DISSERTATION

ONTOGENY AND TAXONOMY OF HUMPBACK CHUB, BONYTAIL, AND ROUNDTAIL CHUB LARVAE AND EARLY JUVENILES

Submitted by

Robert T. Muth

Department of Fishery and Wildlife Biology

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 1990

COLORADO STATE UNIVERSITY

March 22, 1990

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY ROBERT T. MUTH ENTITLED ONTOGENY AND TAXONOMY OF HUMPBACK CHUB, BONYTAIL, AND ROUNDTAIL CHUB LARVAE AND EARLY JUVENILES BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Advisor

Department Head

ABSTRACT OF DISSERTATION

ONTOGENY AND TAXONOMY OF HUMPBACK CHUB, BONYTAIL, AND ROUNDTAIL CHUB LARVAE AND EARLY JUVENILES

The cyprinid genus *Gila* includes three closely related fishes in the *G. robusta* superspecies complex that are endemic to the Colorado River Basin. These fishes are the Colorado roundtail chub *G. robusta robusta* and the federally endangered humpback chub *G. cypha* and bonytail *G. elegans*. Inability to identify young of these fishes has been a major impediment to research, management, and recovery efforts. To facilitate description and identification, over 750 known-identity wild or cultured larvae and young-of-the-year juveniles of these fishes, representing several local populations, were analyzed for developmental and morpho-meristic features. Diagnostic value of each morphological feature examined was evaluated, and artificial keys were developed.

Most developmental events occurred at a smaller size in bonytail than in humpback or Colorado roundtail chub. Transformation to the juvenile period, gut loop formation, and end of finfold absorption occurred at a smaller size in Colorado roundtail chub than in humpback chub and bonytail. Humpback chub hatched and first acquired rays in the pectoral and pelvic fins at smaller size than Colorado roundtail chub.

Within-taxon variability in extent of surface melanophore pigmentation was high. No taxon-specific differences in melanophore distribution were noted.

Humpback chub metalarvae greater than 15 mm standard length and especially juveniles tended to have a nearly horizontal, subterminal mouth. Bonytail and Colorado roundtail chub generally had slightly oblique, terminal mouths.

Bonytail were readily distinguished from humpback and Colorado roundtail chub by several meristics, including postvent and total myomeres or vertebrae (juveniles), gill rakers (juveniles), and modal number of dorsal fin principal rays or pterygiophores (postflexion mesolarvae). Counts of most meristic series, except for anal fin principal rays or pterygiophores (postflexion mesolarvae), were very similar between humpback and Colorado roundtail chub. Bonytail had 10 or more dorsal fin principal rays or pterygiophores, 133 or more total gill rakers, and typically 20 or more postvent and 49 or more total myomeres or vertebrae. Humpback and Colorado roundtail chub had 110 or fewer total gill rakers, typically 19 or fewer postvent and 47 or fewer total myomeres or vertebrae, and typically 9 dorsal fin principal rays or pterygiophores. Humpback chub and bonytail typically had 10 anal fin principal rays or pterygiophores compared to 9 for Colorado roundtail chub.

Six morphometrics were diagnostically useful in taxon separation of metalarvae or juveniles. Bonytail juveniles tended to have a narrower caudal peduncle than juvenile humpback and Colorado roundtail chubs. Humpback chub and bonytail had a longer caudal peduncle relative

to trunk length than Colorado roundtail chub. All fins were longest in humpback chub and shortest in Colorado roundtail chub.

Robert T. Muth
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, CO 80523
Spring 1990

ACKNOWLEDGEMENTS

My sincere thanks go to my advisor, Dr. Clarence A. Carlson, Department of Fishery and Wildlife Biology, and to committee members Dr. Robert J. Behnke, Department of Fishery and Wildlife Biology, Dr. Paul W. Mielke, Statistics Department, and Mr. Thomas P. Nesler, Colorado Division of Wildlife.

Thanks are also extended to Mr. Darrel E. Snyder, Larval Fish Laboratory, for his technical expertise, assistance, and guidance throughout this study. Darrel's dedication to the study of fish early life history provided inspiration for my work.

Mr. Edmund J. Wick, Larval Fish Laboratory, helped obtain the Colorado roundtail chub adults. Ms. C. Lynn Bjork, Larval Fish Laboratory, prepared the drawings.

DEDICATION

To my wife Mary Lee

TABLE OF CONTENTS

LIST OF TABLES

Appendix Tables

LIST OF FIGURES

Appendix Figures

INTRODUCTION

This study was mainly concerned with description and identification of larvae and young-of-the-year (YOY) juveniles of three closely related fishes in the *Gila robusta* superspecies complex (Smith et al. 1979) of the subgenus *Gila*. These fishes are the humpback chub *G. cypha*, bonytail *G. elegans*, and Colorado roundtail chub *G. robusta robusta*. Primary study objectives were to (1) describe and analyze selected developmental, morphometric, and meristic features of known-identity wild or cultured humpback chub, bonytail, and Colorado roundtail chub larvae and YOY juveniles representing several local populations, (2) evaluate the diagnostic value of each morphological feature examined and identify taxon-specific distinguishing characters, and (3) develop artificial keys to the early life stages of these three chubs. Secondary objectives were to (1) examine procedures and characters used in larval-fish taxonomy and (2) describe selected meristic features of cultured F1 young from bonytail X Colorado roundtail chub and bonytail X humpback chub crosses.

The North American cyprinid genus *Gila* comprises three subgenera, 15 recognized species, and many subspecies of widespread western chubs that are characterized by high inter- and intra-specific variability in morphological characters (Uyeno 1961; Lee et al. 1980; Robins et al. 1980; Minckley et al. 1986). Holden (1968) and Rinne (1976) provided annotated listings of synonymies for the subgenus *Gila* of the Colorado

River Basin. Fishes of the *G. robusta* superspecies complex are endemic to the Colorado River Basin. An ancestor of this group probably existed in the basin by Miocene or Plio-Pleistocene time (Uyeno 1961; Smith 1978; Minckley et al. 1986). Humpback chub, bonytail, and Colorado roundtail chub were historically sympatric and occurred in medium- to large-size river channels. Adults of these fishes are relatively large, often exceeding 40 cm in total length, and their morphology probably represents a gradation in adaptation to the swift, turbulent flows, and high sediment loads found in the basin's rivers (i.e., from the highly specialized humpback chub to the more generalized Colorado roundtail chub). Common names given to these fishes in older literature has caused confusion. Often, the names bonytail and roundtail were used interchangeably for *G. elegans* and *G. robusta*. Other common names for *G. robusta* included squawfish, Verde trout, and Gila trout.

Humpback chub and bonytail are listed as federally endangered species (USDI 1989), and information on their distribution and biology, much of which appears in unpublished papers or reports, was reviewed in their revised federal recovery plans (CRFRT 1989a, 1989b). Both of these species presently occur in very low numbers and, especially in the bonytail's case, have extremely restricted distributions. Behnke and Benson (1983) and Kaeding et al. (1986) suggested that the bonytail is the rarest of all Colorado River Basin native fishes and that viable, reproducing populations probably no longer exist in the wild. Only a few scattered bonytail adults have been reported recently in rivers of the Upper Colorado River Basin, i.e., that portion of the basin above Lee Ferry, Arizona. Large, old bonytail adults still occur in low numbers in Lakes Mohave (Arizona-Nevada) and Havasu (Arizona-California)

of the lower mainstem Colorado River (CRFRT 1989b). Jonez and Sumner (1954) noted bonytail spawning activity in Lake Mohave near Eldorado Canyon in 1954 (year Lake Mohave was impounded), but no young were observed. They presumed that common carp *Cyprinus carpio* ate most of the eggs. Bozek et al. (1984) concluded that successful bonytail reproduction had not occurred in Lake Mohave in recent years. Natural recruitment of bonytail has not been conclusively documented since the 1950s (Minckley et al. 1989). Successful humpback chub natural reproduction still occurs. Breeding populations have been mostly identified by captures of adults in reproductive condition, but juvenile and late-larval humpback chub have been collected (Suttkus and Clemmer 1977; Valdez and Clemmer 1982; Kaeding and Zimmerman 1983; Valdez 1986, 1987; Karp and Tyus 1989; Valdez 1989; Kaeding et al. in press). Highest concentrations of humpback chub now occur in lower reaches of the Little Colorado River, Arizona, and in the Black Rocks and Westwater Canyon reaches of the Colorado River, Colorado and Utah (Valdez and Clemmer 1982; CRFRT 1989a). Douglas et al. (1989) and Tyus and Karp (1989) considered the lower Yampa River within Dinosaur National Monument, Colorado, a critical refugium for humpback chub. Hatchery culture of humpback chub and bonytail has been conducted since the early 1980s (Hamman 1982a, 1982b, 1985), and hatchery-reared young of both species have been stocked in the wild in an attempt to re-establish extirpated populations or supplement existing ones (CRFRT 1989a, 1989b). Success of these stockings is being evaluated. In 1988, 39 hatchery-cultured bonytail adults (7 years old) were implanted with radio transmitters and released in the Green River, Utah, at the upper end of Island Park (about river km 343) or below Chew Bridge (river km 316) to

assess habitat use (Chart and Cranney 1989). Only four of these fish survived to the end of transmitter life. Another stocking of 47 hatchery-cultured, radio-tagged bonytail adults (8 years old) was made in 1989 at the same release sites as in 1988. Only two of these fish survived to the end of transmitter life (T. E. Chart, paper given at the annual meeting of Upper Colorado River Basin endangered-fishes researchers, 1990, Moab, Utah). Final results of this work will be reported in spring 1990 (T. E. Chart, Utah Division of Wildlife Resources, personal communication). Stocking of humpback chub and bonytail in the wild is expected to continue and probably increase.

There are at least four recognized roundtail chub *G. robusta* subspecies and possibly as many as six if the Gila chub *G. r. intermedia* and Moapa roundtail chub *G. robusta* spp. are included; the Gila chub has been raised to specific rank by several western biologists (e.g., Rinne 1976; Minckley 1973) and the Moapa roundtail chub is a distinctive form being considered for subspecific ranking (Carlson and Muth 1989). The Colorado roundtail chub is widely distributed, often common to abundant where found (especially in parts of the Upper Colorado River Basin), and known to reproduce throughout most of its range (Minckley 1973; Rinne 1976; Carlson et al. 1979; Tyus et al. 1982a, 1982b; Valdez et al. 1982; Haynes et al. 1985). The other *G. robusta* subspecies are restricted to the Lower Colorado River Basin and are either federally endangered, proposed for federal listing, or candidates for federal listing (Carlson and Muth 1989; USDI 1989). Tyus et al. (1982a) reported that Colorado roundtail chub were rare in the mainstem Green River, Utah. Possible declines in numbers of large Colorado roundtail chub adults in certain reaches of the Yampa River, Colorado, have been recently noted largely

through qualitative observations (E. J. Wick, Larval Fish Laboratory, Colorado State University, personal communication). Ohmart et al. (1988) stated that Colorado roundtail chub were probably never common or widespread in the lower mainstem Colorado River. The Colorado roundtail chub is listed as protected or of special concern by several basin states (Johnson 1987).

Decline of fishes in the *G. robusta* superspecies complex, and other Colorado River Basin native fishes, has been attributed to man-induced changes in environmental conditions. These changes include modification and loss of habitat, introduction of non-native species, and water pollution (Williams et al. 1985; Stanford and Ward 1986c; CRFRT 1989a, 1989b). Bestgen and Propst (1989) blamed habitat alterations and establishment of non-native predator fishes for decline of roundtail chub in the Gila River drainage, New Mexico. Current knowledge on ecology and management of the Colorado River System was summarized by Stanford and Ward (1986a, 1986b, 1986c), Ward et al (1986), and Carlson and Muth (1989).

Identification and classification of all life stages of Colorado River Basin chubs in the *G. robusta* superspecies complex are problematical and remain troublesome to biologists. Genetic and ecological relationships among these fishes are close and, even with adult specimens, inter- or intra-specific morphological variations are often poorly understood (Smith et al. 1979; Valdez and Clemmer 1982; Rosenfeld 1986; Tyus et al. 1987; Douglas et al. 1989). To complicate matters, congeneric interspecific hybridization, resulting in morphological intermediates or intergrades, might occur in the wild (Holden and Stalnaker 1970; Hamman 1981; Valdez and Clemmer 1982;

Kaeding and Zimmerman 1983). However, results of taxonomic analyses conducted by Smith et al. (1979) and Douglas et al. (1989) on adult humpback and roundtail chub and bonytail (Smith et al.) indicated that these fish coexist as separate, reproductively isolated taxa in certain areas of the Colorado and Green or Yampa rivers. Kaeding et al. (in press) discussed the potential for spatial separation between spawning humpback and Colorado roundtail chub in the Black Rocks area. Hybridization among *Gila* may especially occur in disturbed sections of rivers (Tyus and Karp 1989). It is generally true that extent of hybridization among naturally sympatric fishes tends to be greater in altered environments (Campton 1988). Interpretation of the various *Gila* forms has often opened debate on validity of species-level designation for several chubs and, as Rinne (1976) noted, resulted in classification of fishes very different in morphology as subspecies or ecological variants of a single polymorphic species. Starnes (1990) summarized the taxonomic history of Colorado River Basin *Gila*.

