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The Relationship of Habitat and Spatial Scale Upon the Developmental State and Settlement of Blue Crab Postlarvae in Chesapeake Bay

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THE RELATIONSHIP OF HABITAT AND SPATIAL SCALE UPON THE DEVELOPMENTAL STATE AND SETTLEMENT OF BLUE CRAB POSTLARVAE IN CHESAPEAKE BAY

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ABSTRACT

Developmental state of blue crab postlarvae was identified in planktonic and benthic megalopae from within and outside Chesapeake Bay on various spatial scales. Planktonic megalopae advanced significantly in developmental state from the continental shelf, off the Chesapeake Bay mouth, through upriver stations in the York River, a tributary of Chesapeake Bay. This developmental evidence supports the export-reinvasion theory of blue crab recruitment, and is inconsistent with a retention hypothesis for blue crab larval recruitment. In the tributary, benthic megalopae were significantly more advanced in developmental state than planktonic megalopae. Temporal variation in developmental state was also observed over days and months. In addition, time to metamorphosis was significantly and positively correlated with developmental state. These results suggest that advancement in developmental state of megalopae during reinvasion of the estuary may act as a predictor of likelihood of settlement on a baywide scale.

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INTRODUCTION

BLUE CRAB LIFE HISTORY

Female blue crabs, *Callinectes sapidus* Rathbun, release larvae at the mouth of Chesapeake Bay in early summer through fall (Van Engel 1958, Provenzano et al. 1983). In continental shelf waters larvae develop through seven zoeal stages (Costlow 1967, McConaugha et al. 1983, Epifanio et al. 1989), before metamorphosis into the postlarval stage, or megalopa. The megalopal stage lasts from 20 to 40 days (Sulkin and Van Heukelem 1986), and is followed by metamorphosis into the first juvenile instar, which initiates a benthic existence.

In attempts to elucidate recruitment mechanisms of the blue crab, various authors have examined the distribution of larvae and postlarvae relative to estuarine nurseries. Early zoeal stages are common at the estuary mouths, while later zoeal stages are generally only collected offshore (Johnson 1985, Epifanio et al. 1984). Megalopae have been collected offshore, as well as within the Chesapeake Bay (Sandifer 1973). Thus current theory holds that blue crab larvae are released at the estuary mouth and transported offshore, subsequently to reinvade the estuary as postlarvae. Various details of estuarine reinvasion by blue crab megalopae are unclear. In particular, the relationship between developmental state, habitat features and settlement are little understood, except on relatively small spatial scales (Lipcius et al. 1990).

Several forces have been proposed as causes for recruitment into the estuary, ranging from wind-driven surface circulation (Goodrich et al. 1989, Johnson and Hess 1990, Little and Epifanio 1991), to tidally-related migrations (Epifanio et al. 1984, Epifanio 1988), residual bottom flow (Dittel and Epifanio 1982, Biocourt 1982) or a combination of these (Sulkin and Van Heukelem 1982). Regardless of the mode of transport employed by the megalopa in its reinvasion, it begins a benthic existence upon return to the estuary, followed by metamorphosis to the first juvenile instar. Details of the megalopa's transit from the continental shelf into the estuary may be elucidated by an examination of developmental state relative to several spatial scales relevant to the megalopa's movements.

ONTOGENY AND SETTLEMENT

The retention in, or return to, estuaries by larvae in general appears to have been well explained in terms of stage-specific larval responses to environmental variables (Hadfield 1986). Behavioral and morphological changes have often been noted in fish larvae prior to metamorphosis (see Boehlert and Mundy 1988 for review). Invertebrate larvae tend to go from being photopositive and/or geonegative to being photonegative and/or geopositive (see Cameron 1986 for review). In blue crabs, ontogenetic changes take place between and within zoeal and megalopal stages which reverse taxis and kinesis responses (see Sulkin 1984 for review). Stage I larvae of blue crabs are negatively geotactic, but as zoeal development proceeds, the sign of geotaxis shifts (Sulkin et al 1980). In intermediate stages, response to gravity varies with ambient salinity. By the seventh and terminal zoeal stage, larvae are all positively geotactic (Sulkin et al. 1980). Upon molt to the megalopa, the negative geotactic response is again prevalent (Sulkin and Van Heukelem 1982). Megalopae have a greater sensitivity to pressure changes than late stage larvae and an increased rate of sinking (Sulkin and Van Heukelem 1982). They show evidence of a fall in barokinetic response and movement to deeper in the water column as metamorphosis approaches (Naylor and Isaac 1973, Sulkin and Epifanio 1986).

THE MOLT CYCLE AND METAMORPHOSIS

Growth in crustaceans is effected through the processes leading up to and following ecdysis (Passano 1960). A classification system proposed by Drach (1939) quantifies these stages (A-D), each of which corresponds to specific morphological and physiological transformations of the integument. These molt stages are a means of assessing developmental state. By examining the extent of retraction of the epidermis from the cuticle, molt stages may be quantified easily and objectively, and thereby used in quantitative analysis of developmental state of recruiting postlarvae. The status of the cuticle relative to the epidermis is the key feature in molt staging.

Behavioral and morphological changes associated with the molt cycle have been noted in several crustaceans. These changes affect several areas of behavior. For example, proximity to molting has a strong influence on food consumption in *Idotea baltica*, an isopod crustacean (Strong and Daborn 1980). Tamm and Cobb (1978) revealed dramatic changes in aggressive behavior through the molt cycle of juvenile

American lobster. Subadult spiny lobster also reveal characteristic patterns of behavior as a function of molt stage. These patterns are exhibited as changes in locomotor, feeding and agonistic behavior (Lipcius and Herrnkind 1982). American lobster larvae exhibit differences in swimming behavior as a function of developmental state (Cobb et al. 1983, Ennis 1975).

Blue crabs, as well, exhibit these characteristic changes in behavior as a function of developmental state. Adult crabs partition habitats by molt stage using salt creeks and grassbeds as molting habitats (Hines et al. 1987, Ryer et al. 1990). Blue crab megalopae show evidence of a fall in barokinetic response (Naylor and Isaac 1973) and movement deeper in the water column (Sulkin and Epifanio 1986) as they age.

Past studies have stressed the spatial distribution of crab postlarvae (megalopae) relative to developmental state (Hatfield 1983) or temporal changes in developmental state of blue crab megalopae (Lipcius et al. 1990), but none have examined large and small scale variation in postlarval developmental state relative to the combination of space, time, and habitat type. In this study the developmental state of blue crab megalopae is related to physical and biotic factors. Specifically, molt stage is examined in relation to geographic location over large (10's of km) and small (km) spatial scales as a test of larval export and reinvasion patterns. Habitat and time are examined as factors causing differences in developmental state in relation to settlement sites and temporal patterns. Developmental evidence is provided in support of the export and reinvasion theory for megalopal recruitment into Chesapeake Bay, and in support of the hypothesis that settlement propensity of megalopae likely varies over broad spatial scales in Chesapeake Bay.

