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Variation among Populations of the Troglobitic Amphipod Crustacean *Crangonyx antennatus* Packard Living in Different Habitats I. Morphology

by

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INTRODUCTION

Intraspecific morphological variation in response to habitat differences has been observed in freshwater amphipod populations of epigean species (Minckley and Cole, 1963; Pinkster, 1971, 1972; Pinkster et al., 1970; Strong, 1972) and hypogean species (Ginet, 1960; Holsinger, 1967, 1969; Holsinger and Culver, 1970). Variable morphological characters include body length, allometric relationships between body and appendage lengths, setation and integument coloration. Environmental factors, such as current velocity, available food, temperature, predators, competitors and other biotic and abiotic components are considered responsible for these variations.

In the present study morphological variation was recorded among different populations of the troglobitic (i.e., obligatory cavernicole) amphipod *Crangonyx antennatus*. Certain features of the subterranean environment make it attractive for the study of population variation. Caves represent relatively constant, partitioned habitats which lack the major fluctuations of temperature and humidity normally associated with epigean habitats. Because of the lack of significant autotrophism and relative scarcity of food materials, species diversity and population sizes in caves are generally quite small compared to epigean communities.

C. antennatus offers several unique advantages for the study of population variation in a troglobitic species: 1) it is one of the most common and widespread aquatic troglobites in the southern Appalachian region of the eastern United States (Holsinger, 1969, 1972), and populations are relatively large in the caves investigated in Lee Co., Virginia; 2) it populates two distinctly different subterranean habitats, mud-bottom pools and small gravel-bottom streams, which permits a direct comparison of populations in a small portion

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of the overall species range under different environmental conditions; and 3) this species has been extensively studied ecologically (Holsinger and Holsinger, 1971; Holsinger, 1975a; Holsinger and Dickson, in press; Dickson, 1975, in press; Dickson and Kirk, in press).

In the present study, *C. antennatus* cave populations were examined from mud-bottom pool and small gravel-bottom stream habitats to determine: 1) if body length differences at maturity are evident between populations living in the two distinct habitats; 2) if variation is present in first antennal segment number to body length ratio and integument coloration; and 3) possible influences of environmental differences on population variation.

METHODS AND MATERIALS

Populations of *C. antennatus* were sampled seasonally during 1974 and 1975 in six caves located in the Powell Valley of Lee Co., Virginia. Three of the amphipod populations sampled inhabited caves containing mud-bottom pools (Roadside No. 1, Molly Wagle and Sweet Potato caves) and three of the populations were sampled in caves containing small gravel-bottom streams (Cope, Spangler and Gallohan No. 2 caves). Pool habitats receive water through ceiling drips and seepage, whereas stream habitats receive water from subterranean and/or direct surface recharge. The benthic substrate in the mud-bottom pools is characterized by mud sediments containing relatively large populations of bacteria and fungi, in contrast to stream habitats which contain bottom gravels (1-3 cm diameter) and sparse benthic sediments with small microbial populations (Dickson, 1975; Dickson and Kirk, in press). Because of the evidence for potentially well-developed dispersal ability (Holsinger, 1969, 1975a) and high migration rates of *C. antennatus* (Culver, 1973a, in press), the hydrology of the Powell Valley (Holsinger, 1975b) and the close proximity of the investigated caves (within a 5 km radius), the populations sampled were not considered to be genetically isolated.

Ten sample sites of 0.09 m^2 were randomly selected in stream and pool areas of each cave during seasonal sampling periods. All *C. antennatus* observed within the sample sites, including any present in the top 5 cm of gravels in the stream habitats, were collected until 25 amphipods were obtained in each cave. Amphipods were collected with a modified 15 ml asepto syringe and preserved in 70% ethyl alcohol for later examination in the laboratory.

Coloration of the integument was recorded in each cave prior to preservation (because of alcohol bleaching), along with specific information from each of the random plots including the number of *C. antennatus*, presence and number of potentially competitive species (isopods, *Asellus recurvatus* and *Lirceus usdagalun*), substrate type, presence and type of detritus and current velocity. Average water temperature, evidence of flooding and the number of potential predators (salamander, *Gyrinophilus porphyriticus* and crayfish, *Cambarus bartonii*) within 1 m^2 of the sample plots were also recorded.

In the laboratory, amphipods were measured from the base of the first an-

Table 1. Environmental parameters of the sampled *C. antennatus* habitats in six Lee Co., Virginia caves. Seasonal collections listed as: I-August, II-November, III-February and IV-June. An environmental parameter not present in a habitat is indicated by N.P.

