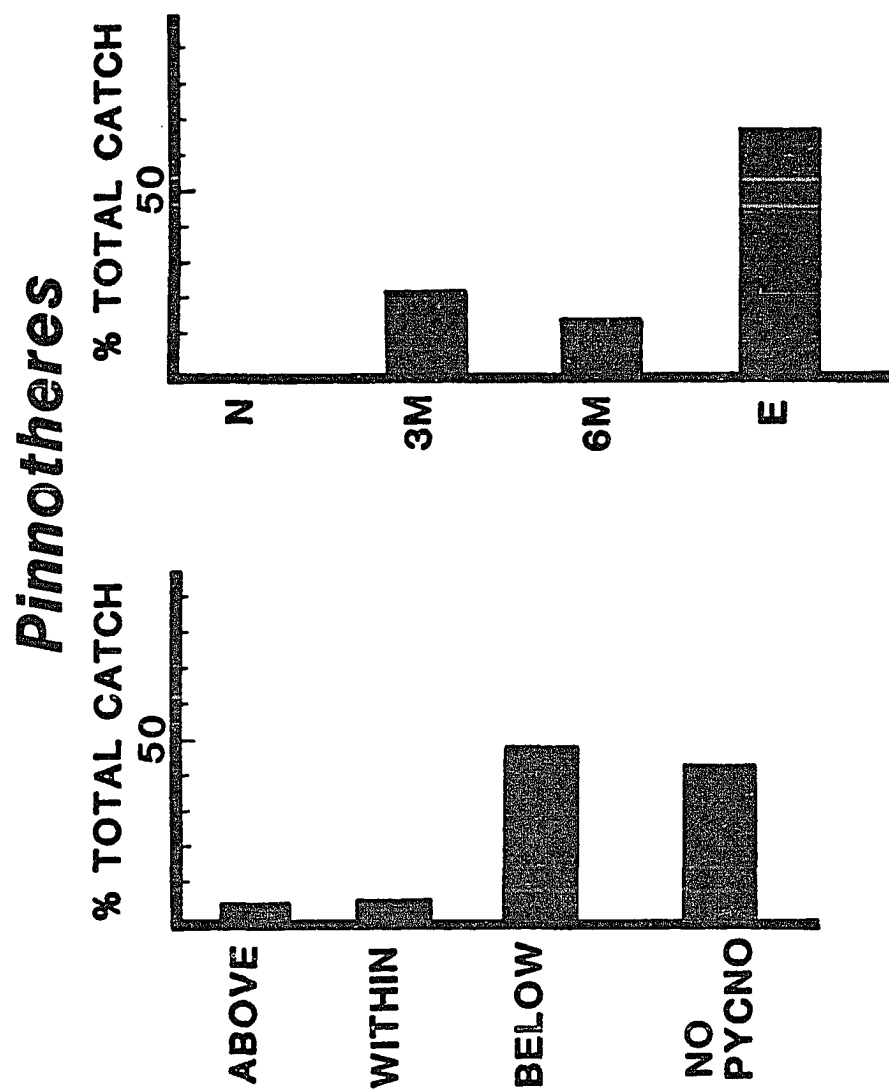


Figure 10a. Percent total catch of Hexapanopeus angustifrons versus depth, where N = neuston, 3M = 3 meters, 6M = 6 meters, and E = epibenthos.

Figure 10b. Percent total catch of Hexapanopeus angustifrons relative to the pycnocline.

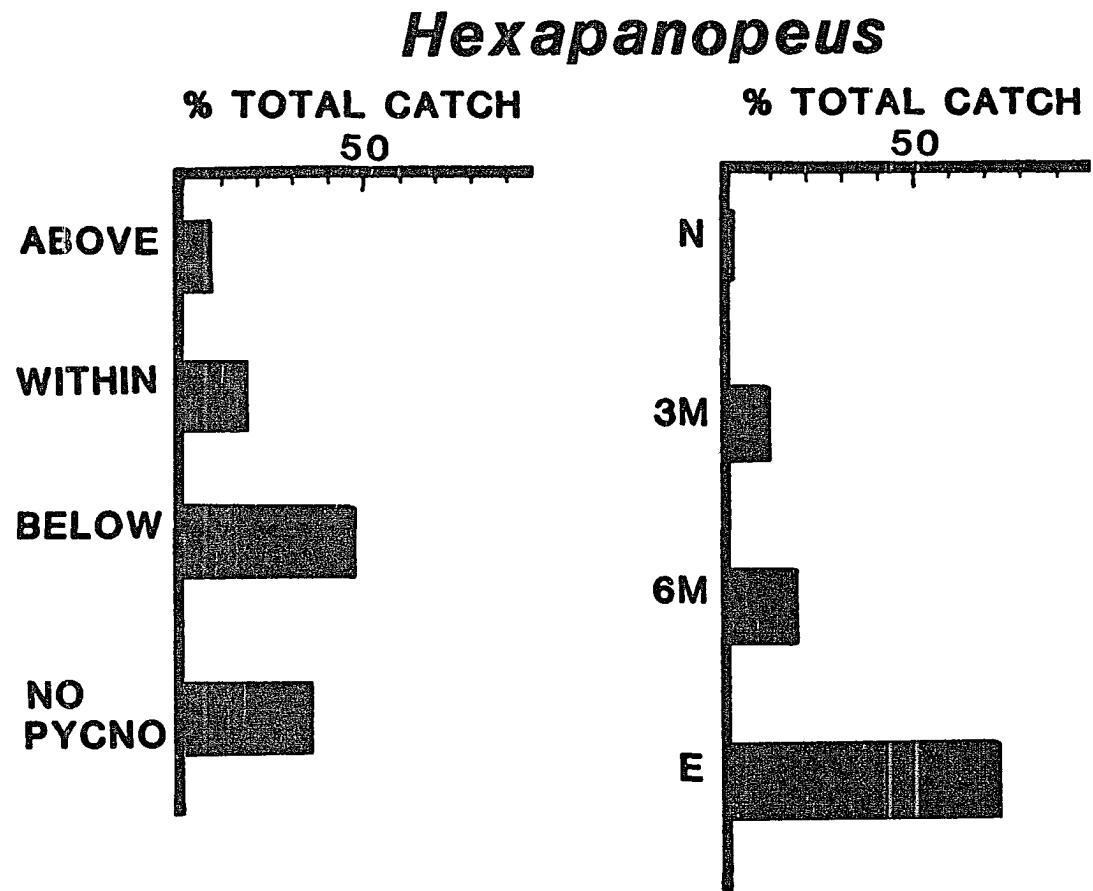


Figure 11a. Percent total catch of Panopeus herbstii  
versus depth, where N = neuston, 3M = 3 meters,  
6M = 6 meters, and E = epibenthos.

Figure 11b. Percent total catch of Panopeus herbstii  
relative to the pycnocline.

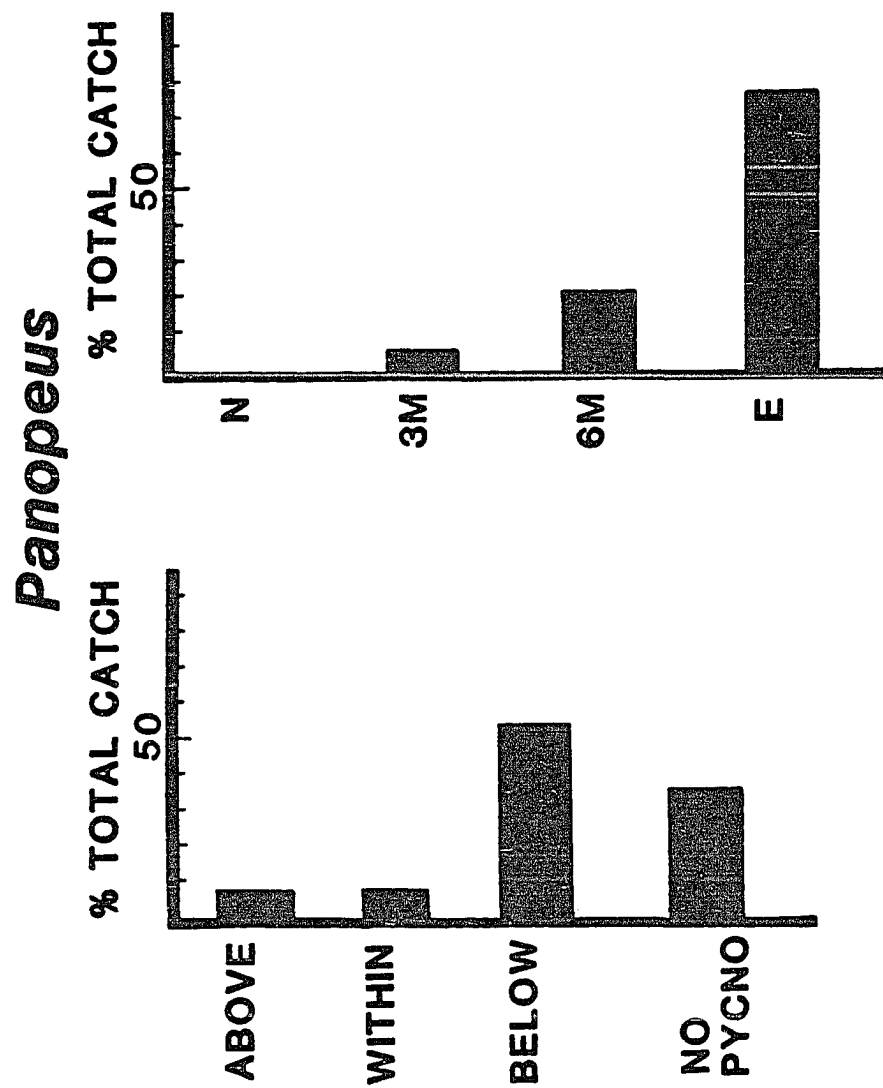


Figure 12a. Percent total catch of Neopanope sayi versus depth, where N = neuston, 3M = 3 meters, 6M = 6 meters, and E = epibenthos.

Figure 12b. Percent total catch of Neopanope sayi relative to the pycnocline.