METHODS

Molt Staging and Time to Metamorphosis

Molt staging has been used successfully to assess developmental state in crustaceans since Drach (1939). This technique inspects microscopic changes in the integument of numerous crustacean body parts, such as pleopods (Aiken 1973), rostra (Anger 1983), scaphognathites (Van Herp and Bellon-Humbert 1978) and maxillipeds (Hatfield 1983). By examining the extent of retraction of the epidermis from the cuticle, molt stages may be identified easily and objectively, and thereby used in the quantitative analysis of developmental state of recruiting postlarvae. Molt stage was identified in planktonic megalopae by examining setal development and the extent of epidermal retraction from the cuticle in the uropods and second maxillipeds under a compound microscope (45X). Molt stages were based on Aiken's (1973) morphological criteria (Table 1).

To verify the consistency of the molt staging technique, the frequencies of each molt stage observed in the uropods were compared with their corresponding stages observed in the maxillipeds. A paired t-test compared uropod versus maxilliped molt stages for 471 megalopae. The Pearson product moment correlation coefficient was also calculated to show the degree of linear relationship between uropod and maxilliped molt stages.

Megalopae were collected in 1-m diameter, 750-micron mesh neuston nets at maximum nocturnal flood tide off the VIMS pier (station R2, Fig. 1) on 27 July 1989 and molt staged. They were held separately in aerated bowls containing York River water at 17 ± 1ppt and 21 ± 2°C. Every 3 hours, each of 24 megalopae ($n \geq 4$ for each stage) were checked for metamorphosis. Time elapsed until metamorphosis into the first juvenile instar was recorded. Time to metamorphosis was regressed on initial uropod molt stage using simple linear regression.

Developmental State Along the Axis of the York River and Chesapeake Bay

To quantify spatial variation in developmental state over a geographic range, molt stages of megalopae from two transects were examined, one from the continental shelf off the mouth of Chesapeake Bay into the York River and one along the axis of flow within the York River (Fig. 1). Duplicate samples of 10 megalopae each were collected for the bay transect on 5 September and 5 October 1990 at each of four locations during nocturnal flood tide. Stations sampled were: offshore, east of the bay mouth (station B1, 22 km outside the bay mouth); near the bay mouth (station B2); in the bay mainstem (station B3, 26 km inside the bay mouth); and in the York River (station B4, 50 km from the bay mouth). For the river transect, samples were collected at maximum nocturnal flood tide on 18 October 1989. Two replicate samples of at least 10 megalopae each were taken at three locations: near the river mouth (station S, 5.9 km upstream), 12 km upstream, and (station R2) 18.7 km upstream. All megalopae were collected in a pair of 750-micron mesh, 1-m diameter neuston nets. Each sample provided a single, independent datum as a proportion in premolt stages for subsequent statistical analysis. Molt stage was identified in the uropods and maxillipeds within two hours of collection, as described previously. For the baywide data in 1990, proportion premolt was correlated with distance from the shelf. At the stations where premolt megalopae occurred in greater than 50 % of the sample (station B3 and station B4), analysis of variance was performed on premolt stage by the factors location and month. In addition, molt stage was correlated with distance upriver for the river transect data of 1989.

Spatial and Temporal Variation in Developmental State

To quantify spatial and temporal variation in developmental state of megalopae within the York River, molt stages of megalopae were examined during two recruitment episodes starting on the full moon (16-21 September and 15-20 October 1989) in two habitat types (plankton and benthos), and at two locations (upriver and downriver). The downriver station, Sandy Point (station S, Fig. 1), was located 1.4 km from the mouth of the York River and characterized by shallow beds of eelgrass, *Zostera marina*, and widgeongrass, *Ruppia maritima*. The second location, VIMS (station R2, Fig. 1), was 10.6 km upriver from Sandy Point and also characterized by shallow eelgrass beds. These seagrass beds serve as a settlement habitat for blue crab megalopae (Orth and van Montfrans 1990).

At each of the two sites, replicate samples of 10 megalopae were taken from the plankton and benthos. Plankton samples were collected at maximum nocturnal flood tide with paired neuston nets (750-micron mesh). Benthic samples were collected using a suction sampler swept along the bottom in seagrass beds on the morning following the corresponding plankton sample (Orth and van Montfrans 1987).

Samples were molt staged (using the uropods) within two hours of collection to preclude advancement through the molt cycle. In addition, October samples were also molt staged in the maxillipeds. Log-likelihood analysis of molt stage frequencies (Sokal and Rohlf 1981) was used instead of ANOVA because of incomplete replication of habitat types at the downriver location. Individual megalopae were widely dispersed and only together in the sampling apparatus for a short time. Each megalopa was, therefore, assumed to be independent. A four-factor, log-likelihood analysis was conducted on uropod molt stage frequencies for both months; the factors were: habitat, location, day, and month. A three-factor log-likelihood analysis was conducted on maxilliped molt stage frequencies; the factors were: habitat, location and day.

RESULTS

Molt Staging and Time to Metamorphosis

Time to metamorphosis was significantly and negatively correlated with uropod molt stage (Fig. 2; $Y = 51.7 - 19.0X$, $r^2 = 0.73$, $P < 0.01$). Megalopae in early premolt took 21 - 47 hours to molt, while those in the most advanced stages molted in 3 - 6 hours. Hence, time to metamorphosis is inversely related to developmental state, even over the relatively narrow range of molt stages examined here.

Maxillipeds were significantly more advanced in molt stage than uropods (Fig. 3; paired t-test, $t = 52.7$, $df = 470$, $P < 0.01$). The range in uropod molt stages was between D_0 1.0 and D_1'' 3.5, while maxilliped molt stages ranged from D_0 1.0 to D_3' 5.5. Maxilliped and uropod molt stages were positively correlated (Fig. 3; $r = 0.622$, $df = 470$, $P < 0.001$).

Developmental State Along the Axis of the York River and Chesapeake Bay

Along the Chesapeake Bay transect, the proportion of megalopae in premolt was significantly and positively correlated with distance from the shelf ($Y = 0.278 + 0.00896\,X$, $r^2 = 0.67$, $P < 0.01$, Fig. 4). Those megalopae within the estuary were much more advanced in developmental state than those near the bay mouth and offshore, though there was a substantial proportion in premolt on the continental shelf (Fig 4). For the stations with the most developmentally advanced megalopae (bay mainstem and York River), molt stage proportions differed by station and month.

There were proportionally fewer megalopae in advanced molt stages during September than during October (ANOVA, F = 6.84, df = 1, 64, $P = 0.01$). Megalopae from the station in the bay mainstem were significantly less advanced than those collected at the York River station (ANOVA, F = 11.06, df = 1, 64, $P < 0.01$). Developmental state was significantly and positively correlated with distance upriver in the York River transect ($Y = 1.53 + 0.0233X$, $r^2 = 0.06$, $P = 0.04$). Those megalopae upriver were more advanced than those near the mouth (Fig. 5), though the absolute difference was small relative to that in the bay transect.