Cave	Habitat	Overall[1] food rating	Current[2] velocity rating	Density *C. antennatus* (no./m^2)				Density isopods (no./m^2)				Predator[3] sightings				Average water temperature (C°)			
				I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Gallohan No. 2	stream	1	1	16.7	5.6	3.3	7.8	3.3	4.4	24.4	14.4	0	0	0	0	13.5	12.5	11.7	11.6
Spangler	stream	2	2	130.0	30.0	15.6	18.9	24.4	30.0	16.7	44.4	0	0	0	0	14.5	11.5	11.1	13.3
Cope	stream	3	3	14.4	12.2	11.1	6.7	16.7	0	3.3	5.6	3	2	4	2	13.4	10.4	12.2	—
Sweet Potato	pool	4	N.P.	34.4	64.4	24.4	71.1	3.3	0	1.1	3.3	1	0	0	0	12.5	11.0	11.7	12.2
Molly Wagle	pool	5	N.P.	—	20.0	26.7	41.1	N.P.				0	0	0	0	—	9.9	9.4	10.0
Roadside No. 1	pool	6	N.P.	251.1	164.4	140.0	128.9	N.P.				1	0	0	0	12.0	9.9	8.9	10.0

[1] Based on quantitative (Dickson, 1975; Dickson and Kirk, in press) and qualitative comparisons of the amount and type of available food (small mammal dung, mud sediments and plant detritus) for *C. antennatus* in each habitat. (1-lowest, 6-highest).

[2] Based on average current velocity in habitats determined by calibrated pitot tube. Ratings: 1) <3.5 cm/sec, 2) 3.5 cm/sec and 3) >3.5 cm/sec.

[3] The number of potential amphipod predators observed within 1 m^2 of sample plots.

tennae to the base of the telson as an indication of total body length (Holsinger, 1967). Sexual maturity was determined in the male by the presence of calceoli (small, paddle-shaped structures) on the second antennae in addition to papillae and in the female by long marginal setae on the oostegites which may be retained during successive molts (Hynes, 1954; Holsinger, 1967). The number of first antennal segments (in addition to the first peduncular segment) was also recorded for each amphipod. Because of sexually dimorphic size differences between mature male and female *C. antennatus*, statistical analyses were conducted separately for each sex.

RESULTS

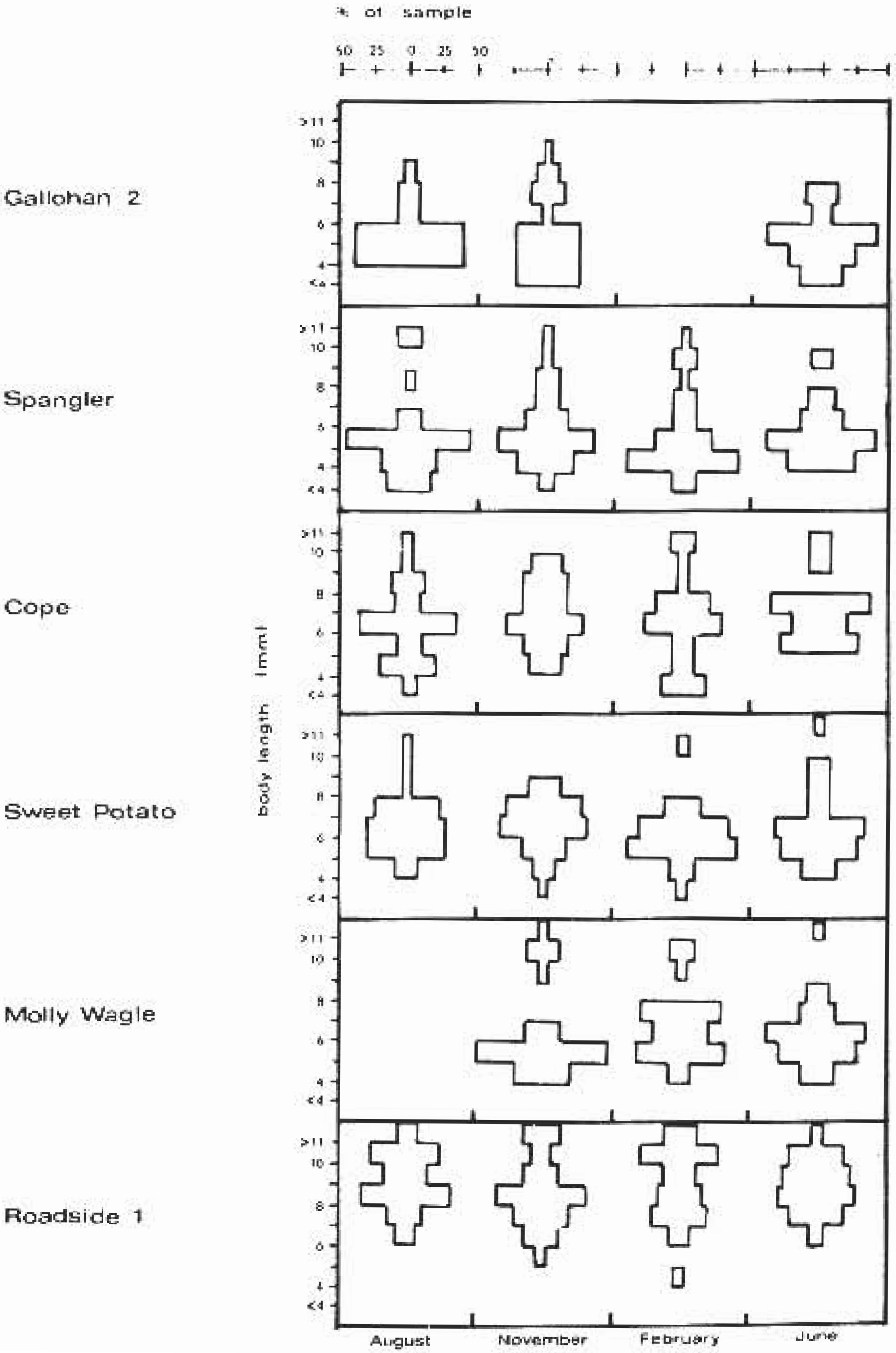
The environmental parameters recorded for each cave are presented in Table 1. In general, mud-bottom pool habitats are characterized by greater quantities of available food, higher *C. antennatus* densities, lower water temperatures, lower isopod densities and fewer predators than the small gravel-bottom stream habitats.