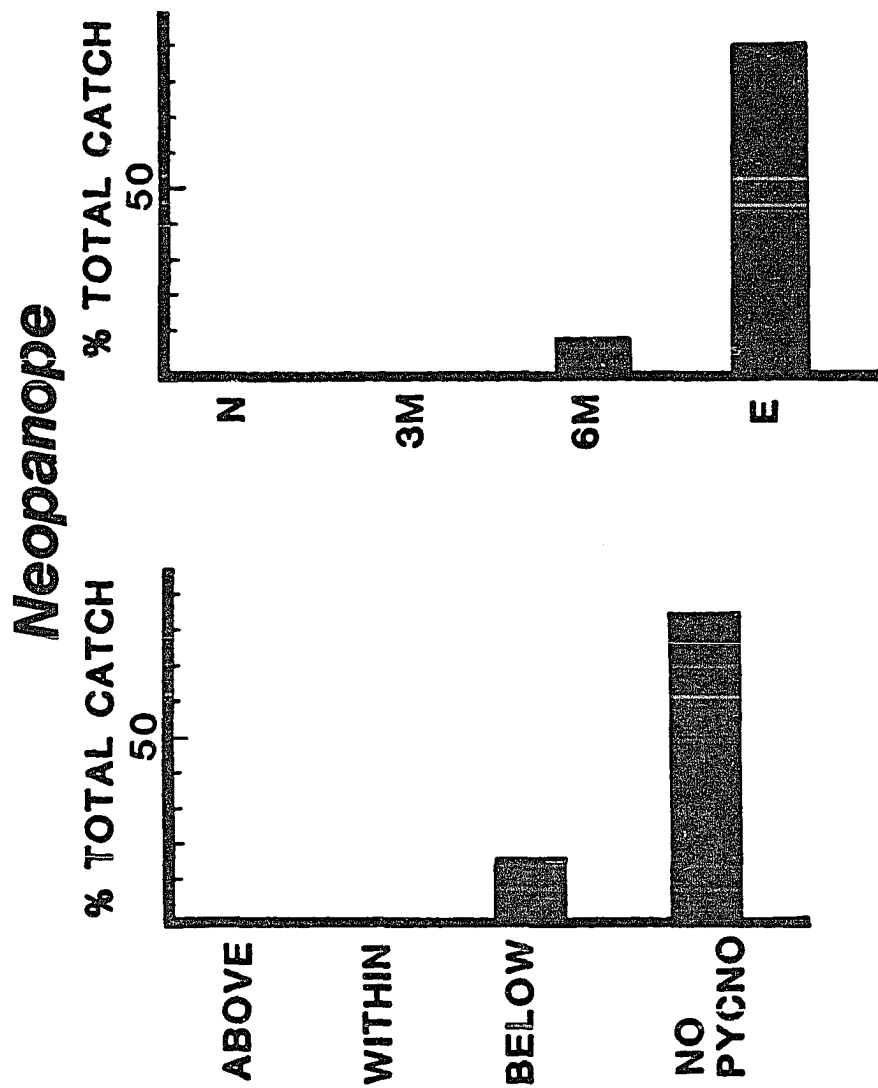
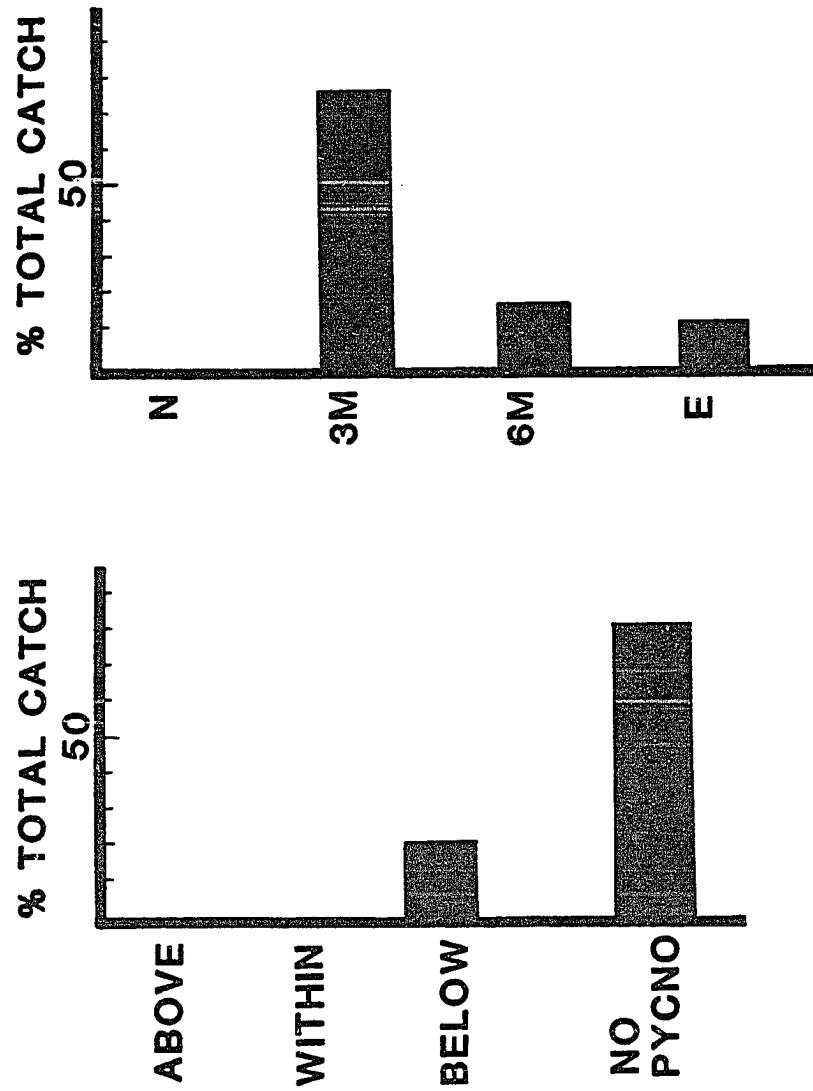




Figure 13a. Percent total catch of Rhithropanopeus harrisii versus depth, where N = neuston, 3M = 3 meters, 6M = 6 meters, and E = epibenthos.

Figure 13b. Percent total catch of Rhithropanopeus harrisii relative to the pycnocline.

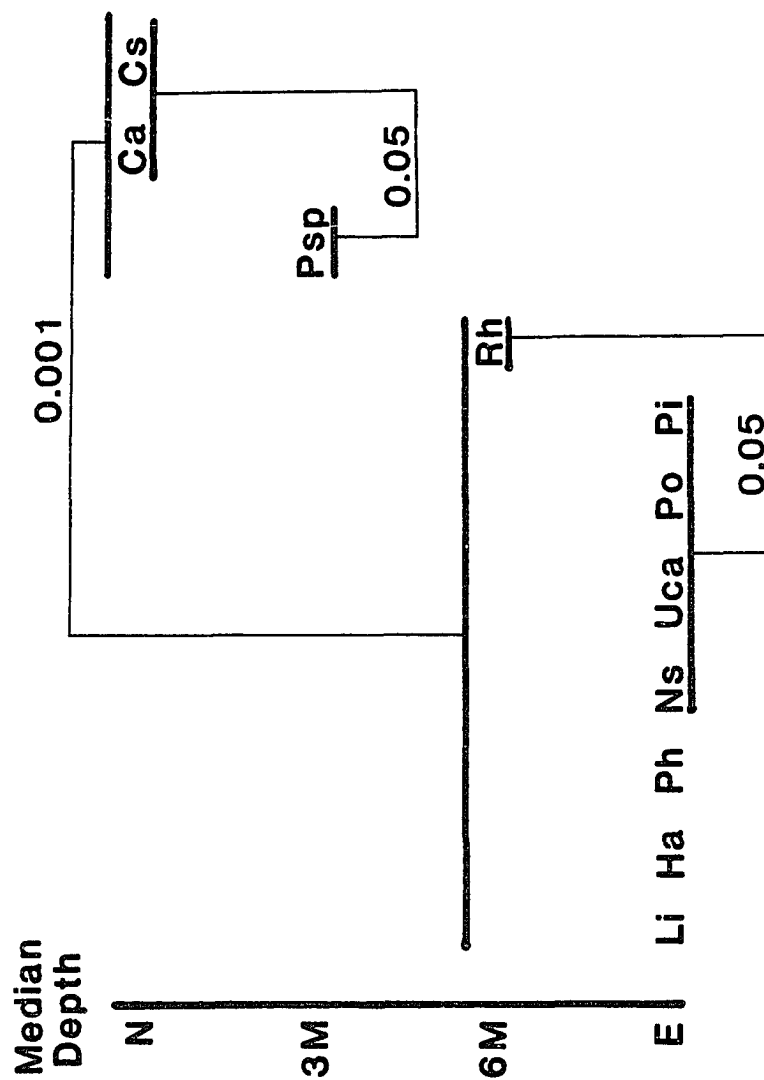
## *Rhithropanopeus*



To statistically evaluate differences in vertical distribution between species when a pycnocline was present, the Kolmogorov-Smirnov two sample test was applied. Callinectes, Cancer and Portunus were distributed very significantly ( $\alpha = 0.001$ ) higher in the water column than all other species (Figure 14). Of those species with megalopae abundant in the bottom waters, Rhithropanopeus was distributed significantly ( $\alpha = 0.05$ ) shallower than Neopanope, Uca and Pinnixa (Figure 14). Hence, megalopae which were previously divided among shelf species, retained estuarine species and non-retained estuarine species, may be further subdivided according to their position in a stratified water column.

When the megalopal vertical distribution of each species is compared between conditions with and without a pycnocline, a number of species are found to have significant shifts in vertical distribution. Callinectes and Cancer are both found very significantly ( $\alpha = 0.001$ ) deeper under conditions of no pycnocline (Table 4). Conversely, Rhithropanopeus, Pinnotheres and Libinia were found to be distributed significantly shallower when a pycnocline was not present (Table 4). All other species were found to have an insignificant change in depth.

Figure 14. The median depth of the studied species, when a pycnocline was measured in the water column. The numbers on the fine lines connecting groups indicate the significance (alpha value) of the differences in vertical distribution. Cs = Callinectes sapidus, Po = Pinnotheres ostreum, Ns = Neopanope sayi, Pi = Pinnixa sp., Ha = Hexapanopeus angustifrons, Li = Libinia spp., Ph = Panopeus herbstii, Ci = Cancer irroratus, Psp = Portunus sp., Rh = Rhithropanopeus harrisii



Species		Percent Catch				Sig.	Shift in median Z
		N	3M	6M	E		
<u>C. sapidus</u>	P	78.1	3.8	6.2	11.9	****	down
	NP	49.5	11.3	13.7	25.5		
<u>Portunus sp.</u>	P	18.5	81.5	0	0	NSC	
	NP	100	0	0	0		
<u>Cancer irroratus</u>	P	76.4	8.5	12.3	2.8	****	down
	NP	4.3	16.6	76.7	2.5		
<u>Libinia spp.</u>	P	0.1	4.2	3.6	92.1	****	up
	NP	5.1	8.6	62.2	24.1		
<u>H. angustifrons</u>	P	0	13.1	17.5	69.0	NSC	
	NP	0	1.4	18.7	79.8		
<u>Neopanope sayi</u>	P	0	1.4	0	98.6	NSC	
	NP	0	0	8.9	91.1		
<u>Panopeus herbstii</u>	P	0	3.7	27.0	69.3	NSC	
	NP	0	6.1	15.1	78.8		
<u>R. harrisii</u>	P	0	2.4	64.3	33.3	**	up
	NP	0	93.0	2.5	4.5		
<u>Pinnixa sp.</u>	P	0.4	0.5	5.6	93.5	NSC	
	NP	0	1.7	3.9	94.3		
<u>P. ostreum</u>	P	0	4.2	9.6	86.2	*	up
	NP	0	42.2	13.3	44.5		
<u>Uca spp.</u>	P	0.4	2.9	2.4	94.3	NSC	
	NP	0	0.5	5.8	93.7		

Table 4. Percentages of megalopae occurring at each of the sampled depths, in water columns with (P) and without (NP) pycnoclines. The levels of significance (alpha value) are represented as, 0.05 = \*, 0.01 = \*\*, 0.005 = \*\*\*, 0.001 = \*\*\*\*, NSC = no significant change. The direction of the vertical shift in distribution under conditions of no pycnocline is indicated as up or down.

### Discussion

The present study offers a significant improvement in the study of several aspects of larval dispersal patterns. This study intensively sampled the frequently neglected megalopal stage, which is more apropos of the larval dispersal pattern than the early zoeal stages. The extremes of the water column were sampled as well as two additional mid-depth levels. This study is based on 713 collections of megalopae in large volume samples which were intensively collected from estuarine and shelf conditions over the peak of the larval season.

The megalopal stage of brachyuran development has been sampled inadequately or not sampled at all, in most reported work concerning larval distributions. It is often easy in retrospect to criticize some aspect of a field study, particularly a study of meroplankton, since fiscal restraints often force the implementation of a compromised sampling plan. With this in mind, the following are suggestions for improvements in the catch of brachyuran megalopae.

Cronin (1979) has discussed the need in all field studies of larvae for a vertical sampling scheme which is more intensive than just surface and bottom tows. The Rhithropanopeus harrisii larvae of his study were most

abundant at mid-depth; hence, near surface and bottom samples do not represent the actual vertical distribution. Furthermore, the results of the present study as well as others (Smyth 1980, McConaughy et al. 1981 and Provenzano et al. in press), demonstrate that for some meroplankton, near surface and near bottom samples are an inadequate representation of even the extremes of the water column, because many larval forms concentrate in the neuston and epibenthos.

In most reports of brachyuran larval distributions the sample volume is typically an order of magnitude too small to capture significant numbers of megalopae, yet the megalopa is widely regarded as the brachyuran larval stage most influential in recruitment (Knudsen 1960; Costlow 1967; Tagatz 1968; More 1969; Williams 1971, 1974; Sandifer 1975; Smyth 1980; Sulkin et al. 1980). The average megalopal concentration for all the species of this study was circa 2 megalopae per cubic meter; thus, to capture an average of 50 megalopae per sample, the sample volume should be at least 25 cu m. Of course, the less common species would require an even greater sample volume. In published studies which used samples of only a few cubic meters the megalopal catch is negligible. In such cases, the larval distributions are based wholly or at least predominantly on the distribution of the early zoeal stages. Such studies, clearly, do not illustrate the complete larval dispersal pattern, but the distribution of



the gravid adults (e.g. Sandifer 1975). The limitations of distribution studies based solely on zoeae, small sample volumes, or surface and bottom tows must be kept in mind during the following discussion.

