

Plasticity of fish body shape. The effects of diet, development, family and age in two species of *Geophagus* (Pisces: Cichlidae)

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Received 25 July 1990, accepted for publication 9 October 1990

Fish body shape is affected by the genetic makeup of an individual as well as environmental influences, such as diet, development, growth rate and nutrition. Fishes in the family Cichlidae exhibit tremendous morphological diversity in body shape and morphology related to feeding. Certain aspects of cichlid feeding morphology have been shown to be plastic in response to different diets but plasticity in body shape has not been examined previously. Plasticity affects ecological interactions, the direction and rate of evolution, and has ramifications for characters used in systematic studies. I examined the effect of different diets: chironomid larvae (bloodworms) and brine shrimp nauplii, on body shape in two species of the Neotropical cichlid genus *Geophagus* which differ in the size at which young begin feeding on external food sources. The fry of *G. brasiliensis*, a substrate spawner, begin to feed on external food sources earlier than the fry of *G. steindachneri*, a mouthbrooder. I hypothesized that the difference in size at first feeding could lead to a difference in the amount of plasticity inducible in the two species. The magnitudes of changes were mostly similar, although *G. brasiliensis* responded to the different diets with slightly greater changes in some of the head measurements. The pattern of changes in the two species were also similar, with fish fed brine shrimp nauplii developing longer and shallower heads and shallower bodies and tails than fish fed chironomid larvae. I also examined the consequences of considering family and age as additional factors besides diet in *G. steindachneri*. Considering family or age as additional factors in the analyses did not change the conclusion that different diets induce differences, albeit small ones, in body shape. I argue that morphological plasticity is dependent on behavioural flexibility and that it may enhance evolutionary morphological diversification.

KEY WORDS:—Phenotypic plasticity – cichlids – *Geophagus* – trophic polymorphism – variation – body shape.

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INTRODUCTION

Phenotypic variation results from genetic differences among individuals and environmental differences. Environmentally induced change, or phenotypic plasticity, is the potential of a phenotypic character of a genotype to change in response to different environmental stimuli. Since selection acts on phenotypes, the nature and extent of environmentally induced variation can influence the rate and direction of evolution (Waddington, 1942; Schmalhausen, 1949; Via & Lande, 1985; West-Eberhard, 1989), and ecological interactions (Schmalhausen, 1949; West-Eberhard, 1989). Phenotypic plasticity can also affect the outcome of systematic studies (Greenwood, 1965). Fish body shape, a character that can vary among individuals within species (Hubbs, 1926; Barlow, 1961; Kullander, 1986; Ehlinger & Wilson, 1988), is affected by the genetic makeup of an individual, environmental factors such as diet, temperature (Martin, 1949) and nutrition (Lovell, 1989), and interactions between factors such as age and size (Hubbs, 1926).

Phenotypic plasticity is often thought to occur primarily in plants (Bradshaw, 1965); however, studies of fish and aquatic amphibians have also demonstrated considerable plasticity in the shape of certain morphological structures (Collins & Cheek, 1983; Meyer, 1987; refs below). Fish body shape can vary dramatically among closely related species (e.g. cichlids, Fryer & Iles, 1972), and has been shown to vary within species (Kullander, 1986; Ehlinger & Wilson, 1988). Fish shape has important functional effects (Webb, 1984). Despite a number of studies demonstrating morphological plasticity in fishes, none has looked explicitly at body shape. In this paper I examine the pattern and extent of plasticity of body shape in two closely related species of the Neotropical cichlid genus *Geophagus* induced by feeding two diets similar to diets that they naturally encounter.

Recently, a number of studies have demonstrated morphological plasticity in fishes that appears to be adaptive. Grudzien & Turner (1984) showed that a polymorphism related to feeding (trophic polymorphism) in the goodeid fish *Ilyodon*, where the relative jaw width of the two morphs differed was, at least in part, the result of plasticity; however, they were unable to induce the full range of natural variation in lab experiments. A classic case of environmentally induced trophic polymorphism occurs in the arctic charr, *Salvelinus alpinus*. Throughout the Arctic there are two to four morphs characterized by differences in relative head size, colour, behaviour and overall size at sexual maturity. The different morphs have been classified as different species or subspecies (Behnke, 1980). Nordeng (1983) in a rearing experiment showed that

each of the three morphs from the Salangen River could have any of the morphs as offspring. The induced differences appeared to be the result of environmentally induced differences in growth rate and timing of sexual maturation.