Size class distributions, based on body lengths of populations from each of the six caves is shown in Figure 1. The pool habitats are characterized by a higher proportion of individuals located in larger size classes than in the stream habitats. This trend is also apparent in size class distributions of both males (Fig. 2) and females (Fig. 3).

Mean body lengths of both mature males and females (Table 2) were found to be significantly ($P<0.001$) greater in pool habitats than in stream habitats (Table 3; Figs. 2 and 3). No significant ($P>0.05$) seasonal differences in mature body lengths were observed between habitats in either sex (Table 3). Although a significant ($P<0.01$) correlation was found between mature body lengths of males and females with both the overall food rating and *C. antennatus* densities, no significant ($P>0.05$) relationship to either isopod densities or predator sightings was observed (Table 4). Mature male body length was found to be inversely correlated ($P<0.05$) with average water temperatures and positively correlated to current velocity rating (Table 4). Finally, a significant correlation was noted between overall habitat food ratings and both the average water temperature ($r=-0.658$, $n=22$, $P<0.01$) and *C. antennatus* densities ($r=0.663$, $n=23$, $P<0.01$).

Examination of newly released young from both habitats revealed that the number of first antennal segments appears to be a fixed developmental feature at hatching (no. of segments=6, n=48). The number of first antennal segments of pool-dwelling amphipods was found to be significantly ($P<0.001$) greater

Fig. 1. Size class distribution in random samples of *C. antennatus* collected from each cave seasonally. Vertical axis represents amphipod body lengths; horizontal axis, percent frequency. Due to adverse conditions, sampling could not be conducted in Molly Wagle Cave in August and Gallohan No. 2 in February.


% of sample
50 25 0 25 50
Gallohan 2
Spangler
Cope
Sweet Potato
Molly Wagle
Roadside 1
>11
10
8
6
4
<4
body length (mm)
August
November
February
June