#### The Importance of Neuston Samples

The present study, as well as other recent reports, has shown the importance of the neuston layer to larval forms, particularly larval decapods (Grant 1977, Smyth 1980, Provenzano et al. in press). Zoeae of Callinectes are so common in the neuston, that failure to sample this layer may underestimate the total abundance by 90% (Provenzano et al. in press). Furthermore, the megalopa is typically regarded to frequent the bottom waters. However, this study reports the megalopae of Callinectes and Cancer reach maximum abundance in the neuston, while the megalopae of Portunus and other forms are frequently abundant in that layer. Smyth (1980) reported similar results for these genera as well Dromidia and Ocypode.

#### The Importance of the Pycnocline

If a pycnocline was present, the megalopae were typically distributed either above or below the pycnocline. Strong evidence of a megalopal concentration at the pycnocline was not observed, even though at least one of the mid-water tows was usually within the layer of the pycnocline. Sulkin and Van Heukelem (in press) presented evidence of larval concentration at a laboratory produced halocline, albeit their halocline gradients were much

sharper than any encountered in the field. The present study reports Callinectes, Cancer and Portunus remain above the pycnocline and their horizontal distribution reflects published surface drifts in the area. All other species, in my study, reach peak abundance below the pycnocline and with the exception of Rhithropanopeus, were most abundant in the epibenthos. Likewise, their distributions reflect published bottom flows in the area. The importance of the pycnocline might seem incidental except for the fact that five of the eleven species of this study showed significantly different vertical distributions between stratified and homogeneous water columns. Those vertical shifts illustrate that brachyuran larvae may be distributed differently in stratified and well-mixed estuaries and larval distribution patterns are influenced by changes in the mixing regime. The questions remain as to whether these vertical changes are due to the consequences of physical forces (i.e. passive), behavioral responses (i.e. active) or a combination of the two. The answers surely depend on the swimming ability of the particular larval type. For example, barnacle cyprids may be passively distributed in the water column (de Wolf 1973, 1981), while strong swimmers such as brachyuran larvae might be vertically distributed according to active behavioral traits.

#### Retained Estuarine Larvae

Estuarine retention is measured in this study as the percentage of the larval population remaining in the

estuary at the end of larval development. When the majority of the megalopae of an estuarine species were captured within the estuary and peak zoeal abundance was reported to be in the estuary that species was considered "retained." The megalopae of five estuarine species were retained within the Chesapeake Bay. The lowest percentage retention recorded for any of these species was 75%, recorded for Hexapanopeus angustifrons. These retained megalopae are additionally characterized by vertical distributions deep in the water column. Except for Rhithropanopeus, retained estuarine megalopa were most abundant in the epibenthos.

Several authors have proposed that the horizontal distributions of retained estuarine larvae should be narrow for estuarine larval originating from parents in the middle and upper reaches of the estuary as compared to those spawned from species common to the lower estuary (Carriker 1967, Williams 1971, Sandifer 1975). The present evidence shows no decreased horizontal distribution for increasingly estuarine species. On the contrary, the most restricted horizontal distribution belongs to Neopanope sayi, which is most common in the bay mouth. The distribution of each of these retained forms will be discussed below.

#### Pinnotheres ostreum

Sandifer (1972) using near surface and bottom tows described the distribution of the early zoeal stages of this species, in almost the same geographic area as this

study, although he had only one station located seaward of the bay mouth. He found peak concentrations of first zoeae in the York River, whereas in this study peak megalopal concentrations occurred at the Chesapeake Bay mouth. This represents a difference and possible displacement during larval development of circa 32 km. Other investigators have found the zoeae of this species to be common in the middle to lower regions of the estuary (Pinschmidt 1963 and Tagatz 1968), or associated with the mouth of the estuary (Dudley and Judy 1971).

Rhithropanopeus harrisii

The megalopae of this species were most abundant in the Pamunkey River and upper York River, which coincides with reported peak concentrations of the zoeae for this area (Sandifer 1972). All other reports of the distribution of Rhithropanopeus larvae also indicate this species to be most common at the upper reaches of the estuary (Bousfield 1955, Pinschmidt 1963, Van Engel and Joseph 1968, Tagatz 1968, Williams 1971, Cronin 1979, Lambert and Epifanio in press), and vertically concentrated near the level of no net motion (Bousfield 1955, Cronin 1979).

Panopeus herbstii

Megalopae of this species were most abundant in the extreme lower bay and bay mouth. Sandifer (1972) found peak concentrations of the early stages of this species in the lower York River. Again this represents a possible 48 km displacement of the larvae between the earliest zoeal

stages and the megalopae. Dudley and Judy (1971) found Panopeus zoeae commonly and megalopae occasionally off Beaufort Inlet, while Pinschmidt (1963) found somewhat greater numbers of zoeae just inside the same inlet. Tagatz (1968) collected the largest numbers of zoeae in the lower St. Johns River.

Hexapanopeus angustifrons

Megalopae of this species reached peak abundance in the Chesapeake Bay mouth and were the most abundant xanthid of this study. Sandifer (1972) also reported the early zoeae of this species were the most abundant xanthid and reached peak abundance in the Chesapeake Bay mouth. Williams (1971) found the megalopae of this species in relatively high salinities near inlets in North Carolina.

Neopanope sayi

Abele (1972) reorganized the classification of Neopanope texana ssp. such that the subspecies N. texana texana and N. texana sayi became distinct species, with N. texana inhabiting the Gulf of Mexico and N. sayi inhabiting the U.S. east coast.

The megalopae of N. sayi were taken almost exclusively in the epibenthos and were narrowly distributed about the Chesapeake Bay mouth. Sandifer (1972) found a trend of increasing abundance of the late zoeae in bottom samples, while peak abundance of the zoeal stages occurred in his lower bay stations. This represents a possible displacement of circa 16 km between the peak zoeal concentration

reported in his study and the megalopal concentration reported here. Authors working in other estuaries have found peak concentrations of zoeae at other regions of the estuary. Hillman (1964) found the zoeae of this species to be most abundant in his upper and middle estuary stations in the Narraganset Bay, while Tagatz (1968) found the zoeae at stations in the lower St. Johns River.

#### Expelled Estuarine Larvae

Three of the species of this study are found in the estuary as adults, yet 60% or more of the megalopae of these species were captured outside of the estuary. Thus, the net result of the larval development was an expulsion of the majority of the larval population from the estuary. This cannot be dismissed as a maladaptation for two reasons. First, two of the three expelled species, Callinectes sapidus and Uca spp., are extremely successful species within the bay as adults. Second, published accounts, which are discussed later, indicate these two species possess behaviors which promote larval expulsion from the estuary. Although these species are undoubtedly recruited as late megalopae or juveniles, retention is an inappropriate term for this form of recruitment as this strategy differs markedly from that of the retained larvae of the previous section. The individual species and their strategies will be discussed below.

Callinectes sapidus

Studies which report significant distributions of Callinectes sapidus larvae within the Chesapeake Bay have not sampled the neuston of offshore stations. In this study only 17% of the total megalopae of this species were captured within the Chesapeake Bay, but only 2.2% of the total catch was taken west of the Chesapeake Bay Bridge-Tunnel, which at its most western point is only 8 km inside the bay mouth. The maximum megalopal catch occurred in the neuston 33 km seaward of the bay entrance. One offshore neuston sample collected 34,500 megalopa/100 cu m. Likewise, McConaughta et al. (1981) from the same cruise reported concentrations of Callinectes zoeae as high as 250,000 zoeae/100 cu m in the neuston. Each of these catches represents the largest reported field concentrations for this species. The peak abundance of the first zoea was found in the bay mouth (Station 21) (McConaughta et al. 1981), while in this study the megalopal peak abundance occurred offshore at station 16. This represents a seaward displacement of the larval population of at least 27 km.

Published reports for this species suggest several behaviors which promote offshore larval development. Churchill (1919) reported the migration of gravid females to the high salinity areas of the Chesapeake Bay mouth. Upon hatching in the estuary mouth, the first zoea swims towards the sea surface in laboratory studies (Sulkin

1975) and field studies report the greatest frequency of first zoeae in the neuston of the estuary mouth (McConaugha et al. 1981, Provenzano et al. in press), on outgoing tides (Tagatz 1968, Provenzano et al. in press). Subsequent stages are well-documented in offshore waters by this study as well others (Nichols and Keney 1963, Dudley and Judy 1971, McConaugha et al. 1981). Clearly, the larvae of Callinectes are flushed to offshore waters.

Although the megalopa is often suggested as the most likely stage of recruitment for this species (Tagatz 1968, More 1969, Williams 1971, Sandifer 1975 and Sulkin et al. 1980), the results of the present work suggest otherwise. Much of the evidence supporting the megalopa recruitment hypothesis is from reports of the megalopa and late stage zoeae frequenting bottom waters (Tagatz 1968, Sandifer 1973 and Goy 1976); however, none of these studies made extensive use of offshore samples or neuston samples. This study and others that have extensively sampled offshore, particularly those that have sampled the neuston, have found the zoeae and megalopae to be most abundant in surface waters (Smyth 1980, McConaugha et al. 1981, Provenzano et al. in press, Dittel and Epifanio in press). The evidence of this study which shows a megalopal vertical distribution in the surface waters, a capture of only 2.2% of the megalopae west of the bay mouth region and a megalopal peak abundance in offshore waters, suggest



the megalopa may be only facultatively reinvasive. In support of juvenile recruitment, Tagatz (1968) reported invasions of the juveniles of this species in the latter part of the spawning season. Juvenile recruitment would provide recruitment during low to average years, while average to high recruitment years would be encouraged by a wind driven flow of inner shelf surface waters, laden with megalopae, towards the bay. This wind driven flow towards the bay often occurs in late summer or autumn. The shift in surface flow on the inner shelf adjacent to the Chesapeake Bay has been discussed by several authors (Bumpus 1969, 1973; Boicourt 1973, 1981; Wang and Elliot 1978; Wang 1979). Also, a shift in vertical distribution probably occurs as the megalopa molts to the juvenile crab, but the *Callinectes megalopae* reported herein were found slightly deeper in conditions of a well-mixed water column, although the median depth was still above 3 m. During this study the water column was well-mixed most frequently in the late summer.

Uca spp.

Sandifer (1972) found the peak abundance of the early zoeae of this species in the lower Pamunkey River, but he noted that zoeal stages III to V were most abundant in the middle and lower reaches of the York River. This study found that megalopae of this species were most abundant 8 km seaward of the Chesapeake Bay (stations 12 and 19).

Although the shift in distribution is obviously considerable, it cannot be evaluated precisely, since this complex represents three different species, the adults of which occur in different regions of the estuary.

Other reports have shown the zoeae of this species to be abundant in various regions of the estuary or coastal waters. Pinschmidt (1963) found the zoeae to be most abundant in the upper reaches of the estuary, although he found larvae in much lower concentrations throughout the entire estuary. Tagatz (1968) found the zoeae of this species to be slightly more abundant in the lower estuary as compared to the upper reaches. Offshore sampling has shown the zoeal stages and occasionally the megalopal stage to be most abundant at the most inshore stations (Dudley and Judy 1971, Smyth 1980).

Published reports on this species have described behaviors which promote offshore larval development. Bergin (1981) published laboratory evidence of a hatching rhythm in Uca adults which indicates nocturnal high tides are favored hatching periods. Several authors report this cycle results in seaward transport of larvae on the semi-lunar spring ebb tide and ultimate export from the estuary (Christy and Stancyk in press, Lambert and Epifanio in press). The data of the present study suggest the megalopa of Uca, unlike that of Callinectes, could be of predominant stage of reinvasion of the estuary. The percentage

of the Uca megalopal catch found inside the bay was more than double that of Callinectes. Also, the peak abundance of the Uca megalopae captured offshore occurred much closer to the bay mouth (6 km) than the peak for Callinectes. Finally, the Uca megalopae were most common in bottom water, which facilitates movement towards the bay.

Pinnixa sp.