Spatial and Temporal Variation in Developmental State

Uropod

The effect of day on uropod molt stage was not significant in any cases (G-test, G = 3.37, df = 2, $P = 0.19$). In both the plankton and benthos, molt stage frequencies were significantly more advanced in October than September (G-test, plankton - G = 21.01, df = 2, $P < 0.01$, benthos - G = 27.69, df = 2, $P < 0.010$, Fig. 6). This pattern is similar to that observed in the Bay transect. The effect of geographic location on uropod molt stage frequency was only significant in benthic samples from October, such that upriver samples were more advanced than downriver samples (G-test, G = 4.24, df = 2, $P = 0.01$, Fig. 6). Megalopae in September showed no significant effect of geographic location (G-test, G = 1.11, df

= 2, $P = 0.57$, Fig. 6). Molt stages from planktonic megalopae did not differ significantly with location in October (G-test, G = 2.56, df = 2, $P = 0.28$, Fig. 6).

The effect of habitat on molt stage frequency varied over the locations sampled. For upriver stations, planktonic megalopae were significantly less advanced than those of the benthos, although the degree of significance varied with month sampled (G-test, September - G = 6.62, df = 2, $P = 0.04$; October - G = 29.59, df = 2, $P < 0.01$, Fig. 6). At the downriver station, habitat differences were significant only in September (G-test, G = 9.43, df = 2, $P = 0.01$, Fig. 6). At that station in October, there was no significant difference in the molt stages of megalopae collected in the plankton versus those in the benthos (G-test, G = 2.54, df = 2, $P = 0.27$).

Maxilliped

Megalopae showed a significant increasing trend in maxilliped molt stage over the five day period following the full moon in October (G-test, G = 10.89, df = 2, $P < 0.01$). As with the uropod molt stages, maxilliped molt stages were significantly more advanced in the benthos than in the plankton at the upriver location (G-test, G = 24.17, df = 2, $P < 0.01$, Fig. 7). Megalopae collected near the river mouth did not show a significant effect of habitat type (G-test, G = 0.96, df = 2, $P = 0.62$). Benthic megalopae were significantly more advanced in maxilliped molt stage from the upriver station than the downriver station (G-test, G = 11.63, df = 2, $P < 0.01$,

Fig. 7). Megalopae in the plankton showed no trend with location (G-test, $G = 1.83$, $df = 2$, $P = 0.40$).

DISCUSSION

It has been shown that blue crab megalopae undergo a progression in developmental state from the continental shelf into the Chesapeake Bay and one of its tributaries (York River). On a baywide scale, megalopae advance significantly in developmental state with distance from the shelf. There may also be a trend in habitat type on this scale but this has not been investigated. On a riverwide scale, megalopae advance in developmental state with habitat type and to a lesser degree with distance from the mouth of the York River. This progression is consistent with a recruitment model postulating that blue crab megalopae reinvade the Chesapeake Bay after being exported onto the continental shelf as larvae (Sulkin and Van Heukelem 1982), and inconsistent with the hypothesis that estuarine crab larvae and megalopae are retained in Chesapeake Bay (Van Engel 1958). The inconsistency lies in the orderly progression in developmental state from the shelf to the York River; the retention hypothesis would predict a progression from the bay mouth out to the shelf (larvae and megalopae lost from the bay system) and a similar progression from the bay mouth to its tributaries (retained larvae and megalopae). The ontogenetic evidence strengthens the ecological evidence from this study in support of the export and reinvasion hypothesis for blue crab larvae and megalopae.

Data from the 1990 Chesapeake Bay transects described above qualitatively predicted developmental stages in the York River based on the regression equation comparable to those found in 1987-1989 sampling (Lipcius et al. 1990 and the current study) and those expected by the export-reinvasion hypothesis. Molt stages of animals within the York River advanced with distance upriver. Quantitatively, the regression model for the bay transect from the present study predicted that 85% of the megalopae collected on the full moon in the plankton would be in premolt at the York River mouth. For 1987 data (Lipcius et al. 1990), the proportion in premolt was slightly lower (at station A, Fig. 1). The 1989 data have a proportion in premolt higher than that predicted based on the bay transect data. The upriver station (station R2) from the 1987 and 1989 data more closely conform to the prediction of 97% for that location. There, in 1987, 81%-100% of the collected animals were in premolt stages. In 1989, 100% of those collected were in premolt in the York River.

The variation in proportion premolt relative to the predicted values may be due to temporal variation in developmental state. It has been shown that developmental state varies on the order of days and months, and may also vary interannually. Quantitatively, the molt stages predicted by these data are not the same as those from past studies, but qualitatively, the trends are equivalent. The usefulness of molt stage for predicting settlement within the York River is limited. On a baywide scale it is clear that developmental state will act as a good predictor of settlement since those megalopae of the most advanced molt stages are the same as those nearing settlement to the benthos.

Maxilliped molt stages showed an increasing trend in developmental state over a period of days. Planktonic availability of megalopae pulses on and around the new and full moon during the summer and fall months (Olmi et al. 1990). A group of animals may reinvade the estuary at one of these times, advancing in developmental state as they progress upriver. Previous authors have also revealed a similar trend in developmental state over a period of days (Lipcius et al. 1990). Variation in developmental state over timescales of months and years may be the result of variation in the physical factors which influence larval development and transport. The location on the shelf at which a megalopa first appears (and its consequent developmental state at a particular location) will be a function of the duration of zoeal development and the characteristics of the currents in which the zoeae have been entrained (Sulkin and Van Heukelem 1986). Variable wind speeds and river flows are known to cause simulated blue crab larvae to travel at different rates, and Johnson and Hess (1990) found reinvasion of simulated larvae to be variable within and between years. Variations in salinity and temperature will also affect the rate of development of larvae and postlarvae (Costlow and Bookhout 1959, Costlow 1967). Ontogenetic changes in vertical distribution during larval development can influence dispersal not only by subjecting larvae to changes in circulation, but also by influencing length of larval development (Sulkin and Van Heukelem 1986).

Sulkin and Epifanio (1986) suggest that newly metamorphosed megalopae will remain near the surface, whereas advanced megalopae migrate to bottom waters. A wind event could potentially alter the ratio of early:late megalopae and affect monthly and yearly variation in developmental state. Smallscale patchiness, current patterns, and megalopal behavior have all been implicated in the geographic distribution of developmental states in planktonic dungeness crab megalopae (Hatfield 1983).