Unresolved taxonomic questions may hinder efforts to protect and recover endangered species (Douglas et al. 1989). Resolution of problems associated with taxonomy of Colorado River *Gila* was identified as a critical need in recovery plans for the humpback chub and bonytail (CRFRT 1989a, 1989b). Douglas et al. (1989) stated that new approaches must be taken to solve these taxonomic problems. They presented a procedure for segregating Colorado River *Gila* based on ranking of multiple-variable qualitative characters. Rosenfeld and Wilkinson (1989) used electrophoretic techniques to examine protein variation at 23 presumptive loci among bonytail, humpback chub, Colorado roundtail chub, Virgin River roundtail chub *G. robusta seminuda*, humpback X

Colorado roundtail chub hybrids or humpback chub back-crosses, and Newark Valley tui chub *G. bicolor newarkensis*. Possible imperfections in their approach include small sample sizes, inadequate geographical coverage, and failure to analyze the same tissues for all taxa. Rosenfeld and Wilkinson (1989) concluded that, although degree of interspecific allelic divergence was small, taxon-specific alleles may be present. Their work requires verification through additional studies.

Several studies have been conducted on taxonomy or systematics of adult or immature humpback chub, bonytail, and Colorado roundtail chub (e.g., Holden and Stalnaker 1970; Suttkus and Clemmer 1977; Smith et al. 1979; Rosenfeld 1986a; Douglas et al. 1989). However, little taxonomic work has been done on their larvae and early juveniles. Winn and Miller (1954) examined field-collected wild larval and juvenile fish and provided a cursory photograph-illustrated key to postlarvae of six cyprinids, including *G. robusta*, and six catostomids native to the Colorado River Basin in Arizona, New Mexico, and Mexico. They defined postlarva as the period of fish development from completion of yolk absorption to loss of finfold and presence of ossified rays in the pelvic fins. Some data on development and morphology were presented in their work. *Gila* specimens examined by Winn and Miller (1954) probably included Colorado roundtail chub and Gila chub, but all chubs were treated simply as *G. robusta*. Their key did not separate *G. robusta* from Colorado squawfish *Ptychocheilus lucius*, another endemic Colorado River Basin minnow, because larval specimens of Colorado squawfish were not available for comparative study. In Winn and Miller's key, separation of *G. robusta* and Colorado squawfish from other cyprinids was based on pigmentation and mouth position. Suttkus and Clemmer (1977)

examined morpho-meristic characters of wild humpback chub specimens as small as about 25 mm standard length (SL) collected from the Grand Canyon area of the Colorado River. Smith et al. (1979) reported that field-collected wild specimens of humpback chub, bonytail, and Colorado roundtail chub as small as 54, 22, and 20 mm total length (TL), respectively, were identified using morpho-meristic criteria they developed. Snyder (1981) contributed descriptive information and three-view (dorsal, lateral, and ventral) drawings for cultured humpback chub and field-collected wild Colorado roundtail chub larvae and YOY juveniles (I complied the humpback chub morpho-meristics for this study). These two fishes and the bonytail were included in Snyder's (1981) provisional key to late larvae of cypriniform fishes in the Upper Colorado River Basin, Colorado. Identification of these three fishes was based on myomere and dorsal fin and anal fin principal-ray counts, but possible overlap in characters among taxa was acknowledged. Distinguishing meristics for bonytail were based on descriptions of adult characters.

Snyder (1981, 1983) and Snyder and Muth (1988, in press) summarized reasons for studying biology and ecology of early life stages of fish and emphasized the need for more and better taxonomic research on fish larvae. Valdez and Clemmer (1982) stated that one of the major problems confronting biologists working in the Colorado River Basin is identifying larval and YOY juvenile humpback chub, bonytail, and Colorado roundtail chub. Except for areas where allotopic (Rivas 1964) populations of these sympatric fishes occur (Kaeding and Zimmerman 1983), identity of field-collected young *Gila* usually has been left at the genus level or given a "tentative" species designation. Reliable

discriminating characters must be determined before collections of young *Gila* can be used to monitor these fishes and help answer many questions regarding life history and habitat requirements, especially those concerned with reproduction and early life history. Tyus et al. (1987) called for an immediate increase in research on ecology and biology of all upper-basin *Gila*. The purpose of this study was to describe the early life stages of humpback chub, bonytail, and Colorado roundtail chub and determine taxon-specific diagnostic morphological characters to facilitate identification of field-collected larval and YOY juvenile *Gila*.

Information on fish early ontogeny can also be useful in charting phylogenetic relationships (Ahlstrom and Moser 1981; Cohen 1984; Futuyma 1986) because characteristics fixed early in development may be more reliable than those appearing later and tend to be more similar among related species. Strauss and Fuiman (1985) stated that properly conducted studies on early ontogeny, because of the dynamic nature of early development, may be more sensitive in detecting evolutionary parallels and convergence than comparisons of adult form. Use of information on early fish ontogeny in phylogenetic reconstruction was examined by Mabee (1989). Descriptive data provided in this dissertation may help to clarify systematics of fishes in the *G. robusta* superspecies complex.

REVIEW OF PROCEDURES AND CHARACTERS USED IN LARVAL-FISH TAXONOMY

According to Snyder and Muth (1988, in press), less than 20% of North American freshwater and anadromous fishes are adequately described as larvae for identification purposes. Identification of fish larvae is partly an elimination process, and knowledge of the fish fauna in areas being studied and species distribution, biology, ecology, and behavior can facilitate identification by limiting the number of possible species. Familiarity with adult morphology of the fish species being studied is important because some adult characters may be useful in identifying larvae. Larval-fish identification is complex and often depends on combinations of various anatomical characters that may change during development. Balon (1981a, 1985a) viewed early development of fish as a saltatory process. Diagnostic, taxon-specific characters tend to be fewer in number and more subtle among larval fishes than among adult fishes, and exact observations are essential for accurate identification (Powles and Markle 1984; Marliave 1988).

Because anatomy of larval fishes changes with growth and development, a broad knowledge of ichthyology and larval fishes is important, and developmental series are necessary for identification. Sandknop et al. (1984) stated that construction of developmental series depends on specimen availability, duration of development periods, and complexity of ontogenetic change. They suggested that a sufficient number of specimens be used to define the beginning, progression, and

end of important developmental changes in morphology. If complete size series of specimens are available, Berry and Richards (1973) recommended a "dynamic" approach in describing larval-fish development (i.e., the smallest larva is described in detail, and only changes in sets of characters are described thereafter).

Variations in methods of collection, fixation, and preservation of fish larvae can result in significant differential expression of pigmentation or specimen shrinkage and alteration of morphometric characters (Hay 1981; Marliave 1988; Blaxter 1988). Morphological features identified as diagnostic characters may actually be artifacts of specimen fixation and preservation. Snyder (1983) discussed methods for fixing and preserving fish larvae.

Meristic traits (counts of like structures) are among the most useful characters for identifying fish larvae at various taxonomic levels and for studying early physiological processes of fish (Berry and Richards 1973; Powles and Markle 1984; Lindsey 1988). An important attribute of meristic characters is that they are labile during fish embryogenesis, and number of meristic parts can be influenced and changed by the environment. However, meristic traits, unlike morphometric characters, usually become fixed quite early in fish ontogeny. For this reason, meristic traits generally exhibit a higher degree of heritability than morphometric traits. Heritability is defined as the proportion of a population's total phenotypic variation due to genetic differences between individuals (Allendorf et al. 1988).

Almost every meristic series can be modified by the environment, but environmentally induced phenotypic variation in number of vertebrae or myomeres and fin rays has received the greatest attention. Natural

environmental variables known to modify meristic counts include salinity, dissolved oxygen, visible-light radiation, and especially temperature. Response of meristic traits to water temperature is typically a negative relationship, i.e., mean meristic counts tend to be lower as water temperature increases (Lindsey 1988). Hubbs (1922, 1924), and many authors since, reported clinal differences with greater average meristic counts for fish in colder waters. Fuiman (1982) found thermally induced differences in number of postanal and total myomeres for cohorts of age-0 yellow perch *Perca flavescens* from a single genetic stock. Results of experiments conducted by Fahay (1981) showed a negative relationship between number of dorsal fin rays in larval striped killifish *Fundulus majalis* and water temperature.

How meristic series respond to environmental conditions is variable among different species or genotypes of the same species as well as among different meristic series of the same species or genotype. A reasonable explanation for observed phenotypic variation in fish meristics is that the environment changes the number of embryonic segments by differentially influencing rates of tissue-growth and tissue-differentiation processes (Lindsey 1988). Blaxter (1984) considered the lability of many fish meristic characters and stated that environmental variables "fine tune" underlying genetic mechanisms. He suggested that larval-fish taxonomists should be cautious when interpreting small differences in certain meristic values, especially differences related to geographical distributions. Balon (1985b) discussed the interplay among genes, cells, tissues, organs, and the environment in fish ontogeny.

In identification of fish larvae and early juveniles, diagnostically useful meristic series include myomeres, vertebrae, pterygiophores, fin rays and spines, gill rakers, branchiostegal rays, pharyngeal teeth, and scales. Knowledge of the myomere complement for a given species is valuable because myomeres are obvious meristic structures, relatively consistent in number and position, and usually completely formed prior to hatching (Snyder 1981; Snyder and Muth 1988, in press). Many authors have reported that total number of myomeres is nearly, if not exactly, equal to total number of vertebrae (including vertebrae of the Weberian complex in cypriniform fishes).

Powles and Markle (1984) suggested methods to facilitate use of meristic data in larval-fish taxonomy. If possible, frequency distributions of meristic counts or at least modes, frequency of occurrence of modal values, and ranges of meristic counts should be included in taxon descriptions. Expressing meristic data as mean values is commonly practiced but may introduce errors if outlying counts exist.

Berry and Richards (1973) stated that morphometric characters can be of great value in larval-fish studies and are used to (1) compare morphology of larvae with adult and juvenile morphology, (2) study early ontogeny of morphology, and (3) distinguish between larvae of related taxa. Morphometry of biological organisms is typically expressed as percent or per mille of some standard; a proportional ratio. Ratios are raw numerical data from a statistical viewpoint, but they are computed variables (i.e., not derived from direct observation). The underlying rationale for presenting morphometry as a ratio is that ratio values may reveal diagnostic characters not clearly exhibited by the original direct measurements (Simpson 1960). Another reason for using ratios is

to remove effects of body size from the direct measurements (Atchley et al. 1976); possible errors in this reasoning due to allometry will be discussed later. Simpson et al. (1960) and Sokal and Rohlf (1981) examined the unique properties of ratios and reported at least three disadvantages of using ratios to express biological data. First, ratios typically vary more than the direct measurements upon which they are based. Simpson et al. (1960) suggested that, if small differences are important, it may be best to deal with direct measurements. Second, ratios may not be normally distributed, and their use may degrade the power of or invalidate many parametric statistical tests. This problem can often be solved by transformation of the variables. Third, ratios alter the underlying data structure, and information on relationships between the direct measurements is lost. According to Simpson et al. (1960), advantages of using ratios far outweigh the disadvantages, but difficulties must be recognized and understood. Sokal and Rohlf (1981) stated that ratios are widely used in analyses of biological data and often are the only meaningful way to understand certain types of biological problems.

Martin (1949), Marr (1955), Atchley et al. (1976), Fuiman and Corazza (1978), Bookstein et al. (1985), and many others provided evidence supporting use of direct measurements rather than ratios in fish-taxonomy studies. In fish taxonomy, morphometric ratios are frequently over-used or misused, and only rarely are original measurements directly considered or presented. When original variates are presented, they are usually in the form of a body part expressed as percent or per mille of the standard plotted against the original standard measurement. This method is more time consuming than plotting

direct measurements and, according to Weil (1962) and Atchley et al. (1976), does not remove effects of body size because ratio variables are more of a size measure than the original variates. Plotting body-part ratios against original standard measurements has little, if any, value, and plots of this type prohibit statistical treatment of data. Bookstein et al. (1985) discussed the inability of ratios (and other common size-adjustment procedures, e.g., restricting size classes) to automatically adjust for body size. They argued against adjusting body-part measurements for body size in evolutionary or systematic biology studies and recommended the "shear" method (Humphries et al. 1981) for size-free discrimination in multivariate analyses. When morphometry is expressed as a ratio, it is often assumed that there is an isometric growth relationship between body dimensions (i.e., constant relationship between growth of a body part and the standard). However, growth relationships between many body dimensions of larval fish is in the form of allometry (i.e., body part grows slower or faster than the standard). Fuiman and Corazza (1979) stated that relative growth patterns in different fishes must be considered and examined if morphometric characters are to be used to characterize a species. Failure of researchers to account for relative growth patterns in larval fishes has often resulted in fruitless analysis of useless morphometric data. Also, allometric growth of body dimensions may contribute to observed variability in morphometrics among taxa and local populations of the same taxon.

Throughout the larval and early juvenile periods, body dimensions of fish may exhibit isometric as well as allometric growth intervals. Typically, ratios for a particular morphometric character are described

and presented as mean or minimum and maximum values. Problems with this method arise when isometry is strictly assumed, potential for allometry is ignored, and descriptive character values (e.g., mean or range) are computed on specimens from too small or too broad a size or developmental range. If too small a size or developmental range is used, descriptive character values could have been derived from specimens in an isometric-growth stanza that preceded or followed a period of allometry. Specimens falling within an allometric growth stanza could be misidentified. Fuiman and Corazza (1979) provided an example of this scenario. If too broad a size or developmental range is used, indiscriminately including periods of isometry as well as allometry, variability among ratios for a particular morphometric character may be high, and diagnostic qualities of descriptive values could be lost.