Sandifer (1972) found P. chaetoptera zoeae reached peak abundance in the Chesapeake Bay mouth, but the abundance decreased precipitously at his station seaward of the bay mouth. He also found this species to be the most common larval pinnixid. This study most commonly collected the megalopae tentatively assigned to this species (see methods) just seaward of the Chesapeake Bay mouth (stations 12 and 19) which is 16 km seaward of the zoeal maximum observed by Sandifer. A few reports have noted the occurrence of Pinnixa larvae in other areas. Hillman (1964) found P. chaetoptera to be most abundant at his middle bay station. Tagatz (1968) found Pinnixa sp. to be more common in the lower St. Johns River. Dudley and Judy (1971) found Pinnixa sp. zoeae to be common at their most inshore stations. Two reports indicate greater concentrations of pinnixid zoeae near bottom (Dudley and Judy 1971, Sandifer 1972). This study found the megalopa to have a high affinity for the epibenthos and to reach peak offshore concentrations near the bay mouth. Like Uca, the percentage of the Pinnixa megalopal catch found inside the bay was

more than double that of Callinectes. Hence the megalopa of this species may be the predominant stage reinvading the estuary.

#### Retained Shelf Megalopae

Three brachyurans which commonly inhabit the shelf as adults were collected as megalopa. The megalopae of each species were most abundant on the shelf, often in close proximity to the bay mouth. The maximum megalopal intrusion in the Chesapeake Bay by any of these species was represented by Libinia with only 9% of the total catch within the bay. Libinia is known to be tolerant of slight estuarine conditions and is often collected as an adult in the lower Chesapeake Bay (Wass 1972). Interestingly, the megalopae of this species were most abundant in bottom waters, which is often stated to favor transport to the estuary. Conversely, Cancer and Portunus adults are only occasionally found in the lower Chesapeake Bay and are most abundant on the adjacent shelf. The megalopae of each of these species reached maximum concentrations in the neuston and were thus impeded from entering the bay. Each of these species will be discussed below.

#### Cancer irroratus

Bigford (1979a) concluded from laboratory data that stage V zoeae and the megalopa are benthic inhabitants. The results reported here indicate the majority of Cancer megalopae inhabit the neuston in stratified water columns.

While a significant downward shift in vertical distribution occurs in homogeneous water columns, the median depth is nevertheless above 3 m. Dittel and Epifanio (in press) also found the larvae of this species to be most common in surface waters. This near surface distribution as found in the field does not favor the onshore movement of larvae as suggested by Bigford (1979b), except during periods of wind induced surface water transport towards the bay. Sandifer (1972) found the zoeae of this species only occasionally in the lower Chesapeake Bay and bay mouth. His greatest catch was at his most seaward station, just outside the bay mouth. Direct comparisons of Sandifer's zoeal and this study's megalopal distributions are not possible for this and other species distributed offshore, because the larvae were only abundant outside the range of Sandifer's study.

Portunus sp.

These megalopae are distributed in the neuston at the most seaward stations (16 and 17). Other studies report the capture of zoeae of this species, but some accounts only incidentally address the distribution of these larvae. Tagatz (1968) collected the zoeae of these species at his highest salinity stations in the lower St. Johns River. Dudley and Judy (1971) reported the occurrence of the zoeae of P. sayi occasionally and P. gibbesi frequently. The zoeal catch of this genus increased at their most seaward stations (10-13 km offshore). Although quantitative data

was not presented, Smyth (1980) reported Portunus spp. zoeae and megalopae co-occurred with Callinectes in off-shore neuston samples from the shelf region of New Jersey and Virginia.

Libinia spp.

The megalopae of this genus were most common well off-shore (station 18), but unlike other shelf species, these megalopae were found in the epibenthos. Smyth (1980) found Libinia spp. zoeae and megalopae along the inner shelf, but a quantitative analysis was not published. Other investigators have collected the zoeae only occasionally and in numbers too few to indicate distributions (Dudley and Judy 1971, Sandifer 1972).

### Summary and Conclusions

1. Twenty-one stations forming a transect of the lower Pamunkey River, York River, lower Chesapeake Bay and adjacent shelf waters, were sampled every second week from July through September 1980. The distributions of the megalopae of 11 brachyuran species were analyzed.
2. Vertical and horizontal distributions are described for each species in relation to water stratification and salinity, respectively.
3. Horizontal distributions include Rhithropanopeus harrisii, Hexapanopeus angustifrons, Neopanope sayi, Panopeus herbsti and Pinnotheres ostreum are retained in estuarine waters. The megalopae of three other estuarine species, Callinectes sapidus, Uca spp. and Pinnixa sp. are flushed from the estuary, resulting in maximum megalopal abundances on the shelf. The megalopae of three shelf species, Cancer irroratus, Portunus sp. and Libinia spp., are most abundant in shelf waters, and with the exception of Libinia spp., are impeded from entering estuarine waters, due to their vertical distribution.
4. Vertical distributions of megalopae indicate Callinectes sapidus, Portunus sp. and Cancer irroratus are most abundant in the neuston and most commonly found above pycnoclines, when the water column is stratified.

The megalopae of Libinia spp., Pinnixa sp., Uca spp., Hexapanopeus angustifrons, Neopanope sayi, Panopeus herbsti and Pinnotheres ostreum are most abundant in epibenthic waters, while Rhithropanopeus harrisii megalopae are commonly found slightly higher in the water column. These species congregate below the pycnocline when stratified conditions prevail.

5. The megalopae of five species, Callinectes sapidus, Cancer irroratus, Libinia spp., Rhithropanopeus harrisii and Pinnotheres ostreum are found to have significant shifts in vertical distribution when stratified water columns become homogeneous.

6. No evidence of decreased dispersal is found for megalopae originating from parents in middle and upper reaches of the estuary as compared to those spawned from species common to the lower estuary. On the contrary, an estuarine species common in the Chesapeake Bay mouth, Neopanope sayi, exhibited the most restricted distribution of all estuarine species.

7. Differences in vertical distribution, distance from the bay entrance, and the proportion of the catch taken within the estuary, suggest the megalopae are important in reinvasion of the estuary for Uca spp. and Pinnixa sp., but for Callinectes sapidus the megalopae may be facultatively reinvasive.



8. The megalopal distributions of this study suggest three apparent recruitment strategies: retained estuarine, expelled estuarine and retained coastal megalopae.

The megalopae of the estuarine adults, Hexapanopeus angustifrons, Neopanope sayi, Panopeus herbsti, Pinnotheres ostreum, and Rhithropanopeus harrisii are retained in the estuary. The larvae of the estuarine species, Callinectes sapidus, Uca spp. and Pinnixa sp. are expelled from the estuary, necessitating reinvasion.

Each of the shelf species are retained in coastal waters. The megalopae of Cancer irroratus and Portunus sp. are impeded from entering the Chesapeake Bay by virtue of their distribution in the extreme surface layers of the shelf waters. While Libinia spp. megalopae are most abundant offshore, their distribution in bottom waters probably accounts for the 9% of the total catch from the lower estuary.

9. Based on estimates of net epibenthic and surface flows as well as the distributions of larvae near the end of their pelagic phase, I suggest that certain forms (e.g. Pinnixa sp. and Uca spp.), must utilize active behavioral mechanisms to ride tidal currents to reinvade estuarine habitats, rather than depend upon passive non-tidal drifts.

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## APPENDIX

### THE DATA BASE

The data base on the following pages uses the following abbreviations: ST = Station Number, DATE = Julian Date 1980, Z = Depth (m), SP = Species Code, ABUN = Abundance (megalopae/100 cu m), TEMP = Temperature (C°), SAL = Salinity (ppt), SIG-T = Sigma-t, T = Coded Tidal Phase, P = Coded Pycnocline.

The codes are as follows.

SP: 1 = Callinectes sapidus, 2 = Hexapanopeus angustifrons, 3 = Panopeus herbstii, 4 = Neopanope sayi, 5 = unknown, 6 = Uca spp., 7 = Pinnotheres ostreum, 8 = Pinnixa spp., 9 = Libinia spp., 10 = Cancer irroratus, 11 = Portunus spp., 12, 13 = unknowns, 14 = Rhithropanopeus harrisii.

T: 0 = High Slack, 1 = Pre-maximum Ebb, 2 = Maximum Ebb, 3 = Post-maximum Ebb, 4 = Low Slack, 5 = Pre-maximum Flood, 6 = Maximum Flood, 7 = Post-maximum Flood, 8 = Tidal currents weak and variable.

P: 0 = Homogeneous Water Column, 1 = Positioned Above Pycnocline, 2 = Positioned Within Pycnocline, 3 = Positioned Below Pycnocline.

ST	DATE	Z	SP	ABUN	TEMP	SAL	SIG-T	T	P
1.0	183	6	14	23.	27.05	7.02	1.86	6	3
2.0	183	3	14	6.	27.78	12.62	5.80	7	2
2.0	183	6	14	28.	27.20	13.30	6.48	7	3
4.0	183	9	14	37.	25.50	18.15	10.58	0	3
5.0	183	10	14	33.	25.70	19.40	11.46	1	3
10.0	184	8	1	3.	18.50	32.24	23.07	6	3
19.0	184	8	6	53.	16.65	31.93	23.27	8	3
18.0	184	0	1	5.	20.60	25.02	17.06	8	1
18.0	184	0	6	5.	20.60	25.02	17.06	8	1
1.0	198	6	14	113.	28.57	5.34	0.18	6	3
2.0	198	8	14	11.	28.10	13.40	6.29	7	3
3.0	198	8	6	11.	27.70	17.20	9.23	0	3
5.0	198	10	14	4.	27.28	18.94	10.65	2	3
8.0	198	0	1	8.	27.13	19.60	11.19	3	1
8.0	198	0	6	1.	27.13	19.60	11.19	3	1
8.0	198	3	1	4.	25.87	23.90	14.77	3	2
8.0	198	10	1	4.	22.57	28.84	19.42	3	3
9.0	197	0	1	10.	19.50	28.92	20.29	6	1
10.0	197	0	1	22.	24.98	20.49	12.48	6	1
10.0	197	0	12	3.	24.98	20.49	12.48	6	1
10.0	197	6	1	12.	21.10	26.10	17.75	6	2
10.0	197	7	1	6.	19.50	28.92	20.29	6	3
10.0	197	7	6	3.	19.50	28.92	20.29	6	3
21.0	197	0	1	2130.	24.76	23.68	14.93	7	1
21.0	197	0	11	2.	24.76	23.68	14.93	7	1
21.0	197	0	12	73.	24.76	23.68	14.93	7	1
21.0	197	1	1	162.	23.92	23.70	15.18	7	1
21.0	197	6	1	19.	23.48	27.50	18.16	7	3
21.0	197	8	1	24.	23.38	27.50	18.19	7	3
11.0	197	0	1	113.	25.54	22.00	13.45	5	1
11.0	197	1	1	5.	25.50	21.50	13.08	5	1
20.0	197	0	1	2846.	22.80	29.10	19.56	7	0
20.0	197	0	10	1.	22.80	29.10	19.56	7	0
20.0	197	1	1	278.	22.80	29.20	19.63	7	0
20.0	197	6	1	77.	22.80	29.50	19.86	7	0
20.0	197	6	3	6.	22.80	29.50	19.86	7	0
20.0	197	12	1	2996.	22.80	29.60	19.93	7	0
19.0	197	0	1	303.	24.20	31.50	20.97	8	1
19.0	197	1	1	73.	24.20	31.20	20.74	8	2
19.0	197	3	1	24.	20.70	30.60	21.26	8	2
13.0	196	0	1	41.	20.00	28.90	20.15	8	1
13.0	196	0	6	1.	20.00	28.90	20.15	8	1
13.0	196	0	12	1.	20.00	28.90	20.15	8	1
18.0	197	0	1	308.	26.40	29.40	18.74	8	1
18.0	197	1	6	30.	26.20	29.00	18.50	8	1
18.0	197	13	1	72.	16.30	31.20	22.80	8	3
18.0	197	13	6	14.	16.30	31.20	22.80	8	3
14.0	196	0	1	147.	25.90	28.90	18.51	8	1
14.0	196	15	13	20.	16.50	32.70	23.90	8	3
15.0	196	0	1	110.	30.30	28.80	17.06	8	1
16.0	196	0	1	34500.	32.70	30.40	17.46	8	1
16.0	196	0	10	513.	32.70	30.40	17.46	8	1