Habitat type has a significant effect on developmental state of megalopae. Planktonic megalopae were less advanced in developmental state than benthic megalopae. The habitat differences were most pronounced at upriver stations. This suggests either that postlarvae which are more advanced are forced by behavioral or physiological mechanisms to settle, or that postlarvae which have settled on the bottom continue through the molt cycle more rapidly. Since several planktonic megalopae were in late premolt stages, it is less likely that megalopae must settle until they have reached a more advanced 'threshold' molt stage. Behavioral observations are required to determine if megalopae settle because of impending metamorphosis, or if they metamorphose because they have settled. In either case, the progression of molt stages seems to be directly related to the timing of settlement.

The molt staging technique used as a quantitative measure of developmental state was an accurate and reliable indicator of proximity to metamorphosis. Staging of both the uropod and maxilliped produced similar results with respect to relative variation in the factors studied. The condition of the uropods is a better indicator of less advanced molt stages, while the condition of the maxillipeds most clearly discerned more advanced molt stages. A technique combining observation of both the uropod and maxilliped would be most accurate. These results were in agreement with those of another study (Lipcius et al. 1990) which found that developmental state of megalopae varies on smaller spatial and temporal scales. The present study further advances the idea that developmental state influences the timing of megalopal reinvasion and settlement.

Variation in recruitment of the blue crab may be influenced by events occurring at or near the time of settlement and metamorphosis from the larval (or postlarval) to the juvenile form (Keough and Downes 1982, Connell 1985). Factors influencing developmental stages will aid in predicting the necessary conditions for settlement and eventual recruitment into the existing adult population. The ability to evaluate the likelihood of settlement and apply a technique for assessing developmental state will help to interpret modes of settlement of benthic crustaceans.

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Table 1. Description of uropod and maxilliped characteristics visible under 45 X maginfication. After Aiken (1973)

Molt Stage	Description - Uropod and Maxilliped	Visible in uropod	Visible in maxilliped
A B C	no visible retraction of epidermis from cuticle	yes	yes
D_0 1.0	early signs of epidermal retraction	yes	no
D_0 1.5	early signs of retraction; cuticle has double bordered appearance	yes	no
D_0 2.0	epidermis clearly retracting from cuticle	yes	no
D_0 2.5	maximum epidermal retraction	yes	yes
D_1^{I} 3.0	epidermis becomes scalloped	yes	yes
D_1^{II} 3.5	invagination of new setae begins; shafts of new setae not clearly visible	yes	yes
D_1^{III} 4.0	setal shafts well defined, proximal ends not clearly defined	no	yes
D_2^{I} 4.5	barbules and proximal ends of setae clearly visible; bifurcate, not blunt	no	yes
D_2^{II} 5.0	proximal ends of setae blunt; barbules clearly visible	no	yes
D_3^{I} 5.5	shafts of setae are thick and dark, proximal ends blunt	no	yes

FIGURE LEGEND

Fig. 1. Map of Chesapeake Bay showing the locations of sampled stations. Circles represent Bay transect stations. Squares represent York river transect stations. Square 'S' and station R2 were used for habitat and location study. Square 'A' and station R2 were used as sites by Lipcius et al (1990).

Fig. 2. Mean time to metamorphosis (± s.d.) for megalopae of various molt stages. Regression line is shown.

Fig. 3. Comparison of uropod and maxilliped molt stages, expressed as frequency of animals for each stage.

Fig. 4. Mean proportion (± s.d.) of megalopae in premolt stages at bay transect stations. All megalopae collected at the station at 50 km were premolt (s.d. = 0, n = 40). Regression line is shown, as well as locations of continental shelf, Bay mouth and York River mouth.

Fig. 5. Mean uropod molt stages (± s.d.) of megalopae at York River transect stations. Regression line is shown.

Fig. 6. Proportion of megalopae collected for various uropod molt stages in the plankton (PLA) and benthos (BEN) for each station and month. a) downriver September b) upriver September c) downriver October d) upriver October. Asterisk indicates statistically significant differences between molt stage frequencies for factor combinations shown.

Fig. 7. Proportion of megalopae collected for various maxilliped molt stages in the plankton (PLA) and benthos (BEN) for each station. a) downriver b) upriver. Asterisk indicates statistically significant differences between molt stage frequencies for factor combinations shown.

