AN ANALYSIS OF MORPHOLOGICAL VARIATION: A COMPARISON OF SOME STREAM-DWELLING FISHES

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ABSTRACT.—Nine species of fish from two different streams are compared with respect to variation of some non-meristic characters. It appears that pelagic species are more variable than benthic ones and that differences in morphological variation may reflect niche size differences.

INTRODUCTION

Most studies of morphological variation in fishes have considered only meristic characters and many of these have dealt solely with geographic variation (Bryan, 1969; Olund and Cross, 1961). Meristic character variation is often the result of developmental inconsistencies rather than direct adaptive mechanisms (Albaugh, 1969). The present study concerns itself with variation of non-meristic characters among a number of different species. Meristic characters were shown to be almost completely invariable in these fishes in a preliminary study by the authors.

The amount of variation of any morphologic feature or complex of features is related to the amount of selection (or lack of) for precision in that character. The degree of centripetal, or stabilizing, selection determines the degree of variation allowable (Bader and Hall, 1960). Some phenotypic characters may exhibit only narrow ranges of variation, as greater deviations would prove detrimental and thus be selected against. The characters that are permitted some degree of variability and the relative degree of their variability are easily determined. Why only some characters are more variable than others in one species and why the degree of variation of the characters differ between species is another matter.

Thus we attempt here to investigate the relative amounts of morphologic variation in nine species of stream-dwelling fish. The species were divided into two groups according to their feeding habits: mid- or top-water feeders, and bottom feeders. The intent is primarily to determine, by comparing degrees of morphological variation, whether greater selection pressures are placed upon pelagic or benthic feeders.

METHODS AND MATERIALS

The fish were collected by seining from two different and widely separated streams of the Salt Fork and Kaskaskia drainage systems which we will call streams 1 and 2, respectively. Nine species were collected from stream 1 and seven from stream 2 (Table 1). Collections were made in the fall of 1969 and 1970. After eliminating the species caught in small numbers, nine species remained for investigation (Table 1). Ninety-six percent of the total number of fish and 67% of the total species caught in stream 1 were utilized; 95% of the number and 71% of the species from stream 2 were studied. A Mann-Whitney U-test (Siegel, 1968) performed on the coefficients of variation of the nine species from the two streams indicated that there was no significant difference in variation between the two groups; hence the fish were considered as coming from a single population.

TABLE 1

Species	Collected in Stream No.	N	Feeding Location
Fundulus notatus	2	34	Pelagic
Semotilus atromaculatus	1 & 2	81	Pelagic
Notropis lutrensis	2	36	Pelagic
Notemigonus chrysoleucas	1	30	Pelagic
Notropis dorsalis	2	26	Benthic
Pimephales notatus	1	108	Benthic
Ericymba buccata	1	57	Benthic
Campostoma anomalum	1 & 2	61	Benthic
Cyprinus carpio	1	24	Benthic
Notropis spilopterus	1	5*	
Notropis stramineus	1	6*	
Etheostoma blennoides	1	1*	
Hybognathus nuchalis	2	8*	
Phenacobius mirabilis	2	1*	

*Not considered in study due to small sample size

Using dividers, ten characters were measured on each fish. Measurements were made according to Hubbs and Lagler (1958). The characters, measured in mm., were: length of dorsal fin base, length of anal fin base, length of longest pectoral ray, length of longest pelvic ray, head length (anterior portion of snout to posterior part of operculum), head width (greatest dimension of head when jaws and operculae are closed (and operculae lie flat), orbital width, upper jaw length, snout length (anterior point on upper lip to anterior part of orbit), and standard body length.

The measurements of the body parts were expressed as proportions of the standard length since body size varied between individuals. In all species the size range was less than 20 mm, thereby minimizing the effects of allometric growth.

The physical structure of both streams is quite similar, averaging 10-15 feet wide, 2-3 feet deep, and having a gravel bottom covered with organic silt. The stream gradient is low (3 to 4 feet per mile) and the water flow is moderate to sluggish during normal water stages; riffles are gentle and pools generally shallow. Water levels change rapidly and drastically and flooding occurs regularly, especially in the spring and summer, during which the water may rise substantially and erode the stream banks considerably. Water temperatures fluctuate a good deal (as much as 8 degrees C in the summer) and in the winter the streams may freeze to the bottom, forcing fish into deep pools. The water turbidity is usually high, drastically limiting the growth of aquatic vegetation. The two drainages are relatively unpolluted and have a slightly alkaline pH. (See Larimore and Smith, 1963, for further details on the drainages of Champaign County, Illinois).