ST	DATE	Z	SP	ABUN	TEMP	SAL	SIG-T	T	P
16.0	196	1	1	254.	32.80	30.40	17.43	8	1
16.0	196	6	1	677.	31.60	30.40	17.83	8	1
2.0	214	3	6	5.	29.81	16.22	7.86	7	2
4.0	214	9	6	20.	28.24	20.73	11.70	2	3
5.0	214	3	6	9.	28.54	21.34	12.06	3	3
5.0	214	6	6	5.	28.38	21.68	12.36	3	3
5.0	214	10	6	28.	27.88	21.94	12.71	3	3
5.0	214	10	7	5.	27.88	21.94	12.71	3	3
5.0	214	10	8	28.	27.88	21.94	12.71	3	3
6.0	214	0	2	2.	27.80	21.20	12.18	4	1
6.0	214	0	6	1.	27.80	21.20	12.18	4	1
6.0	214	0	7	2.	27.80	21.20	12.18	4	1
6.0	214	0	8	14.	27.80	21.20	12.18	4	1
6.0	214	3	7	16.	27.80	21.80	12.63	4	2
6.0	214	3	8	16.	27.80	21.80	12.63	4	2
6.0	214	6	3	16.	26.40	21.80	13.05	4	2
6.0	214	6	6	8.	26.40	21.80	13.05	4	2
6.0	214	6	8	80.	26.40	21.80	13.05	4	2
6.0	214	13	2	20.	24.80	25.30	16.13	4	3
6.0	214	13	8	69.	24.80	25.30	16.13	4	3
9.0	213	0	1	5.	27.71	23.70	14.07	0	1
21.0	213	1	1	64.	23.20	29.80	19.97	0	2
20.0	213	0	1	32.	23.00	29.30	19.65	0	1
20.0	213	1	1	92.	22.56	30.00	20.30	0	1
20.0	213	11	1	44.	21.84	30.38	20.79	0	3
12.0	212	3	1	5.	23.00	25.70	16.94	8	2
12.0	212	6	1	5.	17.80	29.40	21.07	8	2
19.0	213	0	1	24.	23.30	28.00	18.59	8	1
19.0	213	8	9	29.	15.70	31.70	23.31	8	3
13.0	212	0	1	2.	21.10	28.60	19.64	8	1
13.0	212	0	11	1.	21.10	28.60	19.64	8	1
13.0	212	10	1	4.	14.00	32.70	24.45	8	3
18.0	213	0	1	4.	24.60	27.50	17.84	8	1
18.0	213	0	2	1.	24.60	27.50	17.84	8	1
18.0	213	13	1	37.	13.00	33.00	24.88	8	3
18.0	213	13	6	74.	13.00	33.00	24.88	8	3
14.0	212	0	1	58.	25.00	30.20	19.76	8	1
17.0	212	0	12	1.	25.80	30.00	19.37	8	1
17.0	212	12	5	18.	12.10	31.80	24.13	8	3
15.0	212	0	1	36.	26.00	30.90	19.98	8	1
15.0	212	0	11	1.	26.00	30.90	19.98	8	1
15.0	212	1	1	110.	25.00	31.00	20.36	8	1
15.0	212	1	6	12.	25.00	31.00	20.36	8	1
15.0	212	3	1	420.	22.50	31.50	21.45	8	2
16.0	212	0	5	8.	26.20	28.80	18.35	8	1
16.0	212	0	11	1.	26.20	28.80	18.35	8	1
16.0	212	0	12	13.	26.20	28.80	18.35	8	1
16.0	212	0	13	2.	26.20	28.80	18.35	8	1
16.0	212	22	1	13.	11.30	30.80	23.50	8	3
16.0	212	22	6	26.	11.30	30.80	23.50	8	3
1.0	225	7	14	46.	30.25	6.16	0.28	4	0
4.0	225	6	6	57.	29.36	19.30	10.29	6	3

ST	DATE	Z	SP	ABUN	TEMP	SAL	SIG-T	T	P
4.0	225	9	3	18.	29.40	19.40	10.35	6	3
4.0	225	9	6	18.	29.40	19.40	10.35	6	3
6.0	225	14	1	152.	24.82	25.21	16.06	0	3
6.0	225	14	2	19.	24.82	25.21	16.06	0	3
6.0	225	14	6	57.	24.82	25.21	16.06	0	3
6.0	225	14	7	19.	24.82	25.21	16.06	0	3
6.0	225	14	8	19.	24.82	25.21	16.06	0	3
7.0	225	0	2	1.	28.13	21.91	12.61	0	1
7.0	225	3	2	8.	27.56	22.78	13.43	0	1
7.0	225	6	1	100.	23.75	25.98	16.94	0	3
7.0	225	6	6	10.	23.75	25.98	16.94	0	3
7.0	225	10	1	71.	23.53	26.56	17.44	0	3
7.0	225	10	2	24.	23.53	26.56	17.44	0	3
7.0	225	10	6	24.	23.53	26.56	17.44	0	3
8.0	225	6	1	148.	23.44	26.12	17.13	1	2
8.0	225	10	1	48.	21.85	27.59	18.68	1	3
8.0	225	10	2	48.	21.85	27.59	18.68	1	3
8.0	225	10	7	238.	21.85	27.59	18.68	1	3
9.0	226	0	1	31.	23.70	26.70	17.50	6	1
9.0	226	1	1	18.	23.71	27.18	17.86	6	1
9.0	226	6	1	27.	19.98	28.74	20.04	6	2
9.0	226	6	2	7.	19.98	28.74	20.04	6	2
9.0	226	6	6	14.	19.98	28.74	20.04	6	2
9.0	226	6	9	7.	19.98	28.74	20.04	6	2
9.0	226	10	6	10.	19.20	29.16	20.55	6	3
9.0	226	10	8	10.	19.20	29.16	20.55	6	3
10.0	226	0	1	29.	25.30	25.10	15.84	6	1
10.0	226	1	1	121.	25.25	25.10	15.85	6	1
10.0	226	3	1	288.	24.90	25.40	16.18	6	1
10.0	226	3	2	183.	24.90	25.40	16.18	6	1
10.0	226	3	3	26.	24.90	25.40	16.18	6	1
10.0	226	3	6	105.	24.90	25.40	16.18	6	1
10.0	226	6	2	16.	22.70	26.75	17.81	6	2
10.0	226	6	3	16.	22.70	26.75	17.81	6	2
21.0	226	0	1	24.	24.78	26.98	17.40	7	1
21.0	226	0	12	7.	24.78	26.98	17.40	7	1
21.0	226	1	1	9.	24.37	26.98	17.52	7	1
21.0	226	1	6	18.	24.37	26.98	17.52	7	1
21.0	226	3	6	10.	24.34	27.10	17.62	7	1
21.0	226	6	1	13.	23.20	28.30	18.84	7	2
21.0	226	6	2	13.	23.20	28.30	18.84	7	2
21.0	226	6	6	13.	23.20	28.30	18.84	7	2
21.0	226	8	6	57.	22.73	28.44	19.08	7	3
11.0	226	1	1	22.	24.60	25.60	16.42	5	1
11.0	226	1	9	22.	24.60	25.60	16.42	5	1
11.0	226	3	1	5.	24.50	25.80	16.59	5	1
11.0	226	3	2	26.	24.50	25.80	16.59	5	1
11.0	226	3	3	10.	24.50	25.80	16.59	5	1
11.0	226	3	4	10.	24.50	25.80	16.59	5	1
11.0	226	3	6	89.	24.50	25.80	16.59	5	1
11.0	226	6	1	5.	24.20	26.30	17.06	5	1
11.0	226	8	3	3.	23.20	27.20	18.01	5	3



ST	DATE	Z	SP	ABUN	TEMP	SAL	SIG-T	T	P
11.0	226	8	4	3.	23.20	27.20	18.01	5	3
20.0	226	0	1	3444.	19.60	30.86	21.74	0	0
20.0	226	1	1	3943.	19.30	31.30	22.15	0	0
20.0	226	3	1	36.	18.42	31.50	22.52	0	0
20.0	226	6	1	114.	17.80	31.12	22.39	0	0
12.0	227	12	1	188.	13.18	32.08	24.14	8	3
19.0	226	0	1	569.	21.15	31.95	22.16	8	1
19.0	226	0	6	1.	21.15	31.95	22.16	8	1
19.0	226	6	1	8.	14.94	32.70	24.25	8	3
19.0	226	7	6	95.	14.73	32.36	24.03	8	3
13.0	227	1	1	6.	14.92	31.90	23.64	8	2
18.0	226	0	1	153.	20.52	32.82	22.99	8	1
18.0	226	0	6	5.	20.52	32.82	22.99	8	1
18.0	226	12	1	5.	12.25	32.12	24.35	8	3
18.0	226	12	9	1735.	12.25	32.12	24.35	8	3
14.0	227	17	10	5.	11.62	32.50	24.76	8	3
17.0	227	0	1	25.	22.52	31.73	21.62	8	1
17.0	227	0	10	1.	22.52	31.73	21.62	8	1
17.0	227	3	1	231.	21.43	32.05	22.16	8	2
17.0	227	3	2	41.	21.43	32.05	22.16	8	2
17.0	227	3	3	14.	21.43	32.05	22.16	8	2
17.0	227	3	6	150.	21.43	32.05	22.16	8	2
17.0	227	3	11	27.	21.43	32.05	22.16	8	2
17.0	227	6	1	1964.	14.06	32.82	24.53	8	2
17.0	227	6	2	76.	14.06	32.82	24.53	8	2
17.0	227	6	6	126.	14.06	32.82	24.53	8	2
17.0	227	6	13	13.	14.06	32.82	24.53	8	2
17.0	227	18	1	42.	10.85	33.12	25.38	8	3
17.0	227	18	6	29.	10.85	33.12	25.38	8	3
17.0	227	18	13	4.	10.85	33.12	25.38	8	3
15.0	227	0	1	11194.	21.52	30.88	21.25	8	1
15.0	227	1	1	277.	19.77	30.92	21.74	8	2
15.0	227	3	1	185.	18.50	31.68	22.64	8	2
15.0	227	3	3	4.	18.50	31.68	22.64	8	2
15.0	227	3	6	12.	18.50	31.68	22.64	8	2
15.0	227	3	10	4.	18.50	31.68	22.64	8	2
15.0	227	6	1	334.	12.76	32.10	24.24	8	2
15.0	227	6	2	11.	12.76	32.10	24.24	8	2
15.0	227	6	6	43.	12.76	32.10	24.24	8	2
15.0	227	20	1	180.	10.61	32.80	25.17	8	3
16.0	227	0	6	1.	23.54	31.78	21.37	8	1
16.0	227	3	1	5.	22.40	32.45	22.20	8	2
16.0	227	3	2	5.	22.40	32.45	22.20	8	2
16.0	227	3	6	14.	22.40	32.45	22.20	8	2
16.0	227	6	1	200.	13.66	32.60	24.44	8	2
16.0	227	6	6	200.	13.66	32.60	24.44	8	2
1.0	240	0	1	2.	26.26	9.39	3.84	3	0
1.0	240	3	14	600.	26.37	9.43	3.84	3	0
2.0	240	6	1	26.	26.07	16.46	9.16	4	0
2.0	240	6	7	13.	26.07	16.46	9.16	4	0
2.0	240	6	14	26.	26.07	16.46	9.16	4	0
2.0	240	8	6	22.	26.70	16.50	9.00	4	0