Figure 1

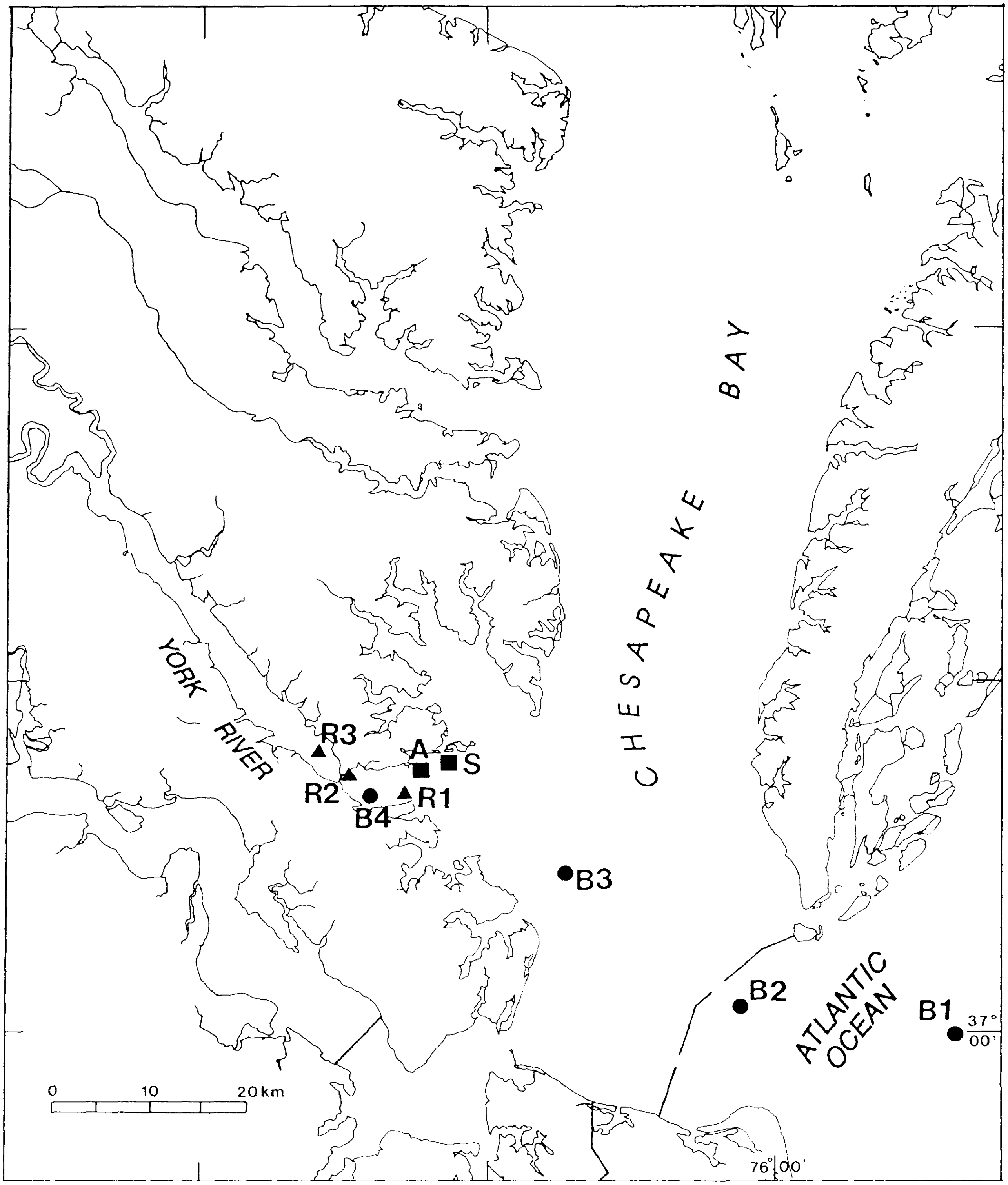
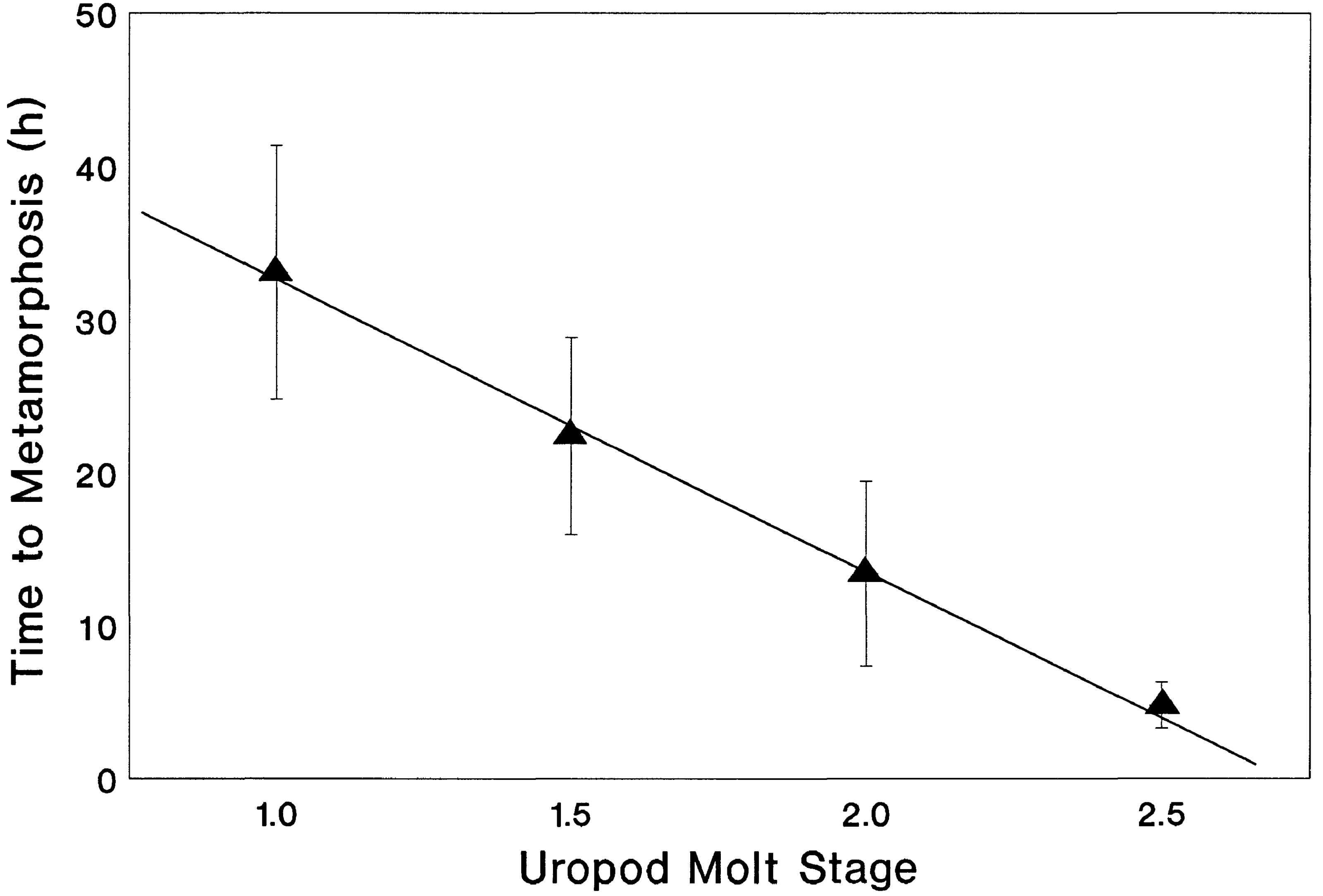