Fish Species Examined

A brief description of each of the nine species studied follows, with the major emphasis on the differences in habitat and food.

Of the five species in the study which can be classified as benthic or primarily bottom dwelling, the carp, *Cyprinis carpio*, alone seems to prefer warm, low gradient streams with an abundance of organic matter. Its tolerance, however, extends over a wide range of bottom types and turbidity levels. Organic detritus and plant matter are the major constituents of the carp's diet (Mauck, *et al.*, in press).

The bluntnose minnow, *Pimephales notatus,* exhibits the highest degree of tolerance of any of the species. It has the ability to survive and spawn in virtually all types of waters, in gradients ranging from 0-100 feet, in areas of high turbidity and pollution, and under conditions of severe competition. Primarily herbivorous, the bluntnose obtains its food by scraping algae from the substrate (Stegman, 1959).

A widespread species, the stoneroller minnow, *Campostoma anomalum,* is closely associated with riffles, especially in low gradient streams. With its ventrally positioned sucker-like mouth, it is particularly adapted to feeding on diatoms, filamentous green algae and other small plants adhering to the riffles' stony substrate (Kraatz, 1923).

The last two benthic minnows, the silverjaw, *Ericymba buccata,* and the bigmouth shiner, *Notropis dorsalis,* closely resemble each other morphologically and in their habits. They possess a similarly shaped head, flattened on its ventral surface, have similar body proportions and coloration, and possess large horizontal mouths. The large mucous ducts visible at the bottom of the silverjaw's head readily distinguishes the two species. Both occur most frequently in gravel- or sandy-bottomed stream sections of moderate gradients, and exhibit similar schooling, feeding, resting and retreat behavior (Hoyt, 1970; Trautman, 1957). Hoyt (1970) states that the silverjaw forms a close feeding association with the bluntnose and stoneroller. In scraping off patches of algae covering the substrate, these two herbivores expose larval insects which constitute the majority of the silverjaw's diet. No food data are available for the bigmouth shiner.

Of the pelagic species, the golden shiner, *Notemigonus chrysoleucas,* appears most frequently in sluggish streams with bottoms chiefly of organic debris and/or sand, substantially covered by vegetation. It utilizes a wide range of food resources which includes mollusks, insects, and a variety of plants (Forbes, 1908).

The northern creek chub, *Semotilus atromaculatus,* is a ubiquitous species which occurs in greatest densities in small streams of medium to high gradients, especially above riffle areas. Mayfly naiads, coleopteran beetles, and plant material compose the largest portion of the chub's diet with larger adults also capturing small fish (Dinsmore, 1962).

The redfin, *Notropis lutrensis,* is an inhabitant of shallow pools of moderate current and is primarily insectivorous. Terrestrial arthropods falling or swept into the water comprise more than two-thirds of its total diet, with aquatic insect larvae and plant material making up the balance (Lewis and Gunning, 1959).

The black-striped topminnow, *Fundulus notatus,* is most frequently found in streams of low or base gradients where at least some aquatic vegetation is present. It is primarily a surface swimmer and its major food items consist of terrestrial arthropods, along with aquatic insects and filamentous algae (Thomerson and Wooldridge, 1970).

Analysis

The means, variances, variances of the logs of the measurements (base e), and coefficients of variation were calculated for each character of each species. By means of an F-test using the variance of the logs, each species was tested against every other for each character to compare the intrinsic variations (Lewontin, 1966). The coefficients of variation were grouped in two ways and Mann-Whitney U-tests were performed on them. The species were divided into pelagic and benthic groups to see if there were any significant differences in the variability of characters between the two groups as a whole.

It appears that the comparison of character variabilities over pairs or groups of species is much more useful for our purposes than comparing the variations of all characters between individual species. This character-comparison technique gives hints as to where selection is acting and how strong it is, rather than merely demonstrating that one species is more variable than another.