One way to address these problems is to partition specimens into discrete size or developmental intervals and then compute morphometric ratios and descriptive character values for each interval. However, this method is often a waste of time and effort and, according to Bookstein et al. (1985), may miss ontogenetic changes in growth and shape. An alternative approach, and the method used in this study, is to use logarithmic graphs and regressions of the original variates (Fuiman and Corazza 1979; Smith 1980; Seim and Saether 1983; and others). Plots are examined for inflection points that indicate change in growth stanzas, and morphometric ratios and descriptive character values are then computed for individual growth stanzas. Linear regression of log-log plots of the original variates has additional taxonomic value. Martin (1949) concluded that only drastic internal or

environmental changes can alter the slope of the regression line, and that the intercept responds to more subtle environmental changes. When comparing taxa, differing slopes may indicate genetically based differences, and differing intercepts may indicate non-genetic differences. Further, when data are graphically presented in this manner, identification can be easily based on proximity of a data point to a regression line. Inclusion of confidence intervals for the regressions simplifies taxonomic decisions (Fuiman and Corazza 1979). This bivariate method is based on linear body measurements and yields one-dimensional information on body form. Another relatively recent morphometric technique that may be considered is the two-dimensional geometric "box truss" method described by Strauss and Bookstein (1982). This technique has been used to analyze evolutionary morphological variation in fishes, but its application to larval fishes has been limited (Strauss and Fuiman 1985). Bookstein et al. (1985) successfully discriminated adult humpback chub, bonytail, and roundtail chub using the shear and box-truss techniques with various morphometric characters. In biological taxonomy, the more straight-forward approaches are usually best, and considerable time and effort can be spent, and often wasted, in statistically manipulating data to produce discriminating characters. Usually, if diagnostic worth of descriptive information is not readily apparent through "simple" examination and comparison, it is doubtful that a more "complex" treatment of the data will provide any new meaningful results. Use of computers in taxonomic analysis of biological data was reviewed by Abbott et al. (1985).

Potential morphological differences between cultured and wild young of the same fish species may confound taxonomic studies (Blaxter

1984). Often, cultured fish are more robust and increase in length slower than wild fish of the same species. Powles and Markle (1984) reported that cultured young fish may exhibit greater meristic variation and are frequently more heavily pigmented than wild specimens. Patterns of melanophore pigmentation are often important in distinguishing larvae of closely related fish species, generally at the species or genus level (Berry and Richards 1973; Kendall et al. 1984). Diagnostic features of melanophore patterns include number and location of individual melanophores and location, shape, and size of groups of melanophores (Kendall et al. 1984). Differences in melanophore pigmentation between cultured and wild fish may be caused by several factors affecting degree of melanophore contraction or amount of melanin in the chromatophores. These factors include variations in background color or brightness, light intensity, and fish nutrition and metabolism (Fujii 1969; Mansfield and Mansfield 1981). Kendall et al. (1984) stated that, generally, relative size and placement of melanophores is under genetic control, whereas degree of melanophore contraction is physiologically determined. Melanophore distribution changes as fish develop and can vary within and among populations. Marliave (1988) noted clinal differences in number of postanal ventral-midline melanophores for larvae of tidepool sculpin *Oligocottus maculosus*.

Snyder (1981) and Snyder and Muth (1988, in press) discussed characteristics useful in identification of cypriniform larvae and YOY juveniles at or above the species level. They identified myomere, vertebra, and dorsal and anal fin principal-ray meristics, size and shape of the body and specific anatomical structures, morphometrics, and melanophore pigmentation as externally visible characters with

potentially high diagnostic value. Additionally, gill-raker and pharyngeal-teeth counts or osteological characters may have diagnostic qualities.

Use of osteological characters for identification of fish larvae has not received much attention, but it has potentially high value in confirming questionable identities or separating taxa for which diagnostic external characters are inadequate (Dunn 1983, 1984; Brothers 1984). Boehlert (1984) and Govoni (1984) reviewed the use of scanning electron-microscopy and histology techniques, respectively, for studying larval-fish anatomy at the microstructural or tissue level. They concluded that these techniques are potentially valuable tools in taxonomic and phylogenetic analyses.

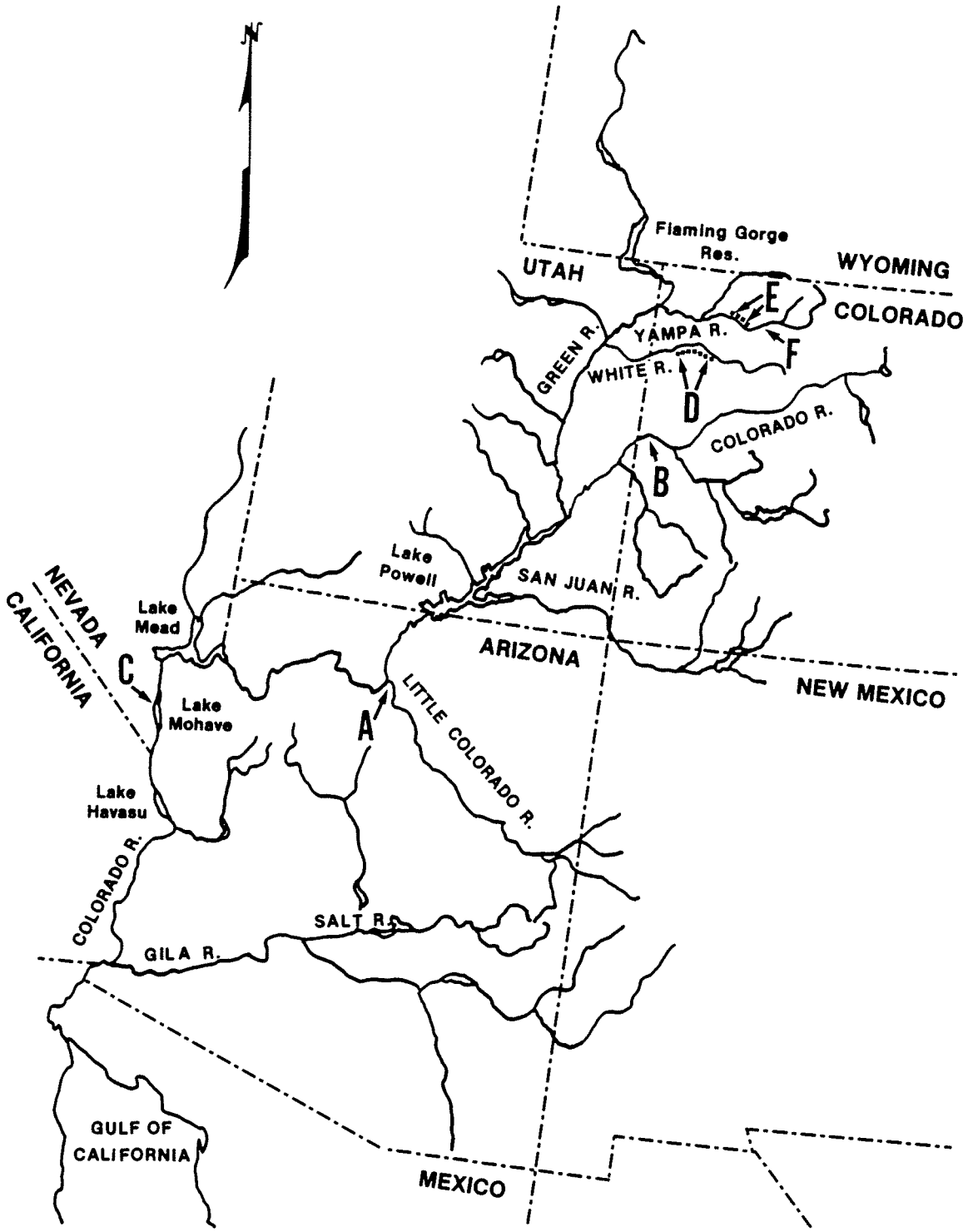
Fuiman et al. (1983) identified four major character states useful in segregating groups of cyprinid larvae occupying waters of North America east of the Continental Divide. These character states included relative preanal length, eye shape, preanal myomere number, and midventral pigmentation.

METHODS

Specimens Examined

Cultured: Hamman (1982b) collected humpback chub brood stock in 1979-1981 from the Little Colorado River near its confluence with the Colorado River, Grand Canyon National Park, Arizona, and from the Colorado River in the Black Rocks area (river km 218-219), Colorado (Figure 1). Total lengths (TL) and weights of females ranged from 355 to 425 mm and 350 to 730 g, respectively. Males were 315-378 mm in TL and weighed 260-470 g. Bonytail brood stock was collected in 1979-1981 from Lake Mohave near Cottonwood Cove, Nevada (Hamman 1982a; Minckley et al. 1989). Females ranged 487-564 mm in TL and weighed 956-1,500 g. Fish in the developmental series were cultured from artificially spawned and naturally or artificially fertilized eggs at Willow Beach (Arizona) National Fish Hatchery (Hamman 1982a, 1982b). Humpback chub young were cultured in 1980 and 1981, and bonytail young were cultured in 1981. To induce ovulation, females were given intraperitoneal injections of a common carp pituitary mixture at a dosage of 4 mg/kg body weight. Genetic integrity was maintained for each humpback chub stock. Fish examined in this study were reared in outside recirculating raceways (each 30.5 X 2.4 X 1.2 m) at water temperatures of 18-23°C. Diet consisted of naturally occurring zooplankton supplemented with a dry commercial trout starter.

FIGURE 1. Capture locations of parental brood stocks or wild larvae and young-of-the-year (YOY) juveniles for developmental study series of *Gila cypha*, *G. elegans*, *G. robusta*, *G. elegans* X *G. r. robusta*, and *G. elegans* X *G. cypha*. **A.** *G. cypha* brood stock and field-collected wild young, Little Colorado River near confluence with Colorado River in Grand Canyon National Park. **B.** *G. cypha* and *G. r. robusta* brood stock, Colorado River in the Black Rocks area. **C.** *G. elegans* brood stock, Lake Mohave near Cottonwood Cove. **D.** *G. r. robusta* field-collected wild young, White River upstream of Rangely. **E.** *G. r. robusta* field-collected wild young, Yampa River in the Government Bridge-Juniper Hot Springs area. **F.** *G. r. robusta* brood stock, Yampa River in the Horse Gulch area.


N
Flaming Gorge Res.
UTAH
WYOMING
COLORADO
E
F
YAMPA R.
GREEN R.
WHITE R.
D
COLORADO R.
B
Lake Powell
SAN JUAN R.
NEVADA
CALIFORNIA
Lake Mead
C
ARIZONA
NEW MEXICO
Lake Mohave
A
LITTLE COLORADO R.
Lake Havasu
COLORADO R.
SALT R.
GILA R.
GULF OF CALIFORNIA
MEXICO

Care was taken to collect Colorado roundtail chub brood stock and young for this study only in localities where historic distribution records precluded the presence of humpback chub and bonytail. Two attempts were made to collect and spawn Colorado roundtail chub brood stock from the Yampa River, Colorado. In March 1983, nine adult Colorado roundtail chub were collected at dusk with a boat-mounted electrofishing unit from near-shore habitats in the Maybell Bridge area (river km 127). Mainchannel water temperature at the time of fish collection ranged from 8 to 11°C. Based on fish size and other characters, four of the nine fish were tentatively classified as female and the rest as male. Females were 430-465 mm in TL and weighed 810-910 g. Males were 390-430 mm in TL and weighed 440-620 g. These fish were brought to the Larval Fish Laboratory, Colorado State University, Fort Collins, and placed in a covered 970-L fiberglass circular tank that received 10°-C well water from a Mino-Cool unit (Blissfield Manufacturing Company, Blissfield, Michigan). Cobble-size rocks had been placed in the tank to provide a more natural substrate. Fish were fed a variety of insect nymphs and larvae (mostly Plecoptera and Trichoptera), that had been picked off rocks taken from the Poudre River in Fort Collins, and fathead minnow *Pimephales promelas* adults. Food was replenished at least twice a week. Following a 7-d acclimation period, tank water temperature was gradually raised over 21 d and maintained at 19°C. Artificial lighting was provided and, during the 21-d period, photoperiod was increased weekly from 10-h light:14-h dark to 12:12 to 14:10. All fish developed orange-red breeding coloration and breeding tubercles soon after 19°C was reached. Seminal fluid was manually expressed from two fish previously classified as male. Each of

the fish classified as female was given two intraperitoneal injections, spaced 2 d apart, of a mixture of fresh common carp pituitaries and Ringer's solution. Dosage was 4 mg/kg body weight. Attempts were made to manually express eggs from injected fish on the day following each treatment. These efforts were unsuccessful, and the work was stopped. Necropsy of all fish showed that the tentative classifications by sex were correct. Females contained numerous small, undeveloped, granular eggs.