ST	DATE	Z	SP	ABUN	TEMP	SAL	SIG-T	T	P
3.0	240	0	1	1.	26.00	18.65	10.81	6	0
3.0	240	6	2	15.	26.40	18.80	10.81	6	0
3.0	240	8	2	24.	26.05	18.54	10.71	6	0
4.0	240	3	7	18.	26.39	20.53	12.10	6	0
4.0	240	6	1	146.	26.41	20.38	11.98	6	0
4.0	240	6	2	194.	26.41	20.38	11.98	6	0
4.0	240	6	6	146.	26.41	20.38	11.98	6	0
4.0	240	6	7	81.	26.41	20.38	11.98	6	0
4.0	240	10	1	73.	26.20	20.35	12.02	6	0
4.0	240	10	2	18.	26.20	20.35	12.02	6	0
4.0	240	10	6	18.	26.20	20.35	12.02	6	0
4.0	240	10	7	18.	26.20	20.35	12.02	6	0
5.0	240	0	1	1.	26.44	22.63	13.65	7	0
5.0	240	3	6	23.	26.35	22.73	13.76	7	0
5.0	240	3	7	46.	26.35	22.73	13.76	7	0
5.0	240	6	1	99.	26.12	23.13	14.12	7	0
5.0	240	6	2	85.	26.12	23.13	14.12	7	0
5.0	240	6	6	99.	26.12	23.13	14.12	7	0
5.0	240	6	7	14.	26.12	23.13	14.12	7	0
5.0	240	10	1	10.	26.18	23.27	14.21	7	0
5.0	240	10	6	10.	26.18	23.27	14.21	7	0
6.0	240	3	2	4.	25.53	21.30	12.93	1	2
6.0	240	3	7	8.	25.53	21.30	12.93	1	2
6.0	240	6	2	75.	25.31	22.04	13.54	1	2
6.0	240	6	3	19.	25.31	22.04	13.54	1	2
6.0	240	6	6	13.	25.31	22.04	13.54	1	2
6.0	240	6	7	13.	25.31	22.04	13.54	1	2
6.0	240	12	2	18.	24.61	23.80	15.06	1	3
6.0	240	12	3	18.	24.61	23.80	15.06	1	3
7.0	240	3	7	11.	25.33	21.01	12.77	1	2
7.0	240	6	1	90.	23.15	24.51	16.00	1	2
7.0	240	6	2	45.	23.15	24.51	16.00	1	2
7.0	240	6	7	441.	23.15	24.51	16.00	1	2
7.0	240	9	1	73.	32.70	25.43	13.76	1	3
7.0	240	9	2	85.	32.70	25.43	13.76	1	3
7.0	240	9	6	17.	32.70	25.43	13.76	1	3
7.0	240	9	7	68.	32.70	25.43	13.76	1	3
8.0	240	0	1	4.	26.50	21.88	13.08	1	1
8.0	240	6	1	30.	23.05	25.46	16.75	1	2
8.0	240	6	2	402.	23.05	25.46	16.75	1	2
8.0	240	6	6	89.	23.05	25.46	16.75	1	2
8.0	240	6	7	30.	23.05	25.46	16.75	1	2
8.0	240	6	8	89.	23.05	25.46	16.75	1	2
8.0	240	10	2	550.	22.59	25.92	17.22	1	3
8.0	240	10	3	373.	22.59	25.92	17.22	1	3
8.0	240	10	6	248.	22.59	25.92	17.22	1	3
8.0	240	10	8	280.	22.59	25.92	17.22	1	3
9.0	242	0	1	171.	24.28	28.50	18.69	1	0
9.0	242	0	2	1.	24.28	28.50	18.69	1	0
9.0	242	0	6	2.	24.28	28.50	18.69	1	0
9.0	242	1	1	29.	24.28	28.62	18.78	1	0
9.0	242	1	6	5.	24.28	28.62	18.78	1	0

ST	DATE	Z	SP	AEUN	TEMP	SAL	SIG-T	T	P
9.0	242	3	1	51.	23.96	28.74	18.96	1	0
9.0	242	6	2	104.	23.38	29.46	19.67	1	0
9.0	242	6	4	295.	23.38	29.46	19.67	1	0
9.0	242	6	7	260.	23.38	29.46	19.67	1	0
9.0	242	6	8	69.	23.38	29.46	19.67	1	0
9.0	242	12	4	3330.	22.85	29.53	19.87	1	0
9.0	242	12	6	3330.	22.85	29.53	19.87	1	0
9.0	242	12	7	3330.	22.85	29.53	19.87	1	0
10.0	242	0	1	87.	24.23	26.18	16.96	2	0
10.0	242	0	4	1.	24.23	26.18	16.96	2	0
10.0	242	1	1	12.	24.23	25.90	16.75	2	0
10.0	242	3	6	8.	23.60	26.72	17.54	2	0
10.0	242	3	7	24.	23.60	26.72	17.54	2	0
10.0	242	3	9	8.	23.60	26.72	17.54	2	0
10.0	242	6	2	74.	23.30	27.50	18.21	2	0
10.0	242	6	3	74.	23.30	27.50	18.21	2	0
10.0	242	6	4	50.	23.30	27.50	18.21	2	0
10.0	242	6	6	25.	23.30	27.50	18.21	2	0
10.0	242	6	7	25.	23.30	27.50	18.21	2	0
10.0	242	8	1	69.	22.96	27.92	18.62	2	0
10.0	242	8	2	2570.	22.96	27.92	18.62	2	0
10.0	242	8	3	310.	22.96	27.92	18.62	2	0
10.0	242	8	4	92.	22.96	27.92	18.62	2	0
10.0	242	8	5	23.	22.96	27.92	18.62	2	0
10.0	242	8	6	1640.	22.96	27.92	18.62	2	0
10.0	242	8	8	803.	22.96	27.92	18.62	2	0
10.0	242	8	9	46.	22.96	27.92	18.62	2	0
21.0	242	0	1	192.	23.98	30.90	20.58	1	1
21.0	242	0	2	29.	23.98	30.90	20.58	1	1
21.0	242	0	6	82.	23.98	30.90	20.58	1	1
21.0	242	0	10	31.	23.98	30.90	20.58	1	1
21.0	242	1	1	5.	23.92	31.25	20.86	1	1
21.0	242	1	2	158.	23.92	31.25	20.86	1	1
21.0	242	1	4	25.	23.92	31.25	20.86	1	1
21.0	242	1	6	329.	23.92	31.25	20.86	1	1
21.0	242	1	10	21.	23.92	31.25	20.86	1	1
21.0	242	3	1	20.	23.98	31.51	21.04	1	2
21.0	242	3	2	34.	23.98	31.51	21.04	1	2
21.0	242	3	6	317.	23.98	31.51	21.04	1	2
21.0	242	6	2	13.	22.99	32.00	21.69	1	3
21.0	242	6	6	38.	22.99	32.00	21.69	1	3
21.0	242	7	2	29.	22.99	32.01	21.70	1	3
21.0	242	7	6	267.	22.99	32.01	21.70	1	3
11.0	242	0	1	2.	24.51	25.28	16.20	3	1
11.0	242	0	10	1.	24.51	25.28	16.20	3	1
11.0	242	1	1	4.	24.98	24.98	15.84	3	1
11.0	242	3	6	4.	24.50	25.20	16.14	3	1
11.0	242	6	2	30.	23.20	27.58	18.30	3	2
11.0	242	6	3	15.	23.20	27.58	18.30	3	2
11.0	242	8	1	371.	23.00	28.42	18.99	3	3
11.0	242	8	2	378.	23.00	28.42	18.99	3	3
11.0	242	8	3	135.	23.00	28.42	18.99	3	3

ST	DATE	Z	SP	ABUN	TEMP	SAL	SIG-T	T	P
11.0	242	8	4	27.	23.00	28.42	18.99	3	3
11.0	242	8	6	54.	23.00	28.42	18.99	3	3
11.0	242	8	8	27.	23.00	28.42	18.99	3	3
11.0	242	8	13	189.	23.00	28.42	18.99	3	3
20.0	242	0	1	69.	23.59	32.39	21.82	0	0
20.0	242	0	10	7.	23.59	32.39	21.82	0	0
20.0	242	1	1	111.	23.60	32.24	21.70	0	0
20.0	242	1	10	14.	23.60	32.24	21.70	0	0
20.0	242	3	1	206.	23.38	31.98	21.57	0	0
20.0	242	3	2	39.	23.38	31.98	21.57	0	0
20.0	242	3	3	3.	23.38	31.98	21.57	0	0
20.0	242	3	6	3.	23.38	31.98	21.57	0	0
20.0	242	3	10	26.	23.38	31.98	21.57	0	0
20.0	242	6	1	100.	23.35	32.13	21.69	0	0
20.0	242	6	6	50.	23.35	32.13	21.69	0	0
20.0	242	6	10	50.	23.35	32.13	21.69	0	0
20.0	242	11	2	349.	23.28	32.20	21.76	0	0
20.0	242	11	3	47.	23.28	32.20	21.76	0	0
20.0	242	11	4	93.	23.28	32.20	21.76	0	0
20.0	242	11	6	604.	23.28	32.20	21.76	0	0
20.0	242	11	8	209.	23.28	32.20	21.76	0	0
20.0	242	11	9	47.	23.28	32.20	21.76	0	0
12.0	241	3	1	4.	23.56	27.32	18.00	8	2
12.0	241	3	3	4.	23.56	27.32	18.00	8	2
12.0	241	3	6	4.	23.56	27.32	18.00	8	2
12.0	241	10	1	649.	21.68	30.48	20.91	8	3
12.0	241	10	2	231.	21.68	30.48	20.91	8	3
12.0	241	10	3	60.	21.68	30.48	20.91	8	3
12.0	241	10	4	34.	21.68	30.48	20.91	8	3
12.0	241	10	6	154.	21.68	30.48	20.91	8	3
12.0	241	10	7	17.	21.68	30.48	20.91	8	3
12.0	241	10	8	1127.	21.68	30.48	20.91	8	3
19.0	242	0	1	29.	23.83	32.38	21.74	8	0
19.0	242	1	1	111.	23.27	32.38	21.90	8	0
19.0	242	1	10	6.	23.27	32.38	21.90	8	0
19.0	242	6	1	84.	23.00	32.64	22.17	8	0
19.0	242	6	2	70.	23.00	32.64	22.17	8	0
19.0	242	6	6	14.	23.00	32.64	22.17	8	0
19.0	242	6	10	225.	23.00	32.64	22.17	8	0
19.0	242	7	2	100.	23.00	32.64	22.17	8	0
19.0	242	7	6	7737.	23.00	32.64	22.17	8	0
19.0	242	7	8	800.	23.00	32.64	22.17	8	0
13.0	241	0	1	2.	23.75	30.30	20.19	8	1
13.0	241	3	6	3.	21.49	30.70	21.12	8	1
13.0	241	6	1	297.	20.98	32.08	22.31	8	2
13.0	241	6	2	95.	20.98	32.08	22.31	8	2
13.0	241	6	3	12.	20.98	32.08	22.31	8	2
13.0	241	6	6	36.	20.98	32.08	22.31	8	2
13.0	241	10	1	23.	20.06	32.10	22.56	8	3
13.0	241	10	2	109.	20.06	32.10	22.56	8	3
13.0	241	10	4	23.	20.06	32.10	22.56	8	3
13.0	241	10	6	31.	20.06	32.10	22.56	8	3

ST	DATE	Z	SP	AEUN	TEMP	SAL	SIG-T	T	P
13.0	241	10	9	31.	20.06	32.10	22.56	8	3
18.0	242	0	1	22490.	23.98	31.83	21.28	8	1
18.0	242	0	10	23.	23.98	31.83	21.28	8	1
18.0	242	1	1	136.	23.26	31.83	21.49	8	2
18.0	242	1	10	5.	23.26	31.83	21.49	8	2
18.0	242	3	1	157.	22.61	32.32	22.04	8	2
18.0	242	3	10	5.	22.61	32.32	22.04	8	2
18.0	242	6	1	100.	22.14	32.50	22.31	8	3
18.0	242	13	1	26.	21.90	32.46	22.34	8	3
18.0	242	13	9	31.	21.90	32.46	22.34	8	3
14.0	241	3	1	4.	22.61	31.00	21.04	8	2
14.0	241	3	3	4.	22.61	31.00	21.04	8	2
14.0	241	3	6	4.	22.61	31.00	21.04	8	2
14.0	241	15	1	649.	19.24	32.71	23.24	8	3
14.0	241	15	2	231.	19.24	32.71	23.24	8	3
14.0	241	15	3	60.	19.24	32.71	23.24	8	3
14.0	241	15	4	34.	19.24	32.71	23.24	8	3
14.0	241	15	6	154.	19.24	32.71	23.24	8	3
14.0	241	15	7	17.	19.24	32.71	23.24	8	3
14.0	241	15	8	1127.	19.24	32.71	23.24	8	3
17.0	241	0	1	249.	23.52	32.43	21.87	8	1
17.0	241	0	6	4.	23.52	32.43	21.87	8	1
17.0	241	0	10	7.	23.52	32.43	21.87	8	1
17.0	241	1	1	69.	23.41	32.47	21.93	8	1
17.0	241	3	1	6.	23.28	32.48	21.97	8	1
17.0	241	3	6	6.	23.28	32.48	21.97	8	1
17.0	241	3	9	6.	23.28	32.48	21.97	8	1
17.0	241	6	1	441.	22.93	32.37	21.99	8	1
17.0	241	6	10	18.	22.93	32.37	21.99	8	1
17.0	241	17	1	454.	20.99	32.56	22.67	8	3
17.0	241	17	6	11.	20.99	32.56	22.67	8	3
17.0	241	17	9	18.	20.99	32.56	22.67	8	3
17.0	241	17	10	4.	20.99	32.56	22.67	8	3
15.0	241	3	1	103.	23.15	31.61	21.35	8	1
15.0	241	3	9	9.	23.15	31.61	21.35	8	1
15.0	241	19	1	24.	19.56	32.57	23.05	8	3
15.0	241	19	9	10.	19.56	32.57	23.05	8	3
15.0	241	19	10	5.	19.56	32.57	23.05	8	3
16.0	241	0	1	8.	24.97	32.61	21.58	8	1
16.0	241	3	1	1207.	24.01	33.08	22.22	8	2
16.0	241	3	10	7.	24.01	33.08	22.22	8	2
16.0	241	6	1	287.	23.56	33.11	22.37	8	2
16.0	241	6	10	8.	23.56	33.11	22.37	8	2
16.0	241	20	1	104.	21.30	32.75	22.73	8	3
1.0	257	3	14	226.	25.87	10.93	5.10	3	0
2.0	257	3	14	11.	25.21	16.77	9.63	3	0
2.0	257	8	6	192.	24.83	16.90	9.84	3	0
3.0	257	3	7	60.	25.59	18.50	10.82	5	0
3.0	257	6	1	67.	25.45	18.20	10.63	5	0
3.0	257	6	6	303.	25.45	18.20	10.63	5	0
3.0	257	6	7	34.	25.45	18.20	10.63	5	0
3.0	257	8	3	19.	25.45	18.20	10.63	5	0