CHESAPEAKE BAY
YORK RIVER
ATLANTIC OCEAN
R3
R2
R1
A
S
B4
B3
B2
B1
37° 00'
76° 00'
0
10
20 km

Figure 2



50
40
30
20
10
0
Time to Metamorphosis (h)
1.0
1.5
2.0
2.5
Uropod Molt Stage

Figure 3

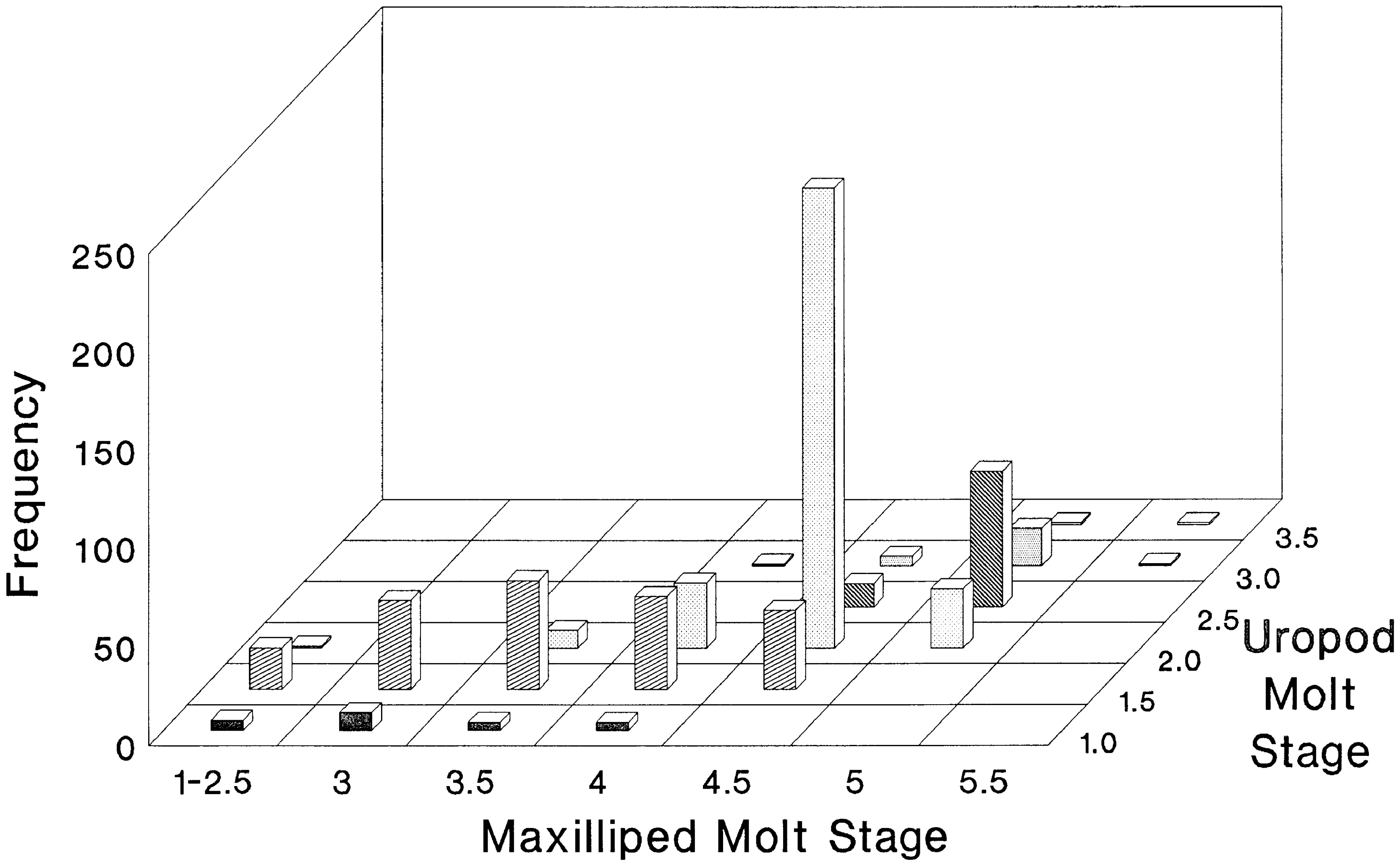

Frequency
250
200
150
100
50
0
1-2.5
3
3.5
4
4.5
5
5.5
Maxilliped Molt Stage
1.0
1.5
2.0
2.5
3.0
3.5
Uropod
Molt
Stage

Figure 4

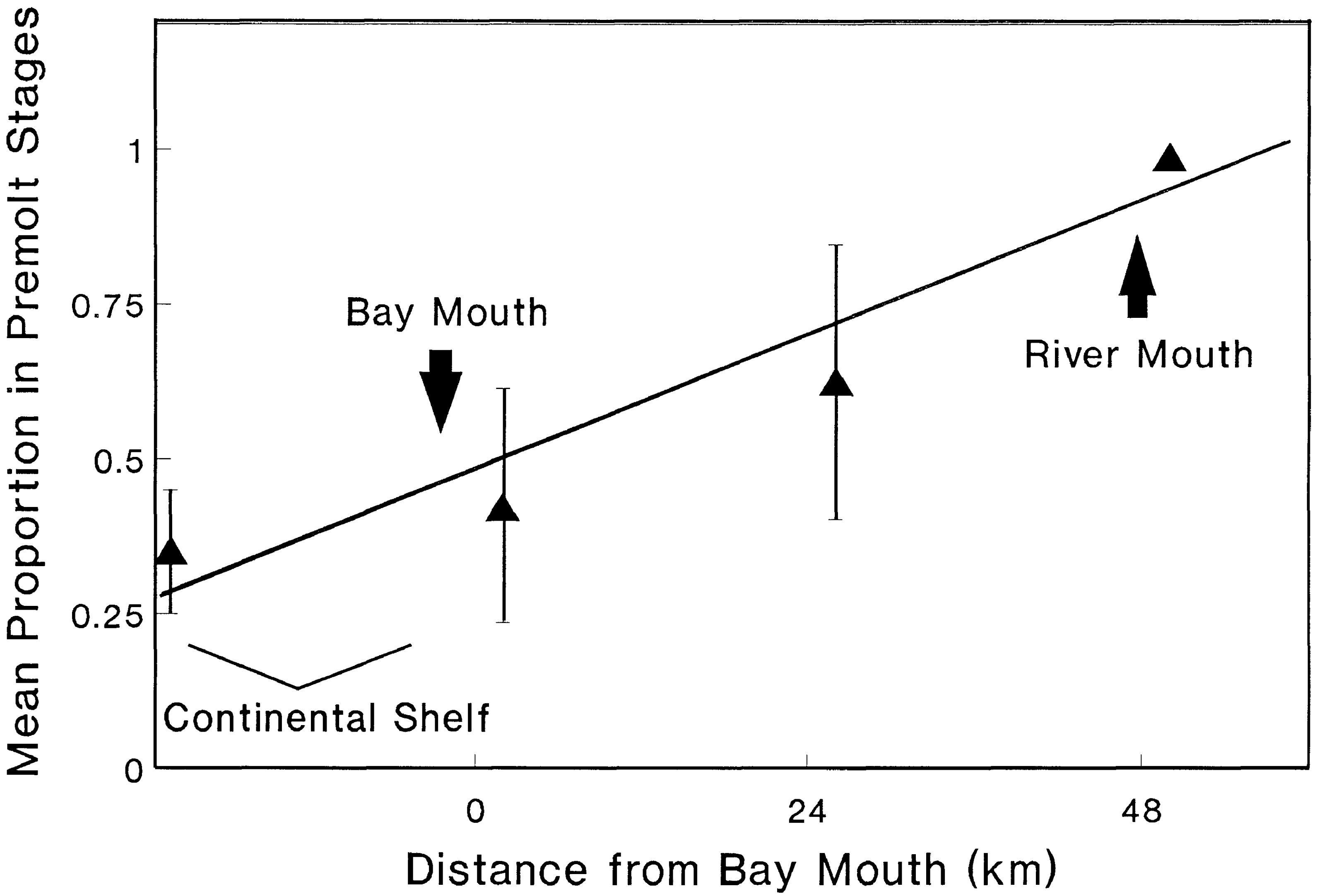

Mean Proportion in Premolt Stages
0
0.25
0.5
0.75
1
Bay Mouth
River Mouth
Continental Shelf
0
24
48
Distance from Bay Mouth (km)