During late June and early July 1983, efforts were made to collect Colorado roundtail chub brood stock from the Yampa River in the Roundbottom-Juniper Hot Springs area, river km 149-199 (Muth et al. 1985). On 13 July 1983, two female and four male Colorado roundtail chub in reproductive condition were collected in the Horse Gulch area, river km 171 (Figure 1). These fish were taken at night with gill nets (38-mm-square mesh) in a near-shore eddy behind a natural rock jetty. At time of fish collection, water temperature in this eddy ranged from 17 to 19°C, water depth from about 1 to 3 m, water velocity from 0.2 to 0.4 m/s, and substrate consisted of silt-covered gravel. Total lengths, weights, and ages of females were 444-455 mm, 880-980 g, and 5-7 years, respectively. Males were 402-450 mm in TL, weighed 480-700 g, and represented ages V-VIII. Eggs were manually stripped, dry fertilized, and water hardened on-site following procedures described by Ball and Bacon (1954). Colorado roundtail chub young were cultured at the Larval Fish Laboratory. Eggs were incubated on wire-screen trays in a flow-through incubator (Heath Tecna Corporation, Kent, Washington) that received 19-°C well water at a rate of 12.3 L/min. During incubation, dissolved oxygen ranged from 7.5 to 8.0 mg/L (100 to 105% saturation),

pH from 7.3 to 7.7, and total water hardness from 410 to 440 mg $CaCO_3$/L. Water quality parameters were measured with HACH field kits (HACH Chemical Company, Loveland, Colorado). Samples of embryos were taken every 4 h. Fish were reared for about 58 d after hatching in flow-through troughs (each 3.0 X 0.3 X 0.2 m) that received 18-20-°C well water at a rate of 6.0 L/min. Artificial lighting was provided, and photoperiod was 14-h light:10-h dark. Throughout the rearing period, dissolved oxygen ranged from 8.0 to 9.0 mg/L (105 to 115% saturation), pH from 7.1 to 7.9, and total water hardness from 450 to 470 mg $CaCO_3$/L. After swim-up (as defined by Blaxter 1988) to end of rearing, fish were fed twice daily, morning and evening, with live *Artemia* sp. nauplii and commercial TetraMin Fry Diet and Staple Food (Tetra Corporation, West Germany). Fish were sampled daily (N = 50/sample) during the first 19 d of rearing. Thereafter, samples were taken every 5 d (N = 50/sample). Samples were collected before the morning feeding.

Cultured F1 young from bonytail X Colorado roundtail chub and bonytail X humpback chub crosses were obtained from Willow Beach National Fish Hatchery (Hamman 1981a). Brood stock consisted of five bonytail females collected from Lake Mohave near Cottonwood Cove in 1979 and 1980 and eight Colorado roundtail chub males and five humpback chub males collected from the Colorado River in the Black Rocks area in 1979 (Figure 1). Females were 457-559 mm in TL and weighed 850-1,300 g. Males were 298-352 mm in TL and weighed 240-420 g. Eggs were artifically spawned and fertilized. Females were given intraperitoneal injections of a common carp pituitary mixture at a dosage of 4 mg/kg body weight to induce ovulation. Fish in the developmental series were reared in an outside recirculating raceway at water temperatures of

16-25°C and fed naturally occurring zooplankton and a commercial trout starter diet.

Collected: A total of 30 wild humpback chub late larvae and YOY juveniles were obtained from Dennis Kubly, Arizona Game and Fish Department, Phoenix. They were collected in late May and early July 1989 from the lower Little Colorado River and the Colorado River below the Little Colorado-Colorado River confluence (Figure 1). Fish were sampled with seines in backwater habitats. Humpback chub is the only *Gila* species presently found in this area, and successful reproduction by humpback chub in the lower Little Colorado River has been documented. Bonytail probably once occurred in this area, but none have been collected in surveys of fishes of the Colorado River in Grand Canyon National Park since closure of Glen Canyon Dam in 1963 (Kaeding and Zimmerman 1983; Maddux et al. 1987). Occurrence of Colorado roundtail chub in the lower Little Colorado River or lower mainstem Colorado River has never been conclusively documented (Carlson and Muth 1989).

Wild Colorado roundtail chub larvae and YOY juveniles were collected by Larval Fish Laboratory and Colorado Division of Wildlife personnel in 1979 during June-August from the White River upstream of Rangely (above river km 154), Colorado, and in 1982 during July and August from the Yampa River in the Government Bridge-Juniper Hot Springs area, river km 149-158 (Figure 1). These fish were collected with fine-mesh seines (0.8-1.6-mm-square mesh), dip nets, and plexiglas light-traps (Muth and Haynes 1984) in near-shore, low-velocity habitats. Water temperature in these habitats at time of fish collection ranged 17-24°C. Light-traps were used to collect larval and YOY juvenile

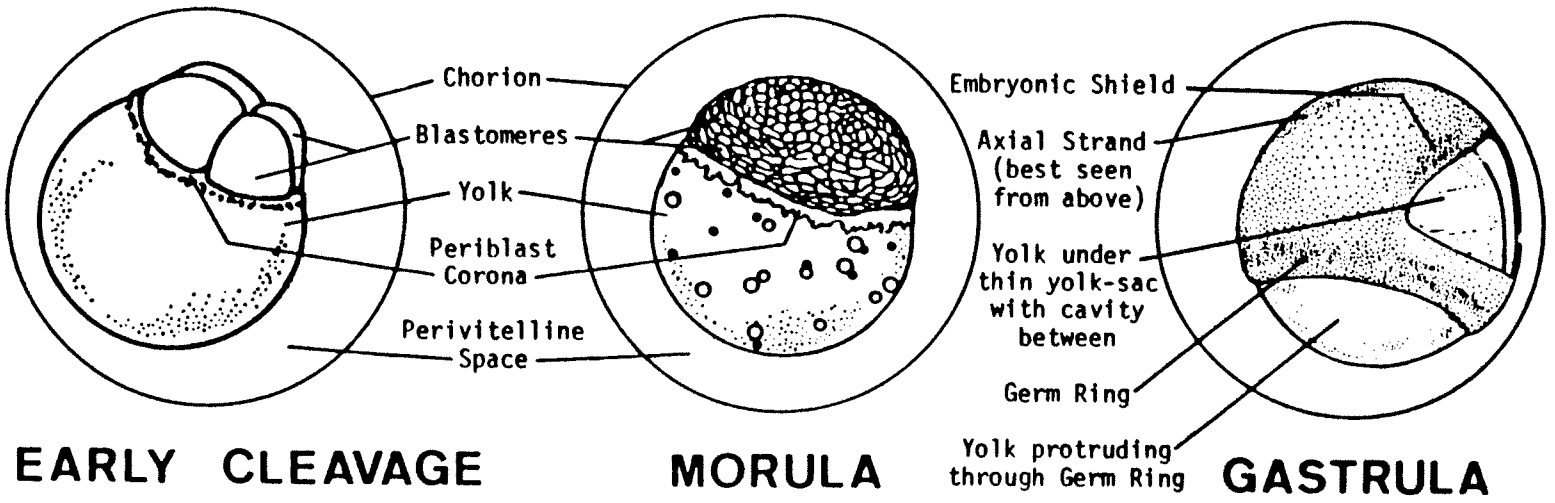
fishes from riverine habitats ineffectively sampled with conventional gear. These habitats included deep eddies, shorelines, or backwaters and areas obstructed by rocks, plants, or debris. Development of light-traps was adjunct to studies on fish early life history conducted by the Colorado Division of Wildlife in the Upper Colorado River Basin. Light-traps were deployed at night for 30 min to 1 h per set.

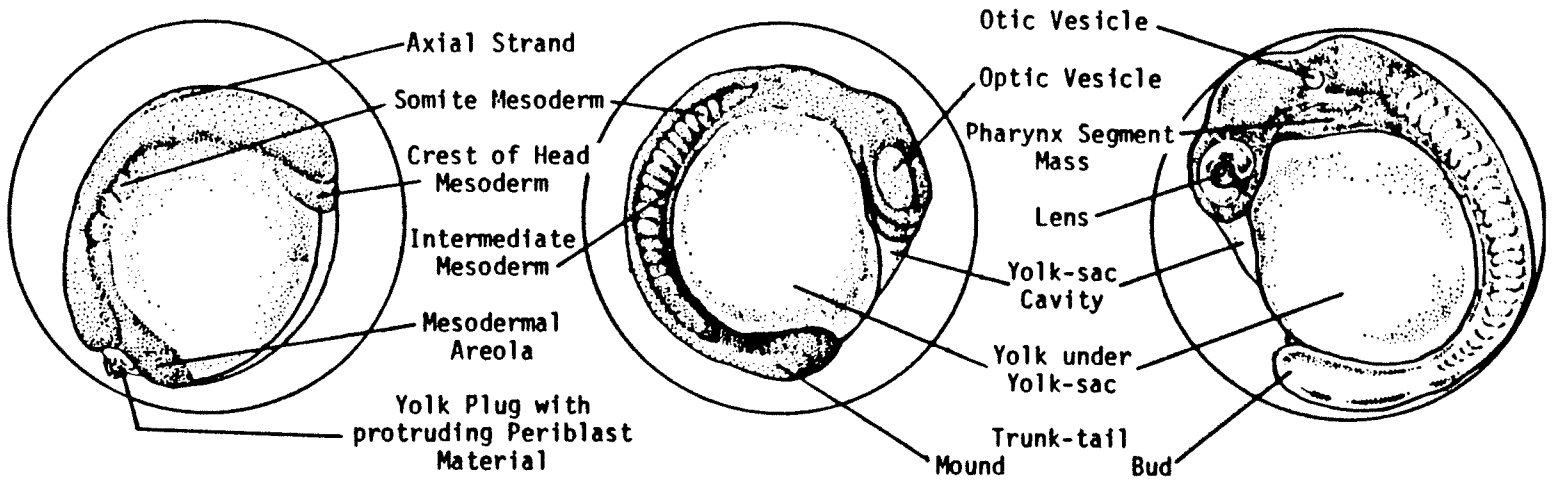
All cultured and field-collected specimens were killed and fixed in 10% formalin and then stored in 3% formalin buffered to near-neutral pH with marble chips or phosphate (Markle 1984). Most specimens on which this study was based are maintained in collections of the Larval Fish Laboratory and are available for examination by other researchers. Associated specimen data (e.g., morphometrics and meristics) are stored in IBM-compatible Lotus 123 or dBase III computer files.

Specimen Data and Observations

Specimens were examined and analyzed for morphometrics, meristics, developmental state, and growth. Hybrid specimens were examined for meristics only. Snyder (1981) and Snyder and Muth (1988, in press) summarized useful characteristics for identification of cypriniform fish larvae, and provided illustrations of selected anatomical features of cypriniform fish eggs, embryos, and larvae (Figures 2, 3). Specimens were studied under a low-power, stereo-zoom microscope fitted with polarizing filters (useful for myomere and fin ray counts) and a measuring eyepiece reticle calibrated against a stage micrometer. Various combinations of reflected, transmitted, and polarized light were used. Measurements were made to the nearest 0.05 or 0.1 mm. Re-measurement of selected specimens, occasionally by a second observer,

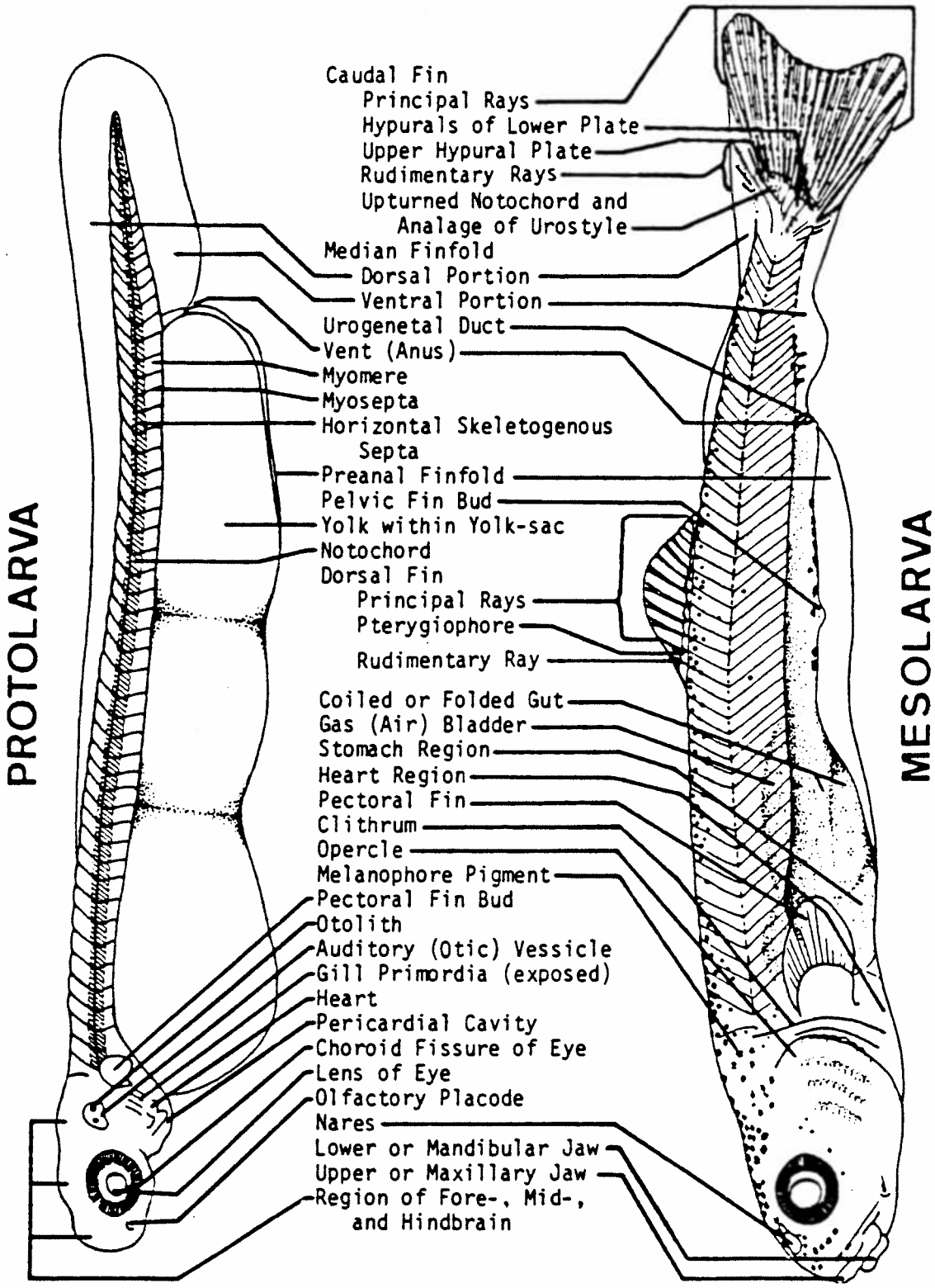
FIGURE 2. Selected anatomical features of cypriniform fish eggs and embryos (from Snyder 1981; based on drawings from Long and Ballard 1976).