Results

The results indicate that the pelagic species measured are significantly more variable ($p < .005$) than the benthic fish in three of nine characters measured (dorsal and anal fin base length, and pelvic fin (length). The benthic fish are not more variable than the pelagic fish for any characters (see Table 2).

Discussion

In general it seems that selection pressures are greater on benthic than on pelagic ones, at least for the three characters indicated. Centripetal selection appears to act with similar vigor on the other characters in both groups. An examination of each of the features studied may clarify the discrepancy in variabilities between the divisions. As shown by a Mann-Whitney U-test, the dorsal fin length is significantly ($p < .004$) more variable in the pelagic fish. The dorsal fin has the logical function of acting as a keel (Lagler, *et al.*, 1962) aiding the fish in maintaining an upright posture, but a thorough study of the function of the dorsal fin would have to be made before the differences in variability of this structure in the two groups could be explained.

Anal fin length ($p < .002$). A similar argument can be made here for the anal fin.

Pelvic fin length ($p < .002$). Selection might aim towards the maintenance of an optimum pelvic fin length in the benthic fishes rather than in the pelagic fishes because the former appear to use the pelvic fin more to maintain their position on the bottom (Allen, 1969).

We at first found the results surprising in that they are almost opposite of what we expected. A preliminary scanning of the situation hinted at a greater pressure of stabilizing selection on pelagic fish due to a seemingly more rigorous habitat. But results indicate the reverse. Although niche width is extremely hard to measure, it is probably safe to assume that the niches are wider and fluctuate more in the pelagic rather than bottom-dwelling species.

The water level, temperature, turbidity, and current velocity change rather continually. These fluctuations may affect the parameters of the pelagic niches more than the benthic ones. Thus the pelagic fish, living in a more variable environment, adapt to the environment by having more variable individuals since the chances that an individual is present which would be optimally adapted to the environment at any one time would be greater in a more variable population. A population which lives in a more stable environment should be less variable as selection pressures are temporally similar. The wider pelagic niches allow greater phenotypic variation by adaptation

TABLE 2—Coefficients of Variation for Each Species/Each Character

	Dorsal Fin	Anal Fin	Pectoral Fin	Pelvic Fin	Head Length	Head Width	Orbit	Upper Jaw	Snout
P. notatus	7.49	12.23	7.37	6.99	4.88	6.62	10.23	12.47	10.61
S. atromaculatus	12.98	11.45	10.35	20.74	4.04	8.24	11.68	12.96	10.21
N. lutrensis	17.05	12.66	10.80	13.71	5.23	13.49	13.27	16.59	12.75
N. chrysoleucas	18.42	14.24	10.39	10.26	6.53	15.01	15.34	19.75	17.12
N. dorsalis	10.90	9.87	9.39	9.55	5.58	7.99	11.63	14.10	10.90
F. notatus	9.40	12.46	9.04	18.79	5.10	9.23	12.64	9.32	12.10
E. buccata	9.59	6.86	5.61	7.50	3.97	6.55	12.86	4.79	6.39
C. anomalum	8.84	8.15	6.79	7.12	5.97	6.91	9.79	12.37	10.34
C. carpio	9.14	9.53	11.76	8.00	7.86	6.07	50.46	43.14	7.35

to the diverse factors in the environment and, as Van Valen (1965) states, morphological variation tends to be greater in populations with wider niches because the variation is adaptive.

We can apply these ideas to the differences in niche width between benthic and pelagic fish. Since the benthic situation may not vary as widely as the pelagic, the benthic environmental range is smaller, and the optimal single phenotype that exists also does not vary as much as the optimal pelagic phenotype since the latter has to be intermediate between more widely different environments. We feel that the data give stimulus to these ideas if not actually supporting them, but we make our conclusions cautiously. The species considered may not adequately represent the two feeding categories and the variation may not be determined solely by selection. Willson (1969) believes that morphological variation generally may not reflect niche size. We feel that differences in morphological variation reflect *difference* in niche size, but a lack of differences in this variation does not necessarily indicate the opposite situation.

Summary

Pelagic- and benthic-feeding fishes from two streams are compared with respect to the morphological variation of nine non-meristic characters. Pelagic species on the whole were found to be more variable, indicating weaker selection pressures on this group. It appears that the niche of the pelagic species is wider since environmental fluctuations are greater in the pelagic environment. Differences in morphological variation may reflect differences in niche size.

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