Cichlid fishes also have been shown to be plastic (Greenwood, 1965; Witte, 1984; Hoogerhoud, 1986; Meyer, 1987). Greenwood (1965) first observed plasticity in cichlids when an aquarium specimen of *Astatoreochromis alluaudi* raised on flake food had papilliform teeth and pharyngeal jaws, in contrast to wild-caught individuals which eat snails and have molariform pharyngeal teeth and stout pharyngeal jaws. He attributed this morphological difference to the different diets that the tank-raised and wild-caught fish ate. Plasticity in cichlids is interesting because they are a morphologically diverse group and a classic example of adaptive radiation, making it intriguing to consider how plasticity might influence evolutionary history (Greenwood, 1965; Meyer, 1990b). Despite a number of studies demonstrating plasticity, none has looked explicitly at body shape, a highly variable character among cichlid species (Fryer & Iles, 1972).

QUESTIONS

This paper addresses questions about body-shape changes induced by different diets in two closely related species in the Neotropical cichlid genus *Geophagus*. By body shape, I mean a collection of homologous measures that express the relative dimensions of the body from head to tail. The two species possess different developmental patterns that may result in different amounts of plasticity being expressed. I examined the following questions at both the interspecific and intraspecific level.

Interspecific comparisons

- (1) Does the size at which a fish begins to feed on exogenous food sources influence the amount of plasticity that is expressed in the two species?
- (2) Do the two species differ in the pattern of changes that are induced?

Intraspecific comparisons

- (1) Do differences in growth rate influence shape, i.e. are two fish of the same size, but different age the same shape?
- (2) How important is heredity, as measured by family effects, and family-by-treatment interactions, in influencing conclusions about the importance of plasticity?

A companion paper (Wimberger, 1991) examines the effects of different diets on skull and jaw osteology.

The fish

In order to address these questions I used two closely related Neotropical cichlids in the monophyletic genus *Geophagus* (Cichoki, 1976; Gosse, 1976; Kullander, 1980), *G. brasiliensis* (Quoy & Gaimard, 1824) and *G. steindachneri* (Eigenmann & Hildebrand, 1910). It is important in comparative studies to use

species as closely related as possible to control, as much as possible, for the effects of phylogenetic history (Lauder, 1982; Ridley, 1983).

Geophagus brasiliensis is a substrate spawner from southern Brazil. The female and male generally spawn on an elevated surface where the eggs adhere. The female guards the eggs, fanning them constantly. They hatch in *c.* 5 days when the young are *c.* 3 mm long. They begin feeding exogenously when *c.* 4 mm long. This contrasts with mode of spawning and parental care in *G. steindachneri* which exhibits the opposite extreme of cichlid mating and parental care. In *G. steindachneri* the female picks up the spawned eggs in her mouth; then the male swims by, releasing sperm which the female sucks up to fertilize the eggs. The female proceeds to hold the eggs in her mouth for *c.* 2 weeks during which time the eggs develop, hatch and the young develop, supported by large yolk sacs until they need to feed on exogenous food sources. At this point the *G. steindachneri* young are *c.* 7–8 mm, about twice the size of *G. brasiliensis* when they first begin feeding.

Possible sources of variation

Why should one expect a difference in the plasticity of feeding-related morphology in organisms that differ in the size at which they begin feeding? I hypothesize that the amount of time that an organism spends developing outside of a given functional context, such as feeding, may affect the amount of plasticity that can be induced in the structures related to the function. For instance, one might expect mouthbrooding cichlids to show less plasticity than substrate spawners for two possible reasons. First, the lack of early environmental influences (in this case food and feeding) during development on the mouthbrooder young may select for increased importance of genetic effects on morphology, and against variation that is environmentally induced. In other words, feeding morphology may be more canalized in young that go through a longer period of time before first feeding. Second, as skeletal elements become more ossified they become less plastic. I have no data on the relative amount of ossification in the young of the two species when they first begin feeding, but it is likely that *G. brasiliensis* is less ossified than *G. steindachneri* by virtue of its smaller size at first feeding.