EARLY EMBRYOS

FIGURE 3. Selected anatomical features of cypriniform fish larvae (from Snyder 1981).


PROTOLARVA
MESOLARVA
Caudal Fin
Principal Rays
Hypurals of Lower Plate
Upper Hypural Plate
Rudimentary Rays
Upturned Notochord and
Analage of Urostyle
Median Finfold
Dorsal Portion
Ventral Portion
Urogenetal Duct
Vent (Anus)
Myomere
Myosepta
Horizontal Skeletogenous
Septa
Preanal Finfold
Pelvic Fin Bud
Yolk within Yolk-sac
Notochord
Dorsal Fin
Principal Rays
Pterygiophore
Rudimentary Ray
Coiled or Folded Gut
Gas (Air) Bladder
Stomach Region
Heart Region
Pectoral Fin
Clithrum
Opercle
Melanophore Pigment
Pectoral Fin Bud
Otolith
Auditory (Otic) Vessicle
Gill Primordia (exposed)
Heart
Pericardial Cavity
Choroid Fissure of Eye
Lens of Eye
Olfactory Placode
Nares
Lower or Mandibular Jaw
Upper or Maxillary Jaw
Region of Fore-, Mid-,
and Hindbrain

showed that most measurements were repeatable to within 0.1 mm. Each specimen was assigned to a developmental phase or period following the combined developmental-interval terminology criteria for fish early life stages of Snyder and Muth (1988, in press). The terminology integrates the principal subdivisions and functions of terminologies presented by Ahlstrom et al. (1976), Snyder (1976, 1981), and Hardy et al. (1978). Elements of Snyder and Muth's (1988, in press) terminology used in this study follow.

Larva: Period of fish development between hatching and the juvenile period. Transition to the juvenile period is based on (1) acquisition of adult complement of fin rays in all fins, including principal and rudimentary fin rays, and (2) loss beyond recognition of all finfold.

Protolarva: Phase of larval development characterized by absence of fin rays in all median (dorsal, anal, and caudal) fins.

Mesolarva: Phase of larval development characterized by presence of at least one fin ray in any of the median fins but either lacking adult complement of principal fin rays in all median fins or lacking pelvic fin buds.

Flexion Mesolarva: Phase of mesolarval development characterized by incomplete adult complement of principal caudal fin rays (posterior portion of notochord flexes upward).

Postflexion Mesolarva: Phase of mesolarval development characterized by presence of adult complement of

principal caudal fin rays (notochord flexion essentially complete).

Metalarva: Phase of larval development characterized by presence of (1) adult complement of principal fin rays in all median fins and (2) pelvic fin buds.

Up to 37 morphometric and 25 meristic characters per specimen were analyzed on over 750 specimens (meristics only for hybrids). Measurements (Figures 4, 5) were made on at least two specimens, if available, in each 1-2-mm TL interval throughout the larval period for each fish group. For juveniles, up to about 50 mm TL, one or more specimens were similarly processed for at least each 5-mm TL interval, if available.

Allometric growth patterns of body dimensions were analyzed following methods described by Fuiman and Corazza (1979) in an attempt to establish and refine diagnostic characters for taxon separation. A similar procedure was also used by Yeager and Wallus (1982), Fuiman (1983), and Strauss and Fuiman (1985). Measurements for each character were plotted against a standard measure (e.g., SL) on log-log coordinates. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines and 95% confidence intervals for each growth stanza were calculated using Bartlett's (1949) method of "best fit" because values of both X and Y variables were measured and therefore subject to error (Kidwell and Chase 1967). One criticism of Bartlett's method is that it may bias the slope estimate (Kuhry and Marcus 1977). However, Sokal and Rohlf (1981) compared regression equations obtained by four different methods,

FIGURE 4. Selected measurements for larval and young-of-the-year juvenile *Gila cypha*, *G. elegans*, and *G. robusta robusta*. **ME** = middle of eye. **BPE** = immediately behind posterior margin of eye. **APM** = anterior margin of most posterior myomere. **SL** is measured to posterior margin of notochord until adult complement of principal caudal fin rays are observed. Thereafter, **SL** is measured to posterior margin of hypural plates. Fin lengths (**D**, **A**, **P1**, and **P2**) are measured along plane of fin from origin to most distal margin.

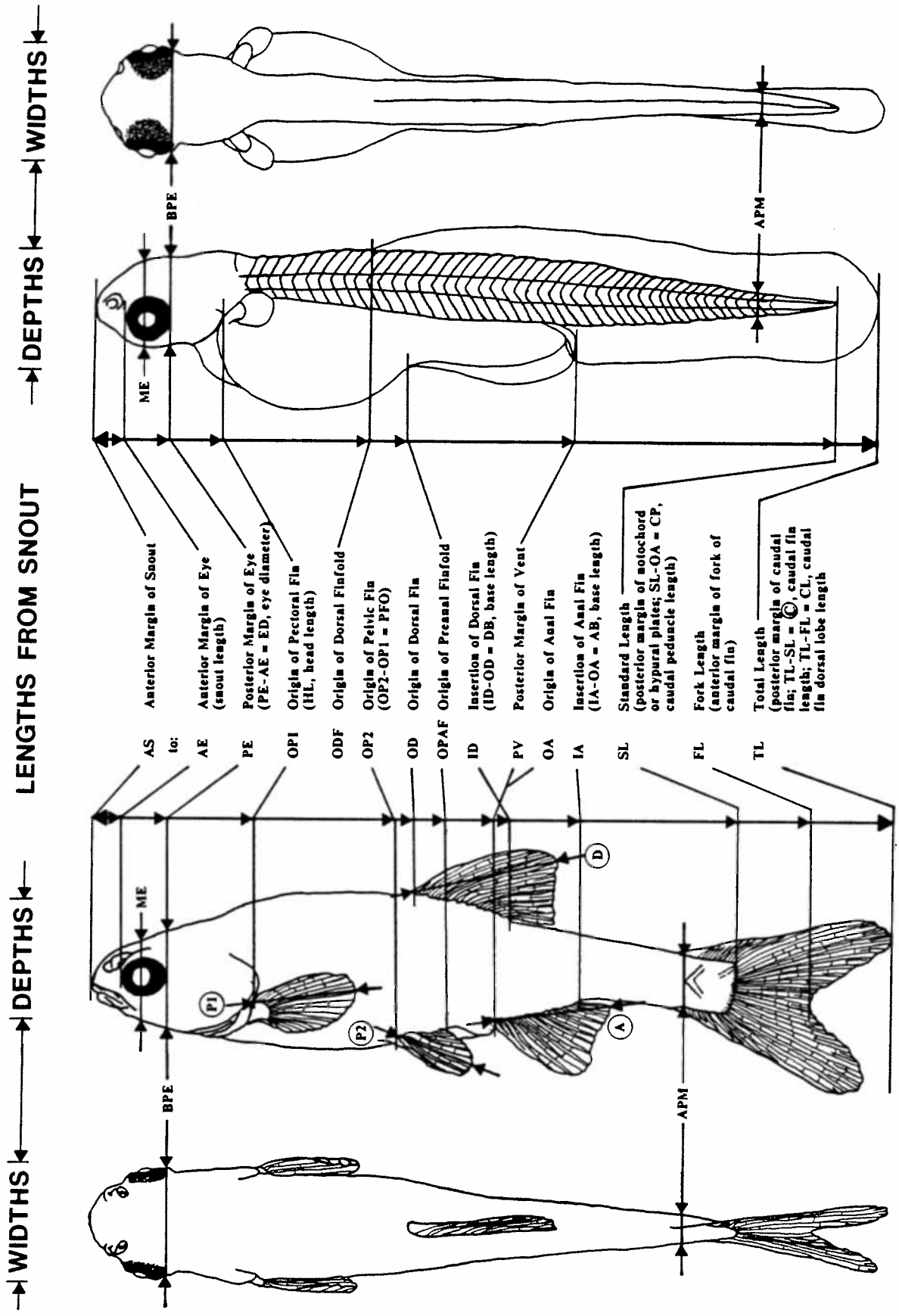
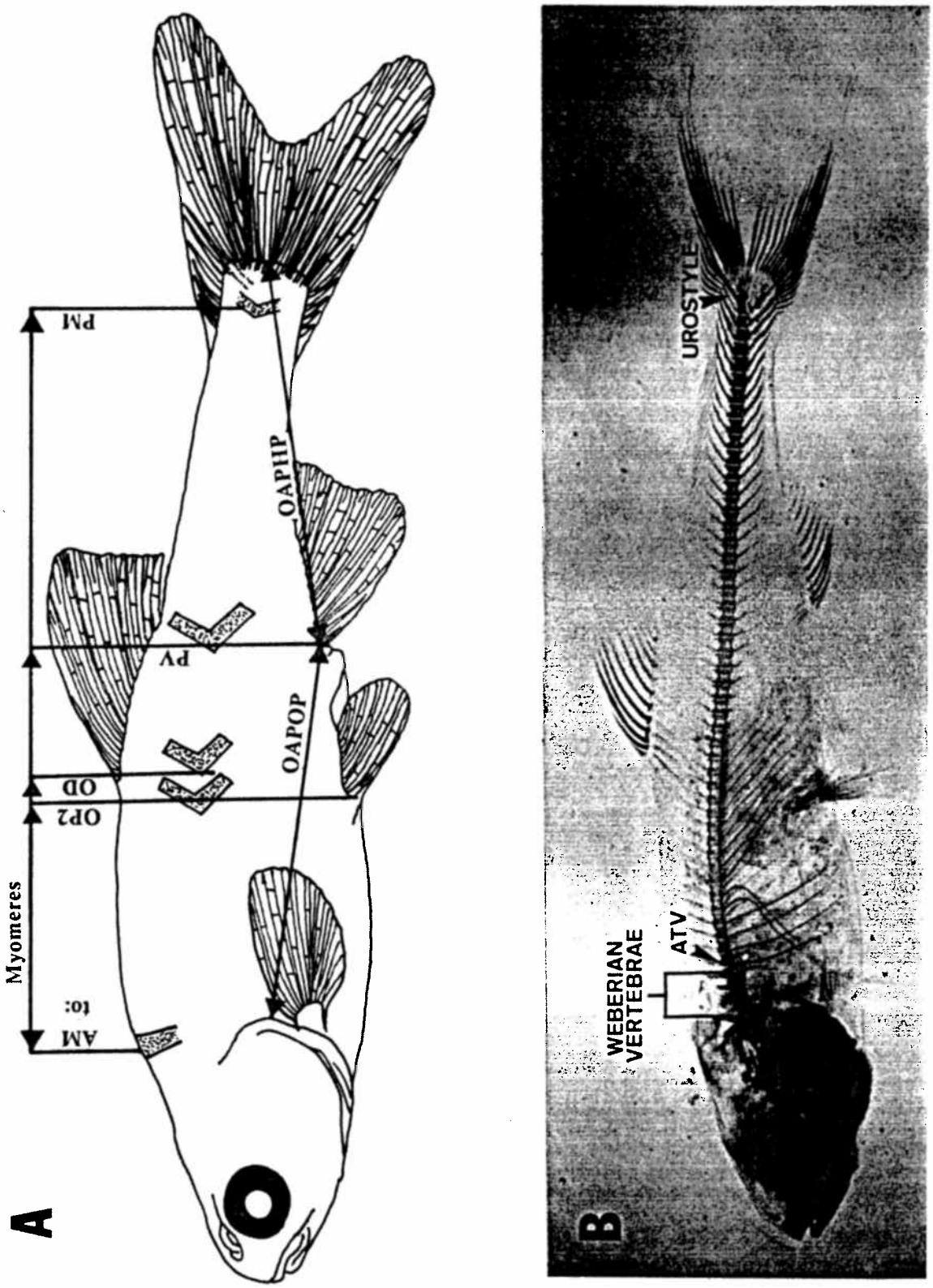

WIDTHS
DEPTHS
LENGTHS FROM SNOUT
DEPTHS
WIDTHS
ME
BPE
APM
AS to: Anterior Margin of Snout
AE Anterior Margin of Eye (snout length)
PE Posterior Margin of Eye (PE-AE = ED, eye diameter)
OPI Origin of Pectoral Fin (HL, head length)
ODF Origin of Dorsal Finfold
OP2 Origin of Pelvic Fin (OP2-OP1 = PFO)
OD Origin of Dorsal Fin
OPAF Origin of Preanal Finfold
ID Insertion of Dorsal Fin (ID-OD = DB, base length)
PV Posterior Margin of Vent
OA Origin of Anal Fin
IA Insertion of Anal Fin (IA-OA = AB, base length)
SL Standard Length (posterior margin of notochord or hypural plates; SL-OA = CP, caudal peduncle length)
FL Fork Length (anterior margin of fork of caudal fin)
TL Total Length (posterior margin of caudal fin; TL-SL = ©, caudal fin length; TL-FL = CL, caudal fin dorsal lobe length
P1
P2
D
A

FIGURE 5. **A.** Selected myomere counts and additional measurements for larval or young-of-the-year (YOY) juvenile *Gila cypha*, *G. elegans*, *G. robusta robusta*, *G. elegans* X *G. r. robusta*, or *G. elegans* X *G. cypha*. **AM** = most anterior myomere. **PM** = most posterior myomere. Method of counting myomeres was as defined by Siefert (1969). **OAPOP** = distance from anal fin origin to posterior margin of opercle. **OAPHP** = distance from anal fin origin to posterior margin of hypural plates. See Figure 4 for definitions of other abbreviations. **B.** Selected vertebra counts (same as for myomeres) for YOY juveniles of all *Gila* examined. **ATV** = most anterior trunk vertebra. In this study, vertebra counts were made on cleared and stained specimens and included the four vertebrae of the Weberian complex and the urostylar vertebra.