ST	DATE	Z	SP	ABUN	TEMP	SAL	SIG-T	T	P
3.0	257	8	6	266.	25.45	18.20	10.63	5	0
4.0	257	3	7	45.	25.63	20.17	12.05	5	0
4.0	257	6	6	163.	25.35	20.65	12.49	6	0
4.0	257	6	7	109.	25.35	20.65	12.49	6	0
4.0	257	9	1	18.	25.40	20.53	12.39	6	0
4.0	257	9	3	72.	25.40	20.53	12.39	6	0
4.0	257	9	6	72.	25.40	20.53	12.39	6	0
4.0	257	9	7	36.	25.40	20.53	12.39	6	0
5.0	257	3	3	9.	25.89	22.19	13.49	7	0
5.0	257	3	7	1379.	25.89	22.19	13.49	7	0
5.0	257	6	3	42.	25.95	22.09	13.40	7	0
5.0	257	6	5	14.	25.95	22.09	13.40	7	0
5.0	257	6	6	14.	25.95	22.09	13.40	7	0
5.0	257	6	7	111.	25.95	22.09	13.40	7	0
5.0	257	9	3	31.	25.97	22.01	13.33	7	0
5.0	257	9	6	10.	25.97	22.01	13.33	7	0
5.0	257	9	8	10.	25.97	22.01	13.33	7	0
6.0	257	0	1	4.	26.12	23.32	14.27	0	0
6.0	257	0	6	1.	26.12	23.32	14.27	0	0
6.0	257	3	6	9.	25.40	23.08	14.30	0	0
6.0	257	6	2	75.	25.24	23.48	14.64	0	0
6.0	257	6	3	50.	25.24	23.48	14.64	0	0
6.0	257	6	7	25.	25.24	23.48	14.64	0	0
6.0	257	13	2	85.	25.14	23.40	14.61	0	0
6.0	257	13	3	127.	25.14	23.40	14.61	0	0
6.0	257	13	6	21.	25.14	23.40	14.61	0	0
6.0	257	13	7	127.	25.14	23.40	14.61	0	0
6.0	257	13	8	21.	25.14	23.40	14.61	0	0
7.0	257	0	1	1.	25.29	23.45	14.60	0	1
7.0	257	0	6	6.	25.29	23.45	14.60	0	1
7.0	257	3	2	14.	25.23	23.82	14.90	0	1
7.0	257	3	6	83.	25.23	23.82	14.90	0	1
7.0	257	3	7	14.	25.23	23.82	14.90	0	1
7.0	257	6	2	184.	25.21	24.13	15.14	0	1
7.0	257	6	3	129.	25.21	24.13	15.14	0	1
7.0	257	6	6	18.	25.21	24.13	15.14	0	1
7.0	257	6	7	18.	25.21	24.13	15.14	0	1
7.0	257	9	2	198.	24.69	25.55	16.35	0	3
7.0	257	9	3	91.	24.69	25.55	16.35	0	3
7.0	257	9	6	335.	24.69	25.55	16.35	0	3
7.0	257	9	7	213.	24.69	25.55	16.35	0	3
7.0	257	9	8	15.	24.69	25.55	16.35	0	3
8.0	257	0	1	15.	25.32	24.27	15.21	0	1
8.0	257	0	6	3.	25.32	24.27	15.21	0	1
8.0	257	6	2	215.	24.73	26.93	17.38	0	2
8.0	257	6	3	50.	24.73	26.93	17.38	0	2
8.0	257	6	6	50.	24.73	26.93	17.38	0	2
8.0	257	10	2	1076.	24.40	27.34	17.78	0	3
8.0	257	10	3	280.	24.40	27.34	17.78	0	3
8.0	257	10	4	37.	24.40	27.34	17.78	0	3
8.0	257	10	6	430.	24.40	27.34	17.78	0	3
8.0	257	10	7	3009.	24.40	27.34	17.78	0	3

ST	DATE	Z	SP	AEUN	TEMP	SAL	SIG-T	T	P
8.0	257	10	8	93.	24.40	27.34	17.78	0	3
8.0	257	10	9	37.	24.40	27.34	17.78	0	3
9.0	259	0	1	4.	0.00	0.00	0.00	4	0
9.0	259	8	6	238.	0.00	0.00	0.00	4	0
9.0	259	1	7	14.	0.00	0.00	0.00	4	0
10.0	259	0	1	2.	25.07	25.51	16.21	4	1
10.0	259	0	6	4.	25.07	25.51	16.21	4	1
10.0	259	0	10	1.	25.07	25.51	16.21	4	1
10.0	259	1	6	34.	25.07	25.83	16.45	4	1
10.0	259	1	7	368.	25.07	25.83	16.45	4	1
10.0	259	3	6	112.	24.78	26.54	17.07	4	2
10.0	259	3	7	280.	24.78	26.54	17.07	4	2
10.0	259	6	7	327.	24.33	28.42	18.61	4	2
10.0	259	11	1	32.	23.40	30.63	20.54	4	3
10.0	259	11	2	1480.	23.40	30.63	20.54	4	3
10.0	259	11	3	301.	23.40	30.63	20.54	4	3
10.0	259	11	4	519.	23.40	30.63	20.54	4	3
10.0	259	11	5	13.	23.40	30.63	20.54	4	3
10.0	259	11	6	9129.	23.40	30.63	20.54	4	3
10.0	259	11	7	4612.	23.40	30.63	20.54	4	3
10.0	259	11	8	58.	23.40	30.63	20.54	4	3
10.0	259	11	9	250.	23.40	30.63	20.54	4	3
11.0	259	0	1	4.	24.79	26.10	16.74	4	1
11.0	259	1	7	14.	24.79	25.82	16.53	4	1
11.0	259	8	6	238.	23.75	29.32	19.46	4	3
12.0	258	0	1	1.	24.05	30.98	20.62	8	1
12.0	258	11	1	8337.	21.38	32.27	22.34	8	3
12.0	258	11	2	887.	21.38	32.27	22.34	8	3
12.0	258	11	6	18625.	21.38	32.27	22.34	8	3
12.0	258	11	7	297.	21.38	32.27	22.34	8	3
12.0	258	11	9	1300.	21.38	32.27	22.34	8	3
19.0	258	0	1	205.	24.70	32.18	21.33	8	0
19.0	258	0	9	37.	24.70	32.18	21.33	8	0
19.0	258	1	1	375.	24.57	32.18	21.37	8	0
19.0	258	1	10	94.	24.57	32.18	21.37	8	0
19.0	258	3	1	737.	23.96	32.35	21.68	8	0
19.0	258	3	6	14.	23.96	32.35	21.68	8	0
19.0	258	3	9	56.	23.96	32.35	21.68	8	0
19.0	258	6	1	198.	24.16	32.40	21.66	8	0
19.0	258	6	6	40.	24.16	32.40	21.66	8	0
19.0	258	6	9	408.	24.16	32.40	21.66	8	0
19.0	258	6	10	26.	24.16	32.40	21.66	8	0
19.0	258	7	1	6.	24.40	32.40	21.59	8	0
19.0	258	7	7	6.	24.40	32.40	21.59	8	0
19.0	258	7	8	3.	24.40	32.40	21.59	8	0
19.0	258	7	9	58.	24.40	32.40	21.59	8	0
19.0	258	7	10	3.	24.40	32.40	21.59	8	0
13.0	258	0	1	1.	25.02	30.15	19.71	8	1
13.0	258	1	12	15.	25.02	30.15	19.71	8	1
13.0	258	3	1	27.	25.02	30.15	19.71	8	1
13.0	258	6	2	45.	22.80	32.24	21.93	8	2
13.0	258	6	6	45.	22.80	32.24	21.93	8	2

ST	DATE	Z	SP	AEUN	TEMP	SAL	SIG-T	T	P
13.0	258	6	9	18.	22.80	32.24	21.93	8	2
13.0	258	6	1	234.	22.80	32.24	21.93	8	2
13.0	258	11	1	38.	22.34	33.02	22.65	8	3
13.0	258	11	6	6.	22.34	33.02	22.65	8	3
13.0	258	11	9	12.	22.34	33.02	22.65	8	3
13.0	258	11	10	6.	22.34	33.02	22.65	8	3
13.0	258	11	13	12.	22.34	33.02	22.65	8	3
18.0	258	0	1	391.	24.51	32.00	21.26	8	0
18.0	258	0	10	5.	24.51	32.00	21.26	8	0
18.0	258	0	12	2.	24.51	32.00	21.26	8	0
18.0	258	1	1	249.	24.51	32.06	21.30	8	0
18.0	258	1	12	12.	24.51	32.06	21.30	8	0
18.0	258	3	1	367.	24.03	32.40	21.70	8	0
18.0	258	6	1	219.	23.76	32.35	21.74	8	0
18.0	258	6	3	7.	23.76	32.35	21.74	8	0
14.0	258	0	1	23.	24.85	29.84	19.53	8	1
14.0	258	1	1	64.	24.93	29.94	19.58	8	1
14.0	258	3	1	143.	24.43	30.80	20.37	8	2
14.0	258	6	1	186.	24.20	31.97	21.32	8	2
14.0	258	6	9	9.	24.20	31.97	21.32	8	2
14.0	258	6	10	9.	24.20	31.97	21.32	8	2
14.0	258	17	9	50.	21.70	32.52	22.45	8	3
17.0	258	0	1	1245.	24.85	32.13	21.25	8	1
17.0	258	0	2	1.	24.85	32.13	21.25	8	1
17.0	258	0	9	3.	24.85	32.13	21.25	8	1
17.0	258	0	10	5.	24.85	32.13	21.25	8	1
17.0	258	0	11	2.	24.85	32.13	21.25	8	1
17.0	258	0	13	1.	24.85	32.13	21.25	8	1
17.0	258	1	1	176.	24.85	31.80	21.00	8	1
17.0	258	1	10	11.	24.85	31.80	21.00	8	1
17.0	258	3	1	195.	24.75	31.75	21.00	8	1
17.0	258	3	9	11.	24.75	31.75	21.00	8	1
17.0	258	6	1	55.	24.13	32.52	21.76	8	1
17.0	258	6	9	11.	24.13	32.52	21.76	8	1
17.0	258	6	10	44.	24.13	32.52	21.76	8	1
15.0	258	0	1	27.	25.48	31.50	20.59	8	1
15.0	258	3	1	35.	25.02	32.40	21.41	8	1
15.0	258	6	1	54.	24.50	32.76	21.83	8	1
15.0	258	6	2	28.	24.50	32.76	21.83	8	1
15.0	258	6	9	14.	24.50	32.76	21.83	8	1
15.0	258	21	1	10.	22.06	33.22	22.88	8	3
16.0	258	0	1	1058.	25.62	31.82	20.79	8	1
16.0	258	1	1	166.	25.62	32.02	20.94	8	1
16.0	258	23	1	22.	21.58	32.58	22.52	8	3
1.0	271	3	14	118.	24.30	12.43	6.64	3	0
2.0	271	3	7	51.	24.04	16.33	9.63	3	0
2.0	271	6	1	20.	23.64	16.26	9.68	3	0
3.0	271	3	7	278.	24.20	18.76	11.40	5	0
3.0	271	6	1	37.	23.48	18.33	11.27	5	0
3.0	271	8	1	187.	23.80	18.33	11.19	5	0
3.0	271	8	8	53.	23.80	18.33	11.19	5	0
4.0	271	3	3	9.	24.64	21.43	13.28	7	0