Figure 5

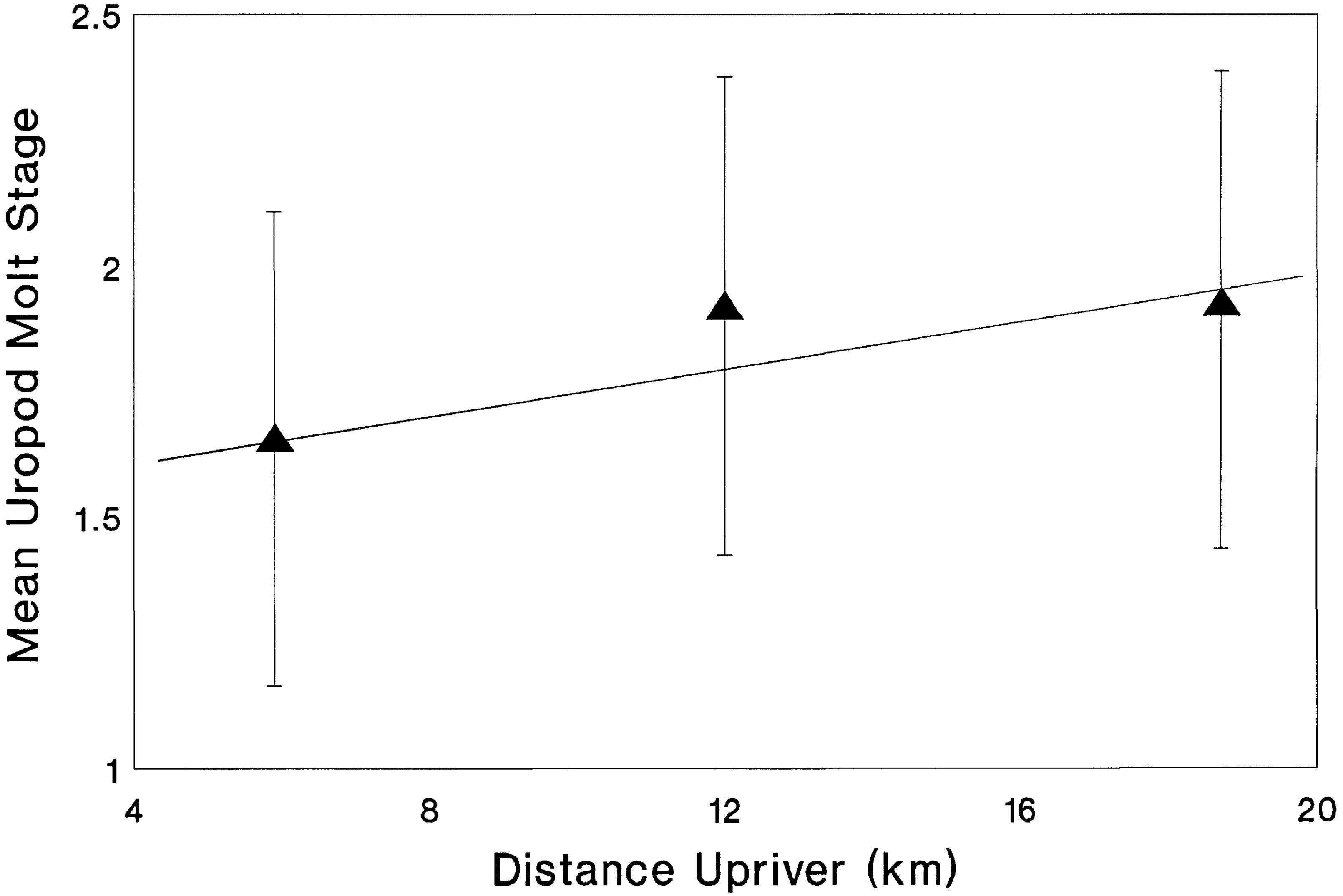

Mean Uropod Molt Stage
2.5
2
1.5
1
4
8
12
16
20
Distance Upriver (km)