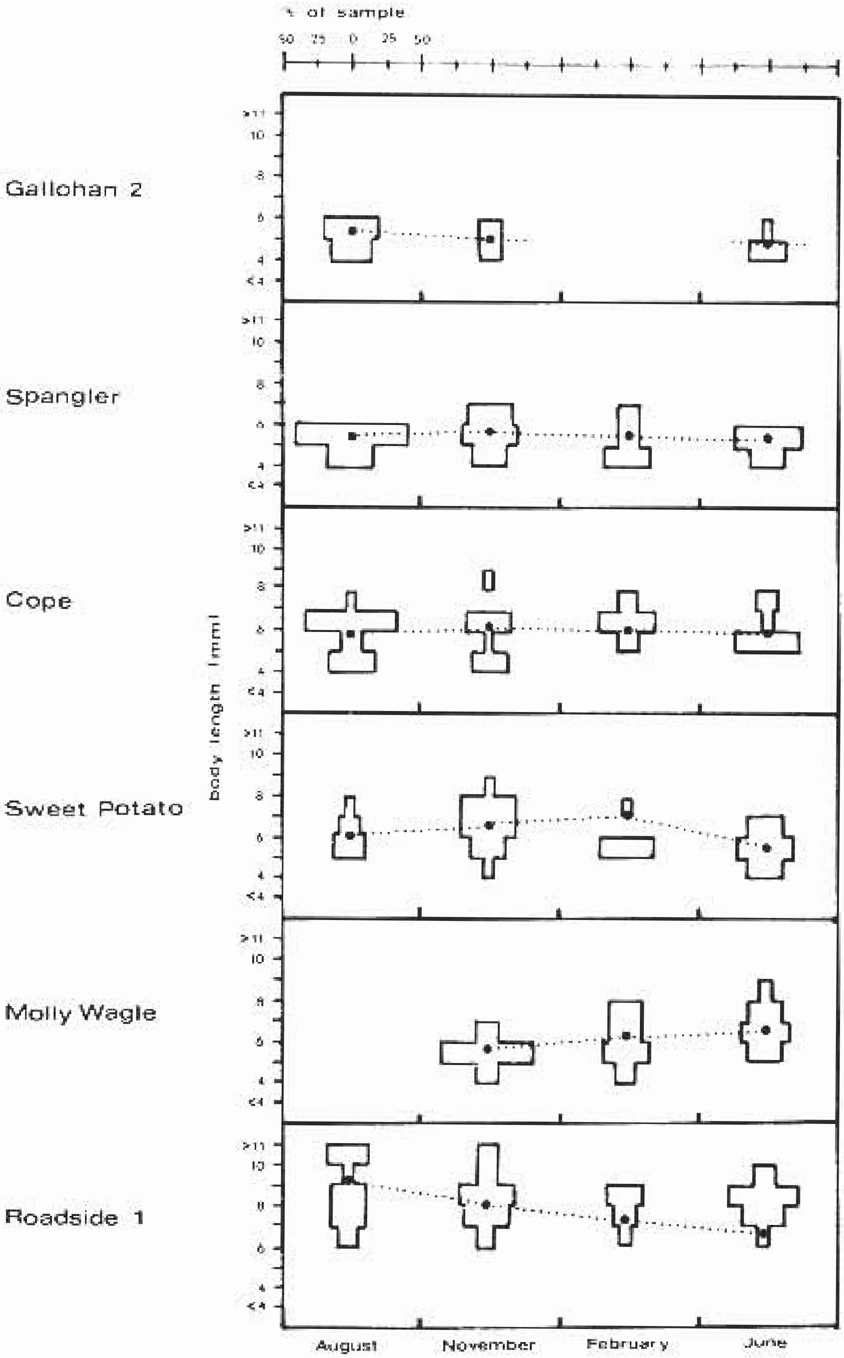


Fig. 2. Size class distribution of males in random samples of *C. antennatus* collected from each cave seasonally. Vertical axis represents amphipod body lengths; horizontal axis, percent frequency. Broken lines represent average mature male body length.