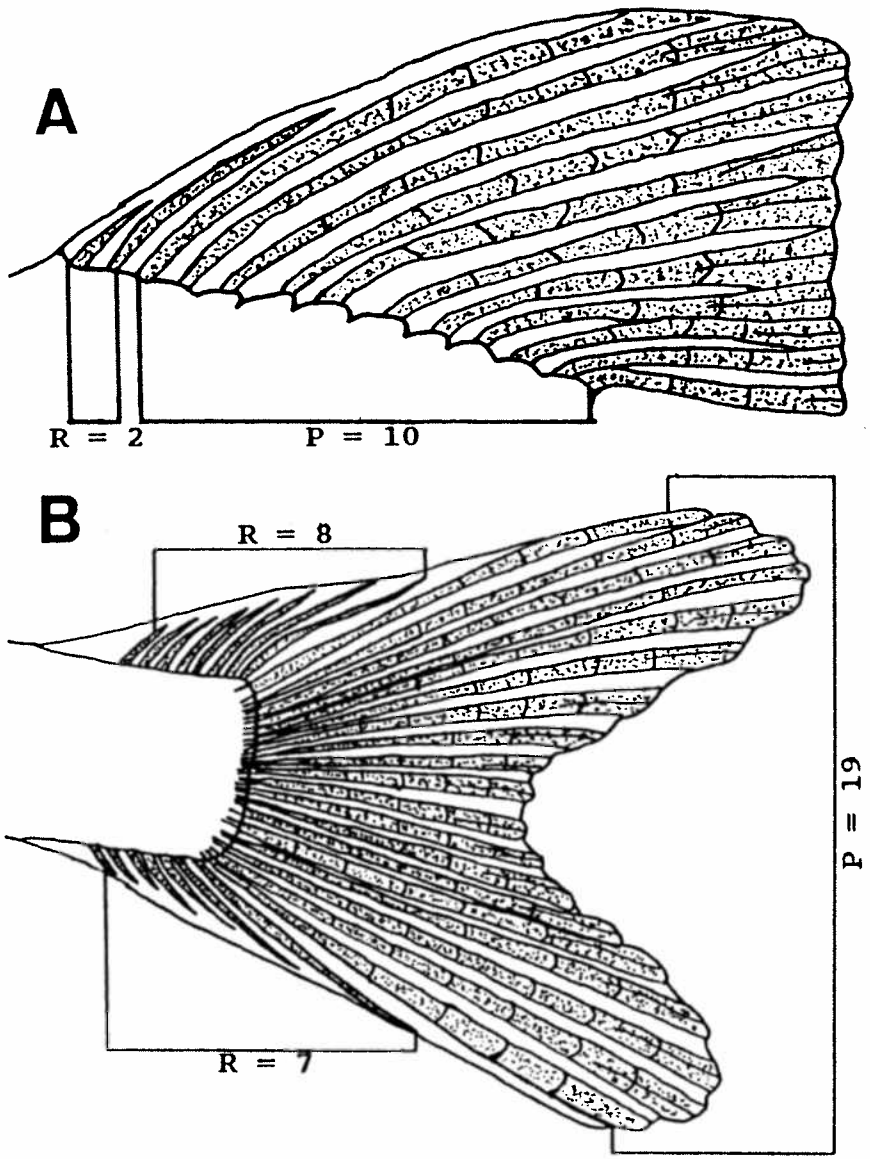

A
PM
OAPHP
PV
OAPOP
OD
OP2
Myomeres
to
AM
B
UROSTYLE
WEBERIAN VERTEBRAE
ATV

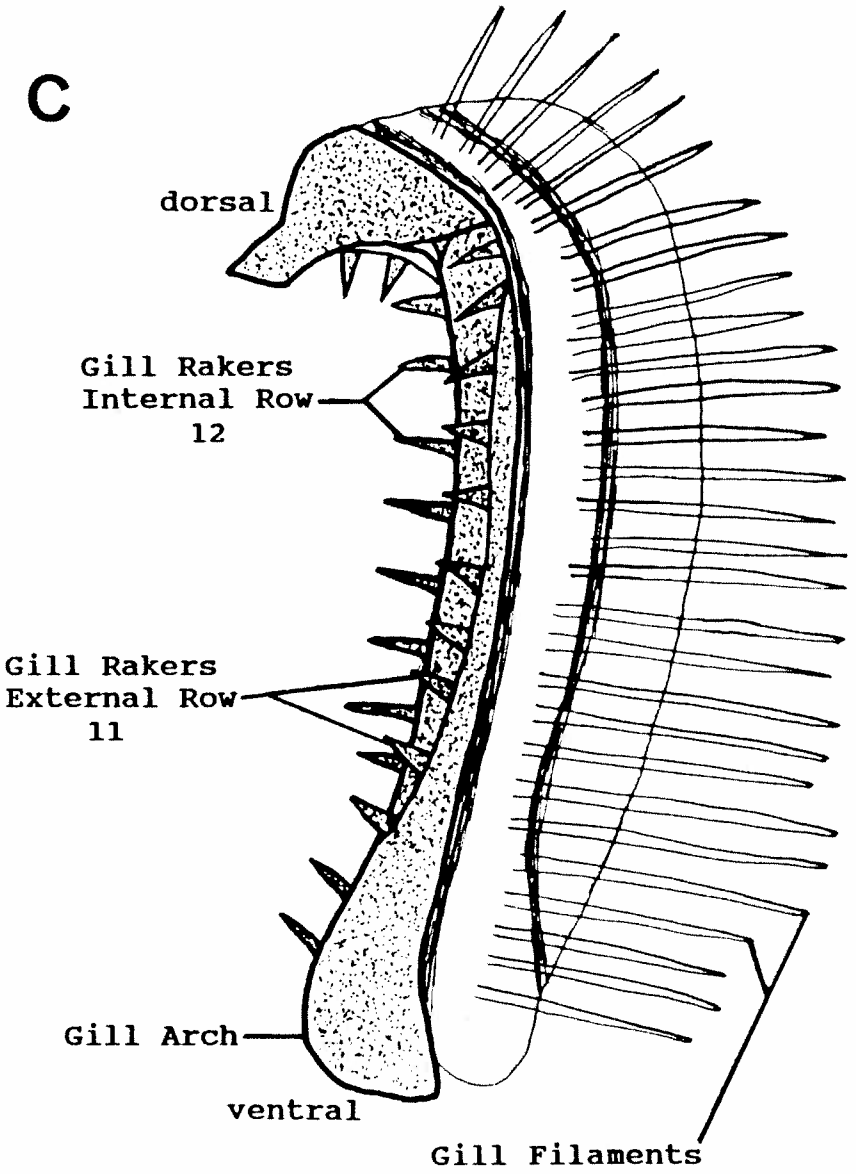
including Bartlett's method, and concluded that computed slopes were similar for all methods.

Huxley's (1932) allometry equation for relative growth was $Y = bX^k$. In its logarithmic form, this equation is linear: $\log Y = \log b + k \log X$, where Y is size of one body part (character measurement), X is size of the other body part (standard measure), k is the growth coefficient constant (slope of log-log line), and b is a constant related to the units of measure (Y-axis intercept or an index of the size of part Y when X is of unit size). Isometric growth is represented by this equation when k equals 1.0. Positive allometry (Y grows faster than X) occurs when k is greater than 1.0, and negative allometry (Y grows slower than X) occurs when k is less than 1.0. Calculated regression equations were used to more accurately estimate inflection points. Measurements for each character were then expressed as percent of the standard measure (morphometrics), and mean, standard deviation, and range for each morphometric were calculated and reported by developmental interval or growth stanzas within each interval. Character measurements for wild humpback chub young were not plotted for regression analysis because only 8 metalarvae and 18 juveniles were examined. Standard length, rather than TL, was used as a standard measure to remove the allometric influence of caudal fin growth.

The method for counting myomeres on larvae was as defined by Siefert (1969), i.e., myomeres anterior to a particular reference point included those bisected by an imaginary vertical line drawn through the body at the reference point (Figure 5). Fin-ray counts were made for all fins on metalarvae and juveniles using observable (presumably ossified) fin rays (Figure 6). Counts were also made of ossified fin

FIGURE 6. Median-fin ray and gill-raker counts for metalarval or young-of-the-year juvenile (sensu Snyder and Muth 1988, in press, see Methods) *Gila cypha*, *G. elegans*, *G. robusta robusta*, *G. elegans* X *G. r. robusta*, and *G. elegans* X *G. cypha*. **A.** Dorsal fin. Method of counting anal fin rays same as for dorsal fin. **B.** Caudal fin. Rudimentary fin rays indicated by **R**, and principal fin rays indicated by **P**. Ray counts for pectoral and pelvic fins include all rays. **C.** Gill arch, lateral view. In this study, gill raker counts were made on gill arches excised from the left side of cleared and stained juveniles.


A
R = 2
P = 10
B
R = 8
R = 7
P = 19


C
dorsal
Gill Rakers
Internal Row
12
Gill Rakers
External Row
11
Gill Arch
ventral
Gill Filaments

rays or skeletal fin-ray supports (pterygiophores) for the median fins on postflexion mesolarvae. Meristic data were also obtained from selected specimens cleared with a sodium borate-buffered trypsin solution and stained for skeletal study. Soft tissue clearing and skeletal staining procedures followed techniques modified by Snyder and Muth (1988) from Pothoff (1984) and Taylor and Van Dyke (1985). Postflexion mesolarvae were dehydrated with ethyl alcohol, stained with a glacial acetic acid-alcian blue solution for cartilage, and cleared. Metalarvae and juveniles were cleared and then stained with a potassium hydroxide-alizarin red solution for bone. A step-by-step description of the clearing and staining procedures is given in Appendix E. Specimens were cleared and stained for examination of vertebra and gill-raker counts on juveniles as well as to verify fin-ray meristics. Reported vertebra counts include the four Weberian-complex vertebrae and the urostylar vertebra (Figure 5). Gill-raker counts were made on gill arches excised from the left sides of specimens and include both external and internal rows (Figure 6). Gill rakers of three hatchery-cultured bonytail adults (8 years old) were also counted (same counting procedure as for YOY juveniles). These fish were obtained from Dexter National Fish Hatchery in November 1989 and were reared from the same group of eggs as the bonytail developmental series. Mode, frequency of occurrence of the modal value, and range were determined for each meristic character and reported by developmental interval.

Central tendency measures (mean or mode) and ranges for each morpho-meristic character by developmental interval or growth stanza within each interval were examined and compared among fishes to identify those with apparent diagnostic value, i.e., those with little or no

overlap in central tendency measures and ranges among fishes. Frequency distribution (by percent) of selected, diagnostically useful morphomeristics was calculated and reported by developmental interval or growth stanza within each interval.

Size or age (days after hatching) at onset of selected developmental events was documented for all specimens analyzed for morphometric and meristic data and for many additional specimens. Events selected included hatching; attainment of eye pigment; loss of yolk and finfold; formation of a gut loop of at least a 90° bend; formation of pectoral and pelvic fin buds; transition to mesolarva (flexion and postflexion), metalarva, and juvenile; formation of first and last principal and rudimentary fin rays in each of the median fins; formation of first and last fin rays in the pectoral and pelvic fins; and initial formation of lateral series of scales. For laboratory-cultured Colorado roundtail chub, timing (hours after fertilization) of onset of selected embryological developmental events was also documented (first reported in Muth et al. 1985). Embryological events selected were classified as to developmental stage following Balinsky's (1948) convention. Stages were cleavage, blastula, late gastrula, late neurula, oval eyes, early tail-bud, finfold, and pigmented eyes.

Growth of cultured specimens of all three fishes was documented by plotting SL measurements against days after hatching on linear coordinates. Data were then analyzed by linear, geometric, and exponential regressions to determine the equation giving the highest coefficient of determination (r^2). Exponential regression was the chosen analysis method because in all cases it accounted for the highest percent of total variation (i.e., highest r^2 value).

Drawings, including dorsal, ventral, and lateral views, of typical specimens were prepared for each larval phase and the juvenile period (YOY portion) of all three fishes to document body form and melanophore (black or brown pigments) pigmentation. Flexion and postflexion mesolarvae were treated as one phase. Enlarged photographs of specimens were traced to assure accurate body proportions and structure locations. Details were completed while examining the photographed specimen under a microscope. Final drawings were idealized (e.g., frayed fins smoothed and curved bodies straightened).