The reason usually inferred for shape differences in most of the intraspecific studies cited above is that differences in the way that fish process different foods sets up different strain regimes in the bones and muscles, which stimulate differential deposition and resorption of the bony matrix (Lanyon, 1984). This process ultimately can lead to differently shaped bones (Lanyon & Rubin, 1985). However, there are several other potential causes of differences in shape which have been ignored in other studies. Hubbs (1926) suggested that environmental differences lead to different growth rates that can lead to shape differences, with slower growing fish assuming adult morphology at a smaller size than faster growing fish. Thus, two fish of the same size, but different age may assume different shapes. In aquarium and pond-raised fish, unequal growth rates tend to be the rule, rather than the exception. Genetic variation may also produce differences in shape. Different genotypes may be differently shaped. How important is genetic variation in masking or exacerbating the effects of different treatments? Nutrition may also be important in determining fish shape.

Certain mineral and vitamin deficiencies are known to cause changes in head shape, growth rate, which in turn can affect shape, and spinal deformities such as lordosis or scoliosis (curvature and fusion of the spine; Lovell, 1989) which also can change overall body shape.

METHODS

I obtained wild-caught adult fish from importers and aquaculture-raised fish from fish farms and hobbyists. I fed these fish on a diet of flake food and bloodworms, which are chironomid (Diptera) larvae. When a pair spawned I separated the young from the parents when the young were 8 to 10 mm standard length. I put half of each brood on a diet of brine shrimp nauplii, *Artemia salina*, and the other half on a diet of frozen chironomid larvae. Each half-brood was placed in a five gallon compartment of a partitioned 10 or 15 gallon aquarium. The fish were fed twice daily to satiation on their assigned diet. Individuals were sacrificed throughout growth in order to obtain growth trajectories for fish on both diets. Fish were sacrificed by being placed in a dilute solution of tricaine methanesulphonate (TMS). They were then fixed in 10% buffered formalin and transferred to 55% ethanol. Fish ranging from 15 to 35 mm for both species were used in the analyses. Thirty-five mm was the maximum size attained by fish on the brine shrimp treatment during the course of the experiment. I used only fish greater than 15 mm standard length to allow individuals to manifest diet-induced differences.

I measured the distances among a set of points that defined a truss (Brookstein *et al.*, 1985, Fig. 1). A truss is a set of measures from homologous landmarks that gives fairly even coverage in both the horizontal and vertical direction of the form being considered. The measurements were made with a video digitizing system, except pectoral fin length and pelvic fin length which were measured with Fowler Ultra-Cal II digital calipers. The points were digitized using a

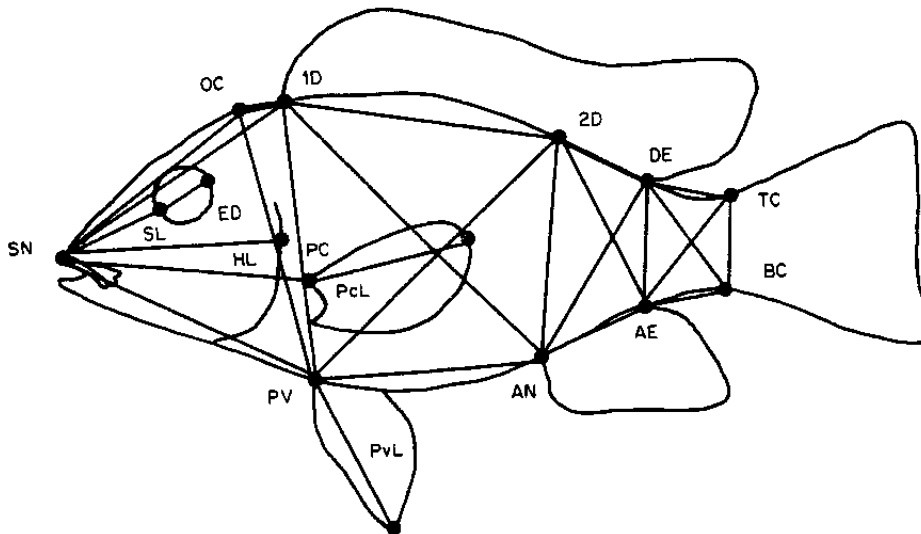


Figure 1. Measurements taken. Points marked with a dot were digitized and the dimensions shown were then calculated.