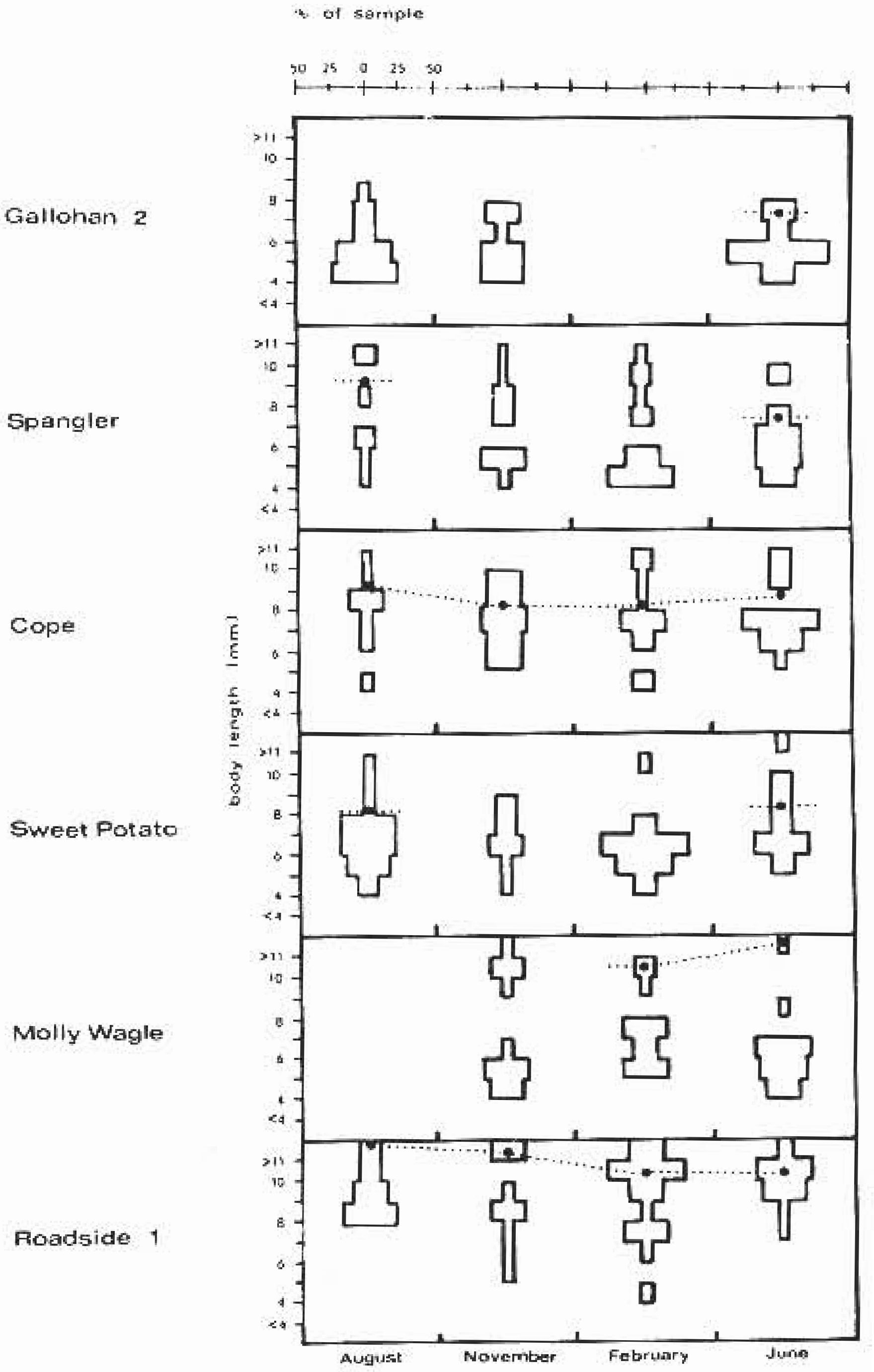


Fig. 3. Size class distribution of females in random samples of *C. antennatus* collected from each cave seasonally. Vertical axis represents amphipod body lengths; horizontal axis, percent frequency. Broken lines represent average mature female body length. The absence of broken lines indicates that no mature females were observed in the seasonal collection.

Table 2. Mean mature body lengths (mm) of *C. antennatus* from seasonal random samples of six cave populations in Lee Co., Virginia.

	August		November		February		June	
	male	female	male	female	male	female	male	female
Gallohan No. 2	5.4 n = 5 SE = 0.15	—	5.1 n = 3 SE = 0.33	—	No collection		4.9 n = 4 SE = 0.13	7.3 n = 1
Spangler	5.4 n = 10 SE = 0.12	9.5 n = 2 SE = 1.15	5.9 n = 10 SE = 0.21	—	5.6 n = 4 SE = 0.34	—	5.2 n = 4 SE = 0.25	7.3 n = 1
Cope	6.0 n = 14 SE = 0.23	9.1 n = 1	6.3 n = 6 SE = 0.49	8.1 n = 3 SE = 0.68	6.2 n = 9 SE = 0.25	8.2 n = 3 SE = 0.70	5.9 n = 4 SE = 0.26	8.8 n = 5 SE = 0.50
Sweet Potato	6.1 n = 6 SE = 0.30	8.2 n = 3 SE = 0.44	6.6 n = 14 SE = 0.25	—	6.4 n = 3 SE = 0.65	—	5.6 n = 11 SE = 0.18	8.3 n = 2 SE = 0.20
Molly Wagle	No collection		5.8 n = 10 SE = 0.15	—	6.4 n = 10 SE = 0.23	10.5 n = 1	6.8 n = 9 SE = 0.25	11.9 n = 1
Roadside No. 1	9.1 n = 12 SE = 0.35	12.4 n = 1	8.2 n = 15 SE = 0.30	11.4 n = 3 SE = 0.12	7.6 n = 6 SE = 0.24	10.4 n = 8 SE = 0.32	6.9 n = 13 SE = 0.39	10.4 n = 5 SE = 0.22

Table 3. Comparison of mature *C. antennatus* body lengths between stream and pool habitats and seasonal collections. The number of first antennal segments is compared between stream and pool populations. Significance is determined by one-way analysis of variance (model-I).