Figure 6

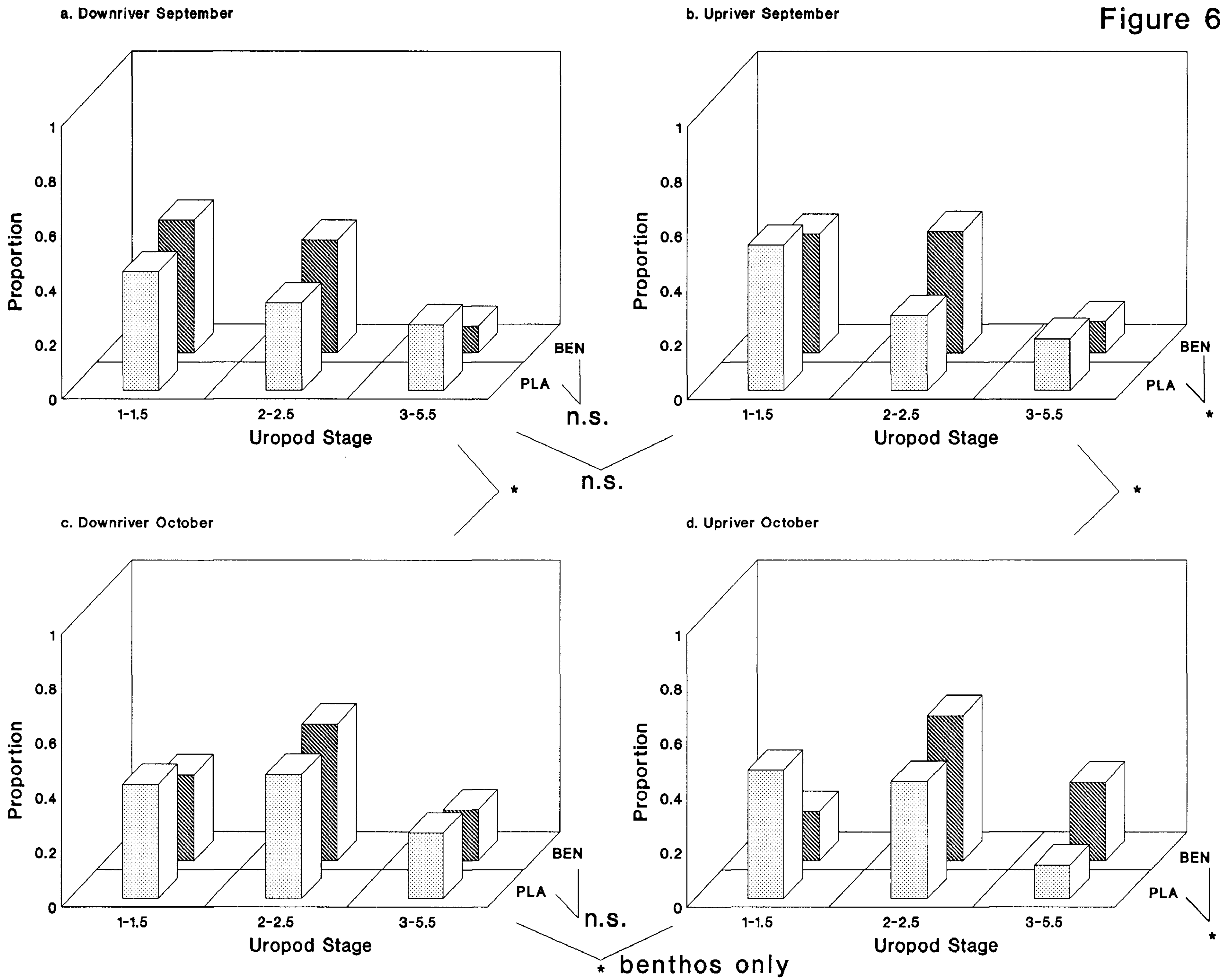
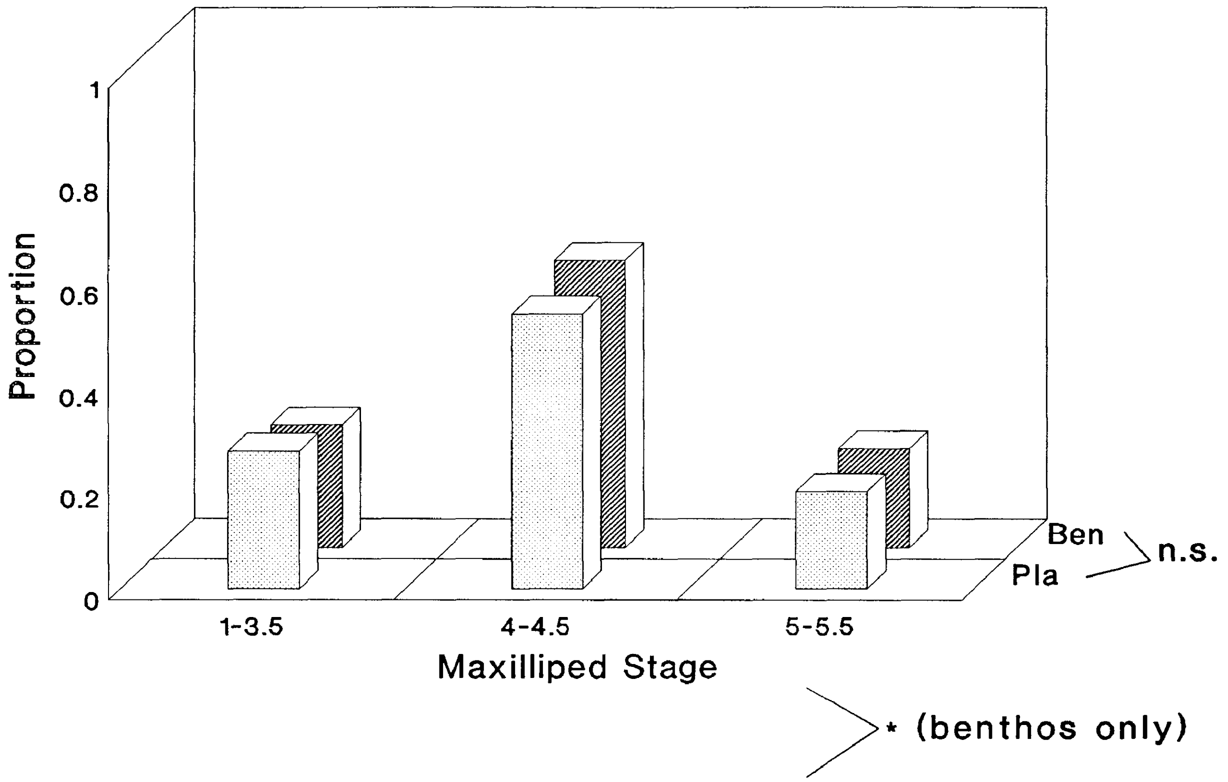
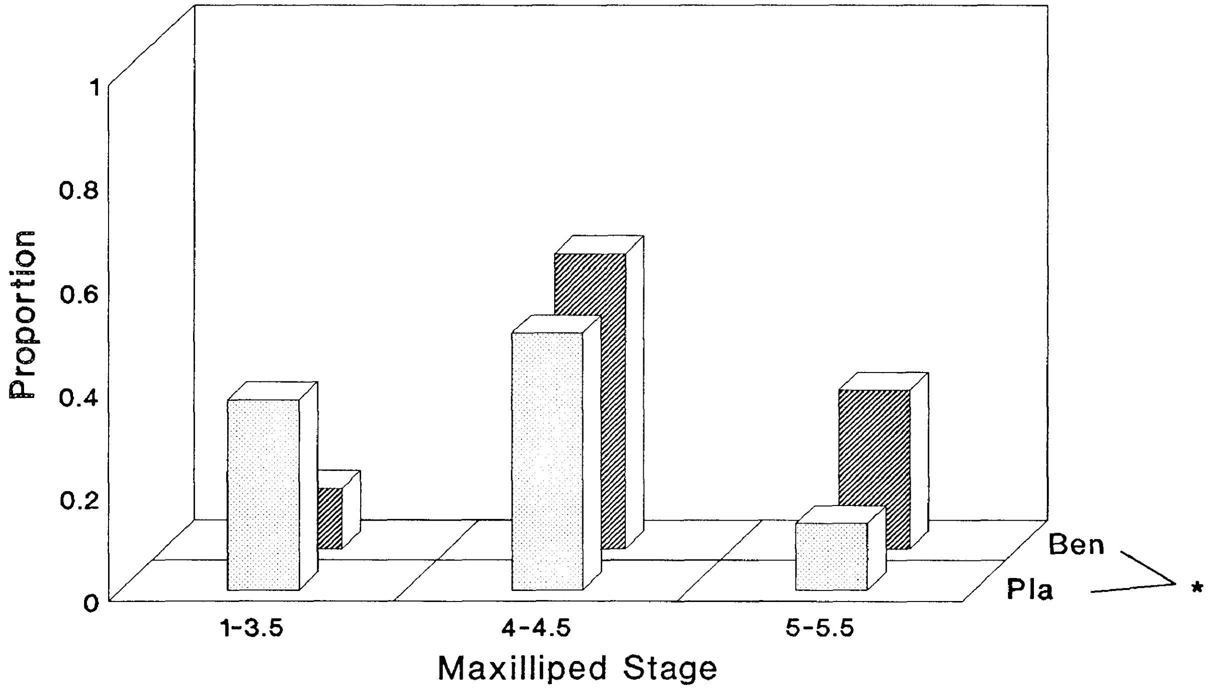

a. Downriver September
b. Upriver September
c. Downriver October
d. Upriver October
Proportion
0
0.2
0.4
0.6
0.8
1
1-1.5
2-2.5
3-5.5
Uropod Stage
BEN
PLA
n.s.
n.s.
*
*
*
*
n.s.
* benthos only

Figure 7

a. Downriver - October



b. Upriver - October



VITA

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