Diagnostic morpho-meristic and developmental characters were used to prepare keys to each developmental interval for all three fishes. Keys were developed with the aid of DELTA-based programs for key generation (Dallwitz 1980; Dallwitz and Paine 1986). Keys were tested for accuracy, clarity, and ease of use by fishery students in the Department of Fishery and Wildlife Biology, Colorado State University.

RESULTS AND DISCUSSION

Results of my work on the three *Gila* taxa are in five interrelated sections. Two sections, Comparative Summary and Keys, are in the main body of the text. The other three sections are appendices: Taxon Accounts (Appendix A), Log-Log Plots of Selected Measurements (Appendix B), and Regression Constants for Log-Log Plots of Selected Measurements (Appendix C). Each taxon account includes (1) a review with references of the fish's status, distribution and habitat, adult morphology and meristics, and reproduction; (2) original data in tables or graphs on size or age at onset of developmental events, growth rates, morphometrics, and meristics for larvae and YOY juveniles (the *G. r. robusta* account provides additional data on timing of embryological events); and (3) drawings, including dorsal, lateral, and ventral views, of typical specimens for each larval phase and YOY portion of the juvenile period (drawings of Colorado roundtail chub mesolarvae through YOY juveniles and of Colorado River humpback chub larvae and YOY juveniles were originally published in Snyder 1981; humpback chub drawings were prepared as part of my study). Selected meristics for *Gila* hybrid specimens are summarized in Appendix D.

Comparative Summary

In this study, cultured specimens were studied for all fishes. Water temperatures and diet during rearing were similar for all three

Gila taxa. Field-collected wild young of certain identity were available for humpback and Colorado roundtail chub. Median water temperatures of collection sites at time of capture were similar to, if not the same as, rearing temperatures for cultured young. All specimens were fixed and preserved in the same manner (field-collected specimens may have remained in fixative longer than cultured specimens). No consistent differences in meristic or morphological characters examined were noted between cultured and wild humpback chub, cultured and wild Colorado roundtail chub, or between humpback chub stocks. Wild humpback chub specimens tended to have slightly longer fins and a slightly longer caudal peduncle than cultured humpback chub specimens. Cultured fish were considerably more robust than wild-caught specimens; consequently, comparative measurements of body depth and width in the trunk region were not taken. Cultured specimens generally exhibited larger and darker melanophores than specimens collected in the field.

Size Relative to State of Development and Age: Youson (1988) stated that presence of certain morphological features or physiological processes along the developmental continuum seems to be more of a function of fish length rather than age, especially in bony fishes. Differences among the *Gila* taxa examined in size relative to developmental state were not great (Tables 1, A-1, A-2, A-7, A-10 to A-12), but they can help in separating taxa when used in combination with other morpho-meristic features. Generally, most developmental processes for humpback and Colorado roundtail chub proceeded at a pace similar to that reported by Snyder (1981). Average egg diameter (mm) after fertilization and water hardening was 2.2 (range = 2.0-2.4) for

TABLE 1. Size at onset of selected, diagnostically useful developmental events for *Gila cypha*, *G. elegans*, and *G. robusta robusta* larvae and young-of-the-year juveniles. Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. See Methods for capture locations of brood stocks and young. Rare or questionable extremes are in parentheses.

Character	*G. cypha* mm SL[a]	*G. elegans* mm SL	*G. robusta* mm SL
Phase/period transitions[b]:			
Embryo to larva	6-7	5-6	7(8)
Proto- to mesolarva	9-10	8	(8)9-10
Flexion to post-flexion mesolarva	10-11	9	10-11
Meso- to metalarva	12-13	11	12-13
Larva to juvenile	21-22	22	19-20
Yolk assimilated	9-10	8-9	9-10
Gut looped, 90° bend	13-15	14-15	12-13
Finfold absorbed	21-22	22	19-20
Onset of first fin rays:			
Dorsal, principal	10	9	10
Anal, principal	10	9	10
Caudal, principal	9-10	8	(8)9-10
Pectoral	10-11	9-10	11-13
Pelvic	11-12	10-11	12-13
Onset of full fin-ray counts:			
Dorsal, principal	12-13	11	12-13
Anal, principal	12-13	11	12-13
Caudal, principal	10-11	9	10-11

[a]See Figure 4 for methods of measuring standard length (SL).
[b]Developmental-interval terminology for fish early life stages as defined by Snyder and Muth 1988, in press, see Methods.

bonytail, 2.7 (range = 2.3-3.3) for humpback chub, and 2.8 (range = 2.7-3.1) for Colorado roundtail chub. Egg maturation in humpback chub and bonytail was induced with hormones (Hamman 1982a, 1982b), whereas Colorado roundtail chub eggs matured naturally (Muth et al. 1985). Minckley and Gustafson (1982) reported that razorback sucker *Xyrauchen texanus* eggs that matured naturally were considerably larger in diameter than hormone-matured eggs. However, they noted that embryos from both sets of eggs were of similar length by time of hatching. In this study, hatching sizes of larvae reflected observed differences in egg size among taxa. Bonytail eggs yielded the smallest larvae, followed by humpback and Colorado roundtail chub, respectively. Through transition to the metalarval phase, bonytail maintained their smaller size relative to developmental state, advancing faster than either humpback or Colorado roundtail chub. After transition to the mesolarval phase through transition to the metalarval phase, development relative to size in humpback chub was similar to that observed in Colorado roundtail chub. Colorado roundtail chub tended to transform to the juvenile period before either of the other two species, followed by humpback chub and bonytail, respectively. For protolarvae and early mesolarvae, yolk was pale yellow, granular, and lacked distinct oil globules. End of yolk assimilation occurred at a slightly smaller size in bonytail than in humpback and Colorado roundtail chub. Gut loop (90° bend) formation and finfold absorption occurred at a smaller size in Colorado roundtail chub than in bonytail and humpback chub. Fin-ray development advanced faster in bonytail than in either of the other two taxa. Humpback and Colorado roundtail chub differed in size relative to onset of first rays

in the pectoral and pelvic fins; they appeared at a smaller size in humpback chub.

Growth rates (SL increment) of cultured specimens for the first 50-65 d after hatching differed among taxa (Figures A-3, A-4, A-18, A-25). Fish from both humpback chub stocks exhibited a similar growth pattern and grew faster than either bonytail or Colorado roundtail chub specimens. Colorado roundtail chub grew the slowest. Maximum estimated daily growth rates for the larval and juvenile periods, respectively, were 0.4-0.5 and 0.8 mm for humpback chub, 0.3 and 0.7 mm for bonytail, and 0.2 and 0.5 mm for Colorado roundtail chub. The slower growth exhibited by Colorado roundtail chub was probably related to their more confined rearing space. Humpback chub and bonytail were reared in 30.5 X 2.4 X 1.2-m raceways, whereas Colorado roundtail chub were reared in 3.0 X 0.3 X 0.2-m troughs (Hamman 1982a, 1982b; Muth et al. 1985). Fuiman (1979) reported a negative relationship between fish density and growth for catostomid larvae reared in the laboratory. In studies concerned with reproduction of wild populations of *Gila*, age-growth regression equations for cultured young developed in my work may be used to estimate spawning dates. Once field-collected larval or YOY juvenile *Gila* have been identified, approximate age in days after hatching for individual fish can be calculated by substituting the SL measurement for the equation variable Y. Size (SL) of field-collected fish must fall within the SL range upon which the equation was based for calculations to be valid. Reported egg-incubation times at water temperatures of 19-21°C were 3-7 d for humpback chub, 4-7 d for bonytail, and 3-5 d for Colorado roundtail chub (Hamman 1982a; Hamman 1982b; Hamman 1985; Muth et al. 1985). By adding incubation time (possibly using a mean or

median value) to calculated post-hatching age, an estimated date at which individual young were spawned (i.e., date at egg deposition and fertilization) can be back-calculated from date of capture. Predicted dates at which individual young were spawned can be aggregated in a frequency distribution to demonstrate beginning and ending spawning dates and peak spawning periods. These data can then be compared with river flow or temperature regimes to help describe physical conditions during spawning. This procedure assumes that growth and incubation time are similar for both wild and cultured young, an assumption which may or may not be valid depending on rearing conditions. Accordingly, back-calculated spawning dates must be considered estimates and should be substantiated by observations of adults in reproductive condition (Nesler et al. 1988). Also, age-growth data for field-collected specimens can be obtained by otolith ageing techniques and used to refine or validate predictive age equations for wild fish.

Haynes et al. (1985) developed a similar age back-calculation procedure to predict spawning times for Colorado squawfish in the Yampa River, Colorado. Their predictive age equations have been used in several studies (e.g., Tyus et al. 1987; Nesler et al. 1988; Osmundson and Kaeding 1989). To develop their age equations, Haynes et al. (1985) used average daily growth data (TL increment) provided by Hamman (1981) for cultured Colorado squawfish young. Age in days after hatching was treated as the dependent variable and regressed against TL (independent variable) on linear coordinates. The age-length relationship for Colorado squawfish young during the first 107 d after hatching was best described by two equations, one for fish less than 22 mm TL and one for fish 22-47 mm TL. The age-length relationship for fish less than 22 mm

TL was S-shaped and was described by a third-degree polynomial: $A = -76.7105 + 17.4949L - 1.0555L^2 + 0.0221L^3$; $r^2 = 0.99$, where A is age in days after hatching, and L is mm TL. For fish 22-47 mm TL, age-length showed a straight-line relationship described by a linear regression: $A = -26.6421 + 2.7798L$; ($r^2 = 0.99$). However, a re-evaluation of analyses performed by Haynes et al. (1985) revealed that when Hamman's (1981) data were plotted on linear coordinates with TL as the dependent variable (the correct method according to Sokal and Rohlf 1981) regressed against age in days after hatching, somewhat different age-length relationships resulted. For fish less than 22 mm TL, the age-length relationship was J-shaped and could be described by an exponential regression: $L = 6.2163e^{0.0375A}$ or $A = \ln(L \div 6.2163) \div 0.0375$; $r^2 = 0.97$. The age-growth relationship for fish 22-47 mm TL was again linear and could be described by a linear regression: $L = 10.0892 + 0.3539A$ or $A = (L - 10.0892) \div 0.3539$; $r^2 = 0.99$. This re-evaluation of age back-calculation procedures developed by Haynes et al. (1985) was not intended to discredit their findings, because the regression analyses they conducted were essentially correct. In fact, when arbitrary TL values were used in both sets of equations, resulting age values were comparable (Table 2). However, the revised age equation for Colorado squawfish less than 22 mm TL is simpler than that developed by Haynes et al. (1985).

Pigmentation: Within-taxon variability in extent of body-surface pigmentation (melanophores) was high, and no taxon-specific differences in melanophore distribution were noted (Figures A-5 to A-15, A-19 to A-22, A-26 to A-32). Some pigment was present in the embryonic eye at

TABLE 2. Comparison of back-calculated ages of Colorado squawfish young from age-length equations developed by Haynes et al. (1985) and from age-length equations developed in this study. Growth data for Colorado squawfish young used to develop these equations were from Hamman (1981). TL is total length.

Age-length equation	TL in mm (L)	Age in days after hatching (A)
For fish < 22 mm TL:		
$A = -76.7105 + 17.4949L - 1.0555L^2 + 0.0221L^3$ (Haynes et al. 1985)	7	2
	14	22
	21	30
$L = 6.2163e^{0.0375A}$	7	3
	14	22
	21	32
For fish 22-47 mm TL:		
$A = -26.6421 + 2.7798L$ (Haynes et al. 1985)	22	35
	35	71
	47	104
$L = 10.0892 + 0.3539A$	22	34
	35	70
	47	104

about 1-2 d prior to hatching, and eyes of recently hatched larvae were moderately to deeply pigmented. Larvae were devoid of body pigmentation at hatching and continued to lack body pigment until the mid- to late-protolarval phase. Body pigmentation was initially observed on the dorsal surface, usually first appearing as scattered pigment in the head and nape regions or as a single row of pigment extending posteriorly from the nape region along the midline. For late proto- through early metalarvae, additional dorsal pigmentation was often in two parallel rows on either side of the midline. Dorsal pigmentation increased and extended laterally as fish grew. Late protolarvae had scattered melanophores on the anterior, ventro-lateral surface, of the yolk sac. Ventral pigmentation was first noted in early flexion mesolarvae and was in two parallel rows on either side of the midline posterior to the vent. The undersurface of the head generally lacked pigment except for scattered melanophores along the opercles and lower jaw. Ventral pigmentation on juveniles was gradually submerged or lost, resulting in white or silvery undersides of the head and body. In late-flexion or early postflexion mesolarva, a dark, oval or "comma-shaped" internal (subcutaneous) basi-caudal pigment spot was present. This pigment spot was readily visible externally until early in the juvenile period; thereafter, it was obscured by musculature and integument. It was still observed in larger cleared and stained YOY juveniles. A similar internal pigment spot is present in young of other Colorado River Basin fish species including common carp, Colorado squawfish, and redside shiner *Richardsonius balteatus* (Snyder 1981). In Winn and Miller's (1954) key to postlarval fishes, presence of this pigment spot

segregated *G. robusta* and Colorado squawfish from loach minnow *Tiaroga cobitis* and speckled dace *Rhinichthys osculus*.