	F ratio	Numerator df	Denominator df	P
Mature male body lengths between habitats	70.7	1	194	<0.001 Sig.
Mature male body lengths between seasons	1.2	3	196	>0.05 N.S.
Mature female body lengths between habitats	173.8	1	34	<0.001 Sig.
Mature female body lengths between seasons	0.4	3	36	>0.05 N.S.
First antennal segment number between habitats	476.8	1	511	<0.001 Sig.

than that of stream-dwelling ones (Table 3). Linear regression analyses (model-II, Bartlett) of the number of first antennal segments to body length produced different slopes in each of the six cave populations (Fig. 4). The three stream populations exhibited greater positive slopes than the three pool populations, with the two extremes, Gallohan No. 2 and Roadside No. 1 caves, being significantly ($P<0.001$) different (Fig. 4).

Live amphipods, observed in the field and in the laboratory, exhibited a distinct difference in body integument coloration from the two habitats. Stream-dwelling amphipods are brownish in color in contrast to pool-dwelling ones which are whitish in color.

DISCUSSION

It has been determined that significant morphological variation exists among populations of *C. antennatus* living in different cave habitats in a small section of the overall range. Environmental differences between habitats apparently influence this variation.

Table 4. Correlation of mature male and female *C. antennatus* body lengths with environmental parameter values (See Table I).

	Overall food rating	Current velocity rating	Population density *C. antennatus*	Population density isopods	Predator sightings	Average water temperature
Mature male body length	$r = 0.853$ $n = 22$ $P<0.01$ Sig.	$r = 0.903$ $n = 11$ $P<0.01$ Sig.	$r = 0.801$ $n = 22$ $P<0.01$ Sig.	$r = -0.487$ $n = 15$ $P>0.05$ N.S.	$r = -0.474$ $n = 6$ $P>0.05$ N.S.	$r = -0.488$ $n = 21$ $P<0.05$ Sig.
Mature female body length	$r = 0.823$ $n = 14$ $P<0.01$ Sig.	$r = 0.488$ $n = 7$ $P>0.05$ N.S.	$r = 0.716$ $n = 15$ $P<0.01$ Sig.	$r = -0.250$ $n = 9$ $P>0.05$ N.S.	$r = -0.440$ $n = 6$ $P>0.05$ N.S.	$r = -0.473$ $n = 14$ $P>0.05$ N.S.