ST	DATE	Z	SP	ABUN	TEMP	SAL	SIG-T	T	P
4.0	271	3	7	164.	24.64	21.43	13.28	7	0
4.0	271	6	1	27.	24.83	21.30	13.13	7	0
4.0	271	6	3	27.	24.83	21.30	13.13	7	0
4.0	271	6	7	13.	24.83	21.30	13.13	7	0
4.0	271	6	8	13.	24.83	21.30	13.13	7	0
4.0	271	10	1	8.	25.09	21.51	13.21	7	0
4.0	271	10	8	8.	25.09	21.51	13.21	7	0
5.0	271	0	7	1.	25.13	23.03	14.34	7	0
5.0	271	3	1	12.	25.12	23.16	14.44	7	0
5.0	271	3	3	12.	25.12	23.16	14.44	7	0
5.0	271	3	7	1283.	25.12	23.16	14.44	7	0
5.0	271	3	8	36.	25.12	23.16	14.44	7	0
5.0	271	6	1	4.	25.22	23.10	14.36	7	0
5.0	271	6	3	24.	25.22	23.10	14.36	7	0
5.0	271	6	6	16.	25.22	23.10	14.36	7	0
5.0	271	6	7	324.	25.22	23.10	14.36	7	0
5.0	271	8	1	70.	24.93	22.97	14.35	7	0
5.0	271	8	3	4.	24.93	22.97	14.35	7	0
5.0	271	8	7	9.	24.93	22.97	14.35	7	0
5.0	271	8	8	18.	24.93	22.97	14.35	7	0
6.0	271	3	1	13.	23.96	23.41	14.95	1	0
6.0	271	3	2	13.	23.96	23.41	14.95	1	0
6.0	271	3	6	13.	23.96	23.41	14.95	1	0
6.0	271	13	1	135.	24.06	23.62	15.08	1	0
6.0	271	13	2	35.	24.06	23.62	15.08	1	0
6.0	271	13	3	14.	24.06	23.62	15.08	1	0
6.0	271	13	4	9.	24.06	23.62	15.08	1	0
6.0	271	13	7	13.	24.06	23.62	15.08	1	0
6.0	271	13	8	26.	24.06	23.62	15.08	1	0
7.0	271	0	7	1.	24.22	24.22	15.49	1	0
7.0	271	3	7	20.	24.00	24.45	15.72	1	0
7.0	271	6	2	4.	23.87	24.68	15.93	1	0
7.0	271	6	7	26.	23.87	24.68	15.93	1	0
7.0	271	10	2	14.	23.80	24.42	15.76	1	0
7.0	271	10	7	28.	23.80	24.42	15.76	1	0
8.0	271	6	2	13.	23.94	26.00	16.90	1	0
8.0	271	6	7	30.	23.94	26.00	16.90	1	0
8.0	271	10	1	187.	24.24	26.02	16.83	1	0
8.0	271	10	2	25.	24.24	26.02	16.83	1	0
8.0	271	10	7	5.	24.24	26.02	16.83	1	0
8.0	271	10	8	10.	24.24	26.02	16.83	1	0
12.0	272	1	4	25.	23.51	27.61	18.24	8	1
12.0	272	1	7	25.	23.51	27.61	18.24	8	1
12.0	272	3	7	63.	23.52	27.59	18.22	8	1
12.0	272	6	1	71.	23.36	28.78	19.16	8	2
12.0	272	6	2	9.	23.36	28.78	19.16	8	2
12.0	272	6	7	57.	23.36	28.78	19.16	8	2
12.0	272	12	2	16.	23.43	30.01	20.07	8	3
12.0	272	12	3	1.	23.43	30.01	20.07	8	3
12.0	272	12	4	3.	23.43	30.01	20.07	8	3
12.0	272	12	7	1.	23.43	30.01	20.07	8	3
12.0	272	12	8	38.	23.43	30.01	20.07	8	3

ST	DATE	Z	SP	AEUN	TEMP	SAL	SIG-T	T	P
19.0	272	0	1	1792.	24.40	32.50	21.66	8	1
19.0	272	0	10	272.	24.40	32.50	21.66	8	1
19.0	272	1	1	438.	24.38	31.68	21.05	8	1
19.0	272	1	2	26.	24.38	31.68	21.05	8	1
19.0	272	1	10	116.	24.38	31.68	21.05	8	1
19.0	272	3	1	190.	22.93	32.26	21.91	8	2
19.0	272	3	2	490.	22.93	32.26	21.91	8	2
19.0	272	3	7	20.	22.93	32.26	21.91	8	2
19.0	272	3	10	50.	22.93	32.26	21.91	8	2
19.0	272	6	1	9.	23.04	32.51	22.06	8	3
19.0	272	6	2	30.	23.04	32.51	22.06	8	3
19.0	272	6	7	39.	23.04	32.51	22.06	8	3
19.0	272	6	8	4.	23.04	32.51	22.06	8	3
19.0	272	6	10	4.	23.04	32.51	22.06	8	3
19.0	272	8	1	19.	23.04	32.51	22.06	8	3
19.0	272	8	2	8.	23.04	32.51	22.06	8	3
19.0	272	8	7	3.	23.04	32.51	22.06	8	3
19.0	272	8	8	19.	23.04	32.51	22.06	8	3
19.0	272	8	9	98.	23.04	32.51	22.06	8	3
19.0	272	8	10	11.	23.04	32.51	22.06	8	3
13.0	272	1	1	15.	23.52	29.60	19.73	8	1
13.0	272	1	2	15.	23.52	29.60	19.73	8	1
13.0	272	3	1	12.	23.54	29.89	19.94	8	2
13.0	272	3	2	106.	23.54	29.89	19.94	8	2
13.0	272	3	3	12.	23.54	29.89	19.94	8	2
13.0	272	3	9	24.	23.54	29.89	19.94	8	2
13.0	272	6	1	100.	23.52	30.87	20.69	8	2
13.0	272	6	2	67.	23.52	30.87	20.69	8	2
13.0	272	6	7	24.	23.52	30.87	20.69	8	2
13.0	272	11	1	6.	23.33	31.88	21.51	8	3
13.0	272	11	2	25.	23.33	31.88	21.51	8	3
13.0	272	11	9	3.	23.33	31.88	21.51	8	3
18.0	272	0	1	30.	22.96	31.68	21.46	8	0
18.0	272	0	10	19.	22.96	31.68	21.46	8	0
18.0	272	1	1	31.	22.71	31.93	21.72	8	0
18.0	272	1	10	188.	22.71	31.93	21.72	8	0
18.0	272	3	1	127.	22.77	32.00	21.75	8	0
18.0	272	3	2	6.	22.77	32.00	21.75	8	0
18.0	272	3	10	105.	22.77	32.00	21.75	8	0
18.0	272	6	1	359.	22.37	32.20	22.02	8	0
18.0	272	6	2	91.	22.37	32.20	22.02	8	0
18.0	272	6	3	13.	22.37	32.20	22.02	8	0
18.0	272	6	9	17.	22.37	32.20	22.02	8	0
18.0	272	6	10	130.	22.37	32.20	22.02	8	0
18.0	272	12	2	13.	22.52	31.68	21.58	8	0
18.0	272	12	9	26.	22.52	31.68	21.58	8	0
18.0	272	12	10	13.	22.52	31.68	21.58	8	0
14.0	272	0	1	1.	23.02	30.50	20.55	8	1
14.0	272	0	3	1.	23.02	30.50	20.55	8	1
14.0	272	0	6	6.	23.02	30.50	20.55	8	1
14.0	272	3	1	262.	23.18	30.50	20.51	8	1
14.0	272	3	2	116.	23.18	30.50	20.51	8	1

ST	DATE	Z	SP	ABUN	TEMP	SAL	SIG-T	T	P
14.0	272	3	3	29.	23.18	30.50	20.51	8	1
14.0	272	3	9	116.	23.18	30.50	20.51	8	1
14.0	272	3	10	29.	23.18	30.50	20.51	8	1
14.0	272	6	1	398.	23.44	32.12	21.66	8	2
14.0	272	6	2	13.	23.44	32.12	21.66	8	2
14.0	272	6	9	81.	23.44	32.12	21.66	8	2
14.0	272	6	10	21.	23.44	32.12	21.66	8	2
14.0	272	16	9	17.	23.30	31.85	21.49	8	3
17.0	272	0	1	9.	22.70	31.77	21.60	8	0
17.0	272	0	9	1.	22.70	31.77	21.60	8	0
17.0	272	0	10	5.	22.70	31.77	21.60	8	0
17.0	272	0	12	9.	22.70	31.77	21.60	8	0
17.0	272	0	13	79.	22.70	31.77	21.60	8	0
17.0	272	3	1	33.	22.80	32.36	22.02	8	0
17.0	272	3	10	11.	22.80	32.36	22.02	8	0
17.0	272	6	1	244.	22.68	32.81	22.39	8	0
17.0	272	6	2	25.	22.68	32.81	22.39	8	0
17.0	272	6	9	13.	22.68	32.81	22.39	8	0
17.0	272	6	10	93.	22.68	32.81	22.39	8	0
17.0	272	17	1	2.	22.66	32.28	22.00	8	0
17.0	272	17	9	3.	22.66	32.28	22.00	8	0
17.0	272	17	10	5.	22.66	32.28	22.00	8	0
15.0	272	0	11	15.	23.38	31.70	21.36	8	0
15.0	272	3	1	84.	23.30	31.78	21.44	8	0
15.0	272	6	1	203.	23.32	31.94	21.55	8	0
15.0	272	6	2	9.	23.32	31.94	21.55	8	0
15.0	272	6	9	27.	23.32	31.94	21.55	8	0
15.0	272	6	10	133.	23.32	31.94	21.55	8	0
16.0	272	0	1	2.	22.98	31.84	21.57	8	1
16.0	272	0	11	8.	22.98	31.84	21.57	8	1
16.0	272	1	1	26.	22.98	31.98	21.68	8	1
16.0	272	3	1	251.	22.66	32.18	21.92	8	1
16.0	272	3	11	39.	22.66	32.18	21.92	8	1
16.0	272	6	1	214.	22.98	32.16	21.82	8	1
16.0	272	6	10	34.	22.98	32.16	21.82	8	1
16.0	272	21	1	6.	21.60	32.42	22.40	8	3
16.0	272	21	9	8.	21.60	32.42	22.40	8	3

## AUTOBIOGRAPHICAL STATEMENT

Born in Beaufort, North Carolina on 24 September 1951. Graduated from University of North Carolina, Chapel Hill in May 1973 with a B.S. in Biology with honors. Graduated from Emory University, Atlanta, Georgia in May 1977 with a M.S. in Biology. Entered the Oceanography Department, Old Dominion University in September 1978.

Honors and awards include: Fellowship, Scholarship, Teaching Assistantship and election to Phi Sigma at Emory University; Teaching Assistantship, Research Assistantship and election to Phi Kappa Phi and Sigma Xi at Old Dominion University.

Since 1973 the following positions have been held: Research Assistant at Duke University, Clinical Toxicology Instructor at Mercer University, and a Microbiologist at the Center for Disease Control, Atlanta, Georgia.

### Publications

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Johnson, D. F. 1981. The use of recruitment mechanisms by the megalopae of selected Brachyuran Crustaceans of the lower Chesapeake Bay and inner Continental Shelf. Estuaries 4:277 (Abstract).

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- Provenzano, A. J., J. R. McConaughy, K. Philips, D. F. Johnson, J. Clark. 1982. Vertical distribution of first stage larvae of the blue crab, Callinectes sapidus, in the mouth of the Chesapeake Bay. Estu. Coast. and Shelf Sci. (in press).