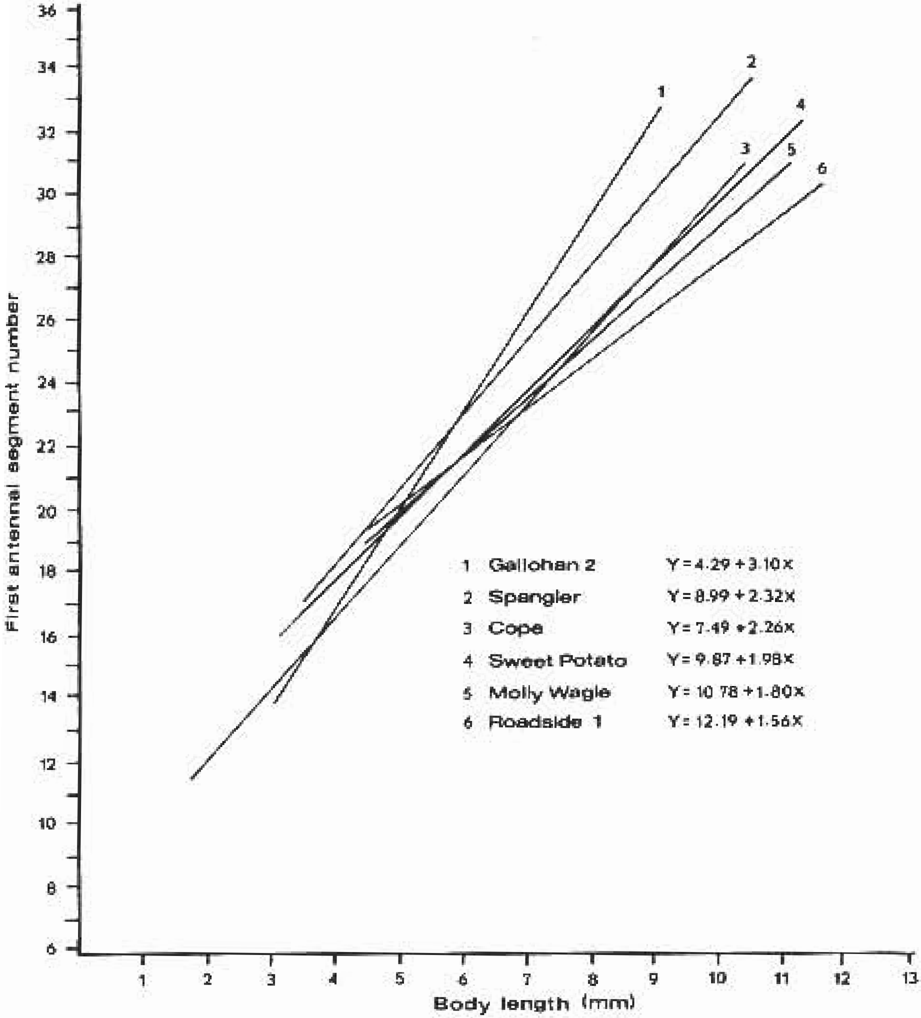


Fig. 4. Regression (model-II, Bartlett) of *C. antennatus* body length plotted against the number of first antennal segments in each of the six caves. A significant difference was found between Gallohan No. 2 and Roadside No. 1 cave populations ($F(1,171)=18.9$, $P<0.001$).

The amount of available food within each habitat appears to be the most important environmental factor affecting mature body length in *C. antennatus*. Results from both this study (Table 4) and a laboratory investigation of morphological variation in juvenile *C. antennatus* reared on different substrates (Dickson, in press) indicate a direct relationship between available food and body length. Similar observations on the amount of habitat food affecting body length were made in cave populations of another troglobitic crustacean, the crayfish *Orconectes pellucidus* (Jegla et al., 1965).

Population densities of *C. antennatus* and average water temperature of the habitats, although indicating a direct relationship with mature amphipod body lengths (Table 4), represent factors which are also correlated with overall food ratings of the habitats and thus probably have no major individual effects on mature body size. This interpretation is supported by studies on populations of other freshwater crustaceans. Population density was not observed to affect mature body lengths in populations of the copepod *Cyclops strenuus strenuus* (Elgmork and Halvorsen, 1976) and the crayfish *Orconectes pellucidus* (Jegla et al., 1965). In a laboratory investigation of the amphipod *Gammarus pulex*, decreased water temperatures were related to decreased biomass production and smaller size (Nilsson, 1974).

Current velocity and incidence of flooding are two of the most frequently cited causes for the selection of small size in stream invertebrates (Pennak, 1953; Houston, 1960; Patrick, 1970). This variation is explained as an adaptation to flowing water habitats through both the decrease of surface area exposed to water currents and the ability of organisms to move deeper into the benthic gravels. Based on observations by Culver (1973a) on the presence of apparently smaller mature *C. antennatus* in benthic gravels of Cope and Gallohan No. 2 caves, size variation in this species was initially thought to represent an adaptation to flowing waters. After comparison of all of the populations investigated, current velocity does not appear to be a primary factor in the selection of smaller body lengths in *C. antennatus,* as larger amphipod body lengths were correlated with greater average current velocities (Table 4).

Severe depression of population densities of *C. antennatus* has been noted due to intense competition with the isopods, *A. recurvatus* and *L. usdagalun* (Culver, 1973a). This effect was also observed in the present study; however, no evidence was found to indicate that population densities of potentially competitive isopods were a major cause of mature body length variation in *C. antennatus* (Table 4). The presence of relatively large populations of amphipod predators also was not found to be associated with smaller *C. antennatus* in the habitats studied (Table 4). These results support Culver's (1973b) observations that the salamander *G. porphyriticus* does not exhibit feeding selectivity for larger prey over smaller prey, thus indicating the apparent absence of predator-influenced selection pressure for small body size.

Another morphological feature found to vary in *C. antennatus* populations was the relationship between body length and the number of first antennal segments. The first pair of antennae in amphipods plays an important role in chemoreception (Kaestner, 1970). The length of the first antennae frequently seems to be an allometric function of body length (Holsinger, 1967; Holsinger and Culver, 1970) and the number of segments added during each molt can vary between individuals of the same species (Geisler, 1944).

The number of first antennal segments in *C. antennatus* was found to be significantly greater in pool populations than in stream populations (Table 3).

This was initially thought to represent an allometric growth function involving additional antennal segments being associated with larger amphipods. After examination of regression slopes representing this linear relationship in the six populations (Fig. 4), it becomes apparent that another factor is also affecting this relationship. The regression lines of the three stream populations are found to exhibit greater positive slopes than the pool populations, indicating that a greater number of first antennal segments per unit body length are associated with the smaller stream amphipods. Although this might be caused by an increase in the number of molts in stream habitat amphipods, the associated increase in metabolic activity which is necessary for ecdysis (Waterman, 1960) would not be expected to occur more frequently in relatively food-poorer habitats. If it is assumed that the chemosensory structures located on the first antennae are utilized to locate food, this population variation could represent a selective adaptation to increasingly food-poor habitats through the accumulation of additional sets of chemoreceptors located on each segment. Although not significant, a trend was observed in juvenile *C. antennatus* in which amphipods reared on food-poor substrates possessed a greater number of first antennal segments than individuals reared on food-rich substrates (Dickson, in press). Increase in numbers of sensory structures in relation to less available habitat food has also been noted in cave populations of amblyopsid fish (Poulson, 1963).

The integumentary pigment of amphipods is composed of various carotenoid-protein complexes which must be obtained from food sources (i.e., leaf and woody detrital material) because of the inability to synthesize them (Beatty, 1949; Kaestner, 1970). Some troglobitic crustaceans are thought to have genetically lost the ability to utilize carotenoids in integumentary pigmentation, while in others it depends on exposure to food materials containing these substances (Beatty, 1942; Maguire, 1961; Wolfe and Cornwell, 1964). The distinct variation in integument coloration between stream and pool populations is apparently due to differences in the type of available food. Populations inhabiting streams possess a brownish integument, probably due to the availability of carotenoid materials in stream detritus. Pool populations possess a whitish integument, apparently because of the lack of allochthonous plant material and the loss of carotenoids from drip water due to percolation through limestone as reported by Beatty (1942). Similar results were found in a laboratory study which correlated integument coloration with food type in young *C. antennatus* (Dickson, in press).

Strong (1972) found through laboratory breeding experiments that morphological variation in isolated populations of the amphipod *Hyalella azteca* was inherited. However, two factors tend to indicate that morphological variation in *C. antennatus* is environmentally rather than genetically induced. The populations of *C. antennatus* investigated are not believed to be isolated genetically for reasons stated under Methods and Materials; and, second, the significant morphological variation observed in juvenile *C. antennatus* from a single clutch under different environmental conditions (Dickson, in press) indicates the presence of morphological flexibility within amphipods from a single habitat.

Studies by Culver (1973a, in press) indicating that *C. antennatus* experiences the most intense competition and exhibits the highest migration rates of all of the aquatic cave crustaceans in Lee Co., Virginia and the evidence for its high dispersal potential between caves (Holsinger, 1969, 1975) suggests that this species has evolved increased vagility to escape competitive pressures. Variability encompassed within the genome and the accompanying ability to adapt to various environmental conditions would enhance this species survival in the habitats encountered during dispersal.

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SUMMARY

Populations of the troglobitic (i.e., obligatory cavernicole) amphipod *Crangonyx antennatus* living in two distinct aquatic habitats were examined for possible morphological variation. Collections were made seasonally for one year in six Lee Co., Virginia caves, three with mud-bottom pools and three with small gravel-bottom streams. Environmental parameters thought to influence population variation were recorded for each of the six caves. Body length of mature amphipods was found to be greater in the mud-bottom pool habitats, whereas stream amphipods possessed more first antennal segments per unit body length. Variation was also observed in integument coloration; stream amphipods were characterized by a brownish integument and pool amphipods a whitish integument. Differences in the type and amount of available food in the two habitats is considered the most important environmental parameter affecting morphological variation. The population variation noted between habitats is believed indicative of the adaptive flexibility of this vagile troglobitic species.

RÉSUMÉ

Une éventuelle variation morphologique a été recherchée chez *Crangonyx antennatus*, Amphipode troglobie (c'est-à-dire cavernicole obligatoire), dans des populations vivant dans deux biotopes aquatiques distincts. Des récoltes saisonnières ont été faites pendant une année dans six grottes du Lee Co. (Virginie), trois d'entre elles présentant des flaques d'eau à fond argileux, les trois autres des cours d'eau à lits de graviers. Les paramètres du milieu susceptibles d'influencer la variation de la population ont été enregistrés dans chacune des six grottes. Les Amphipodes matures des flaques d'eau ont une taille plus grande, tandis que chez ceux des eaux courantes le nombre des premiers segments antennaires est plus élevé, corrélativement à la longueur du corps. La couleur du tégument montre aussi une variation: les Amphipodes des eaux courantes sont caractérisés par un tégument brunâtre, ceux des flaques par un tégument blanchâtre. D'après les différences observées dans le type et la quantité de nourriture disponible dans les deux biotopes, on doit considérer le facteur nourriture comme le paramètre le plus important de la variation morphologique. La variation des populations des deux biotopes montre, selon toute vraisemblance, la souplesse d'adaptation de cette espèce troglobie.

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