Mouth and Snout Morphology: Mouth and snout morphology are important diagnostic characters in distinguishing adult and immature humpback chub from bonytail and Colorado roundtail chub (Miller 1946; Holden and Stalnaker 1970; Suttkus and Clemmer 1977; Smith et al. 1979; Douglas et al. 1989; CRFRT 1989a, 1989b). Adult and older-juvenile humpback chub have a subterminal to inferior mouth that is nearly horizontal (mouth position defined by Scott and Crossman 1973). Their snout is long and fleshy and overhangs the mouth. The mouth of bonytail and Colorado roundtail chub adults and older juveniles is terminal to subterminal, slightly oblique to nearly horizontal, and not notably overhung by the snout. Larger bonytail adults may have a subterminal to inferior mouth. Douglas et al. (1989) proposed and tested a set of seven diagnostic qualitative character states for adults of these three *Gila* that included mouth, snout, and jaw morphology. Under jaw morphology, they reported that posterior extension of the upper jaw is anterior to the eye in Colorado roundtail chub, beneath at least the anterior third of the eye in humpback chub, and clearly beneath the pupil of the eye in bonytail. Suttkus and Clemmer (1977) reported that the subterminal to inferior mouth was apparent in humpback chub specimens as small as about 25 mm SL. Smith et al. (1979) included snout morphology in their diagnosis of humpback chub and bonytail young less than 150 mm SL.

In my study, mouth and snout morphology characters had little or no value in identifying humpback chub larvae. Larger humpback chub

metalarvae (specimens > 15 mm SL) tended to exhibit a somewhat subterminal mouth overhung by the snout. Differences in mouth and snout morphology between humpback chub and bonytail and Colorado roundtail chub were readily apparent only after juvenile specimens reached about 30 mm SL (Figures 7, A-12, A-15, A-22, A-32). Even after this size was attained, within-taxon variability and the somewhat subjective nature of these characters limited their diagnostic value in separating YOY juvenile humpback chub from the other two fishes. Clearing and staining juvenile specimens may facilitate examinations for taxon-specific differences in mouth and snout morphology. Discriminating jaw-morphology character states used by Douglas et al. (1989) were not obvious in specimens examined in this study.

Meristics: Several meristic characters were diagnostically useful (Tables 3-5, A-6 to A-8, A-11, A-18 to A-20). Prevent and especially postvent and total myomere and vertebra counts were comparably higher for bonytail (Table 3). No important differences in these counts were noted between humpback and Colorado roundtail chub. Of the other Colorado River Basin cyprinids, only the Colorado squawfish has a reported total myomere or vertebra count as high as that of bonytail. Colorado squawfish larvae typically have 33-34 prevent, 15-17 postvent, and 48-50 total myomeres (Snyder 1981). Accurate myomere counts are difficult to make on YOY juveniles, but counting can be facilitated by decreasing the angle at which reflected light strikes the specimen. Total myomere and vertebra counts were similar to total vertebra counts reported for adults of these fishes; counts for bonytail tended to be slightly higher than reported values for this species.

FIGURE 7. Mouth and snout morphology of young-of-the-year juvenile *Gila cypha*, *G. elegans*, and *G. robusta robusta*. **A.** *G. cypha*, 33.2 mm SL, cultured from brood stock collected from the Colorado River, Colorado. **B.** *G. elegans*, 34.1 mm SL, cultured from brood stock collected from Lake Mohave, Nevada side. **C.** *G. r. robusta*, 31.7 mm SL, collected from the Yampa River, Colorado. See Methods for clarification of capture locations.

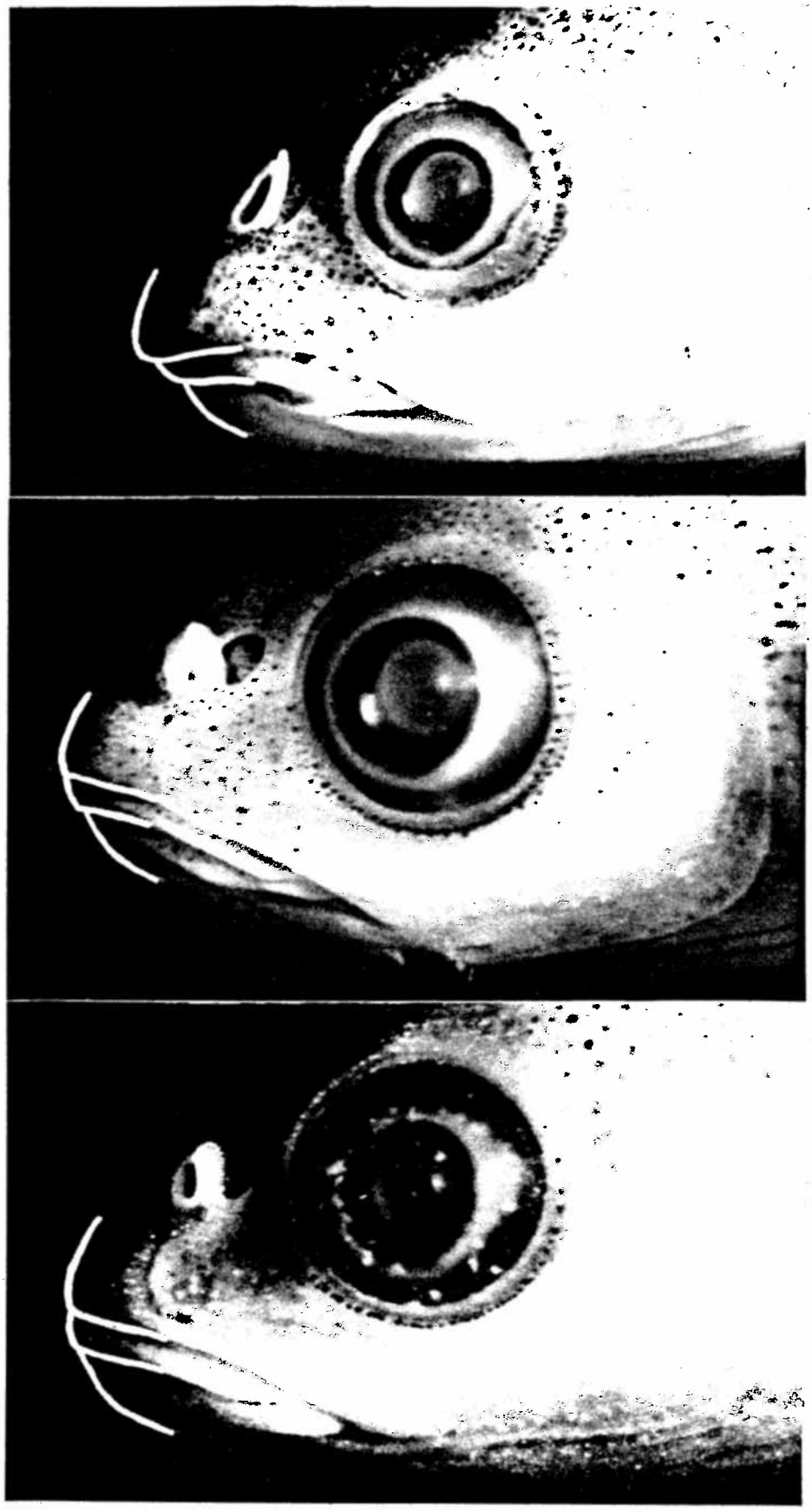

A
B
C

TABLE 3. Frequency distribution of selected, diagnostically useful myomere counts for larval and vertebra counts for young-of-the-year juvenile *Gila cypha*, *G. elegans*, and *G. robusta robusta*. Values in the table are percents of the total number of specimens examined (N per taxon and developmental interval) having a particular myomere or vertebra count. Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. See Methods for capture locations of brood stocks and young. F = flexion; Pf = postflexion. See Figure 5 for method of counting. Developmental-interval terminology for fish early life stages as defined by Snyder and Muth (1988, in press, see Methods).

Taxon and developmental interval	N	Number of myomeres for larvae and number of vertebrae[a] for juveniles																						
		Prevent								Postvent								Total						
		25	26	27	28	29	30	31	32	16	17	18	19	20	21	22	23	44	45	46	47	48	49	50	51	52
G. cypha																										
Protolarvae	67				21	57	22				12	51	34	3						10	52	34	3			
F mesolarvae	56				21	63	16				2	57	36	5						14	39	36	11			
Pf mesolarvae	16			6	6	56	31				6	56	38							13	31	56				
Metalarvae	33		3	9	42	36	9				12	70	12	6					12	36	36	15				
Juveniles	37	3	41	32	24								8	49	43				5	8	41	43	3			
G. elegans																										
Protolarvae	37					3	95	3						38	62								3	32	65	
F mesolarvae	20						75	10	15				15	25	60									25	65	10
Pf mesolarvae	4						100							25	75									25	75	
Metalarvae	34					15	68	9	9				12	68	21								6	74	15	6
Juveniles	16			25	56	19									31	56	13						31	63	6	
G. robusta																										
Protolarvae	20					100					5	65	25	5						10	60	25	5			
F mesolarvae	18			11	28	61						44	56						6	11	56	28				
Pf mesolarvae	22			5	18	55	23					45	45	9							50	41	9			
Metalarvae	55	2	7	25	40	22	4				2	24	60	15					9	29	45	15	2			
Juveniles	31		13	61	26								16	74	10				6	23	61	10				

[a]Counts were made on cleared and stained specimens and include the four Weberian-complex vertebrae and the urostylar vertebra.

Similarly, principal fin-ray counts showed close agreement with reported adult counts, and numbers of dorsal fin and anal fin rays were diagnostic (Table 4). In this study, typical dorsal/anal fin principal-ray counts were 9/10 for humpback chub, 10/10 for bonytail, and 9/9 for Colorado roundtail chub. Typical values for combined principal-ray counts for both fins were 19 for humpback chub, 20 for bonytail, and 18 for Colorado roundtail chub. Typical numbers of caudal fin principal rays and pectoral fin and pelvic fin rays were essentially the same in all three fishes.

Gill-raker counts for juveniles were highly diagnostic in distinguishing bonytail from humpback and Colorado roundtail chub. Counts made on all gill raker series examined were comparably higher for bonytail; total gill-raker counts gave the best taxon separation (Table 5). Gill-raker counts for humpback chub were similar to those observed for Colorado roundtail chub. Lindsey (1988) stated that gill-raker number for a given fish species is largely inherited but, like other meristic traits, may be influenced by environmental conditions. He also reported that the full complement of gill rakers is often not attained until late in the juvenile period, and some fish species may continue to add gill rakers throughout life. The lack of gaps within rows of gill rakers suggested that the full complement of gill rakers was formed. However, some gill rakers were small or did not stain completely, and careful examination was required to accurately count gill rakers.

Rosenfeld (1986b) attempted to downplay this observed difference in gill-raker number between juveniles of bonytail and humpback and Colorado roundtail chub. He stated that results of work performed by Snyder (1981) on cultured larvae and YOY juveniles of these fishes

Table 4. Frequency distribution of dorsal fin and anal fin principal-ray counts for *Gila cypha*, *G. elegans*, and *G. robusta robusta* larvae and young-of-the-year juveniles. Values in the table are percent of total number of specimens examined (N per taxon and developmental interval) having a particular fin-ray count. Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. See Methods for capture locations of brood stocks and young. Pf = postflexion. See Figure 6 for method of counting. Developmental-interval terminology for fish early life stages as defined by Snyder and Muth (1988, in press, see Methods).

		Number of principal fin rays[a]												
		Dorsal fin			Anal fin				Dorsal fin + anal fin					
Taxon and developmental interval	N	9	10	11	8	9	10	11	17	18	19	20	21	22
G. cypha														
Pf mesolarvae	16	100				19	81			19	81			
Metalarvae	33	97	3			18	79	3		18	76	6		
Juveniles	85	85	15			18	81	1		15	70	15		
G. elegans														
Pf mesolarvae	4		100				100					100		
Metalarvae	34		100				79	21				79	21	
Juveniles	52		98	2			60	40				60	38	2
G. robusta														
Pf mesolarvae	22	100				100				100				
Metalarvae	55	100				98	2			98	2			
Juveniles	53	100			2	91	8		2	91	8			

[a]For postflexion mesolarvae, counts were based on pterygiophores using whole specimens examined with polarized light or cleared and stained specimens.

TABLE 5. Frequency distribution of gill-raker counts for Gila cypha, G. elegans, and G. robusta robusta young-of-the-year juveniles. Values in the table are percent of the total number of specimens examined (N, per taxon) having a particular gill-raker count. Counts were made on gill arches excised from the left side of cleared and stained specimens. Data for G. cypha and G. r. robusta are from cultured and field-collected wild young. Data for G. elegans are from cultured young. See Methods for capture locations of brood stocks and young. See Figure 6 for method of counting.

Taxon and gill arch	Number of gill rakers: Total per arch																					Total all arches																							
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	90	91	93	94	96	98	99	100	101	102	103	106	107	109	110	133	137	138	140	143
G. cypha[a]																																															
1st arch					3	14	28	17	33	3		3																																			
2nd arch							11	14	14	44	11	3	3																																		
3rd arch					5		5	19	39	14	11	3	3																																		
4th arch	8	5	8	44	5	14	11	3	3																																						
Total																							8				38	6	14	3	11	6		8	1	1									
G. elegans[b]																																															
1st arch														31	25	31	13																													
2nd arch																	6		25	56		13																									
3rd arch																		19		25	38	19																									
4th arch											13		25	38	19	6																														
Total																																					31	13	25	25	6					
G. robusta[c]																																															
1st arch					6	13	10	52	19																																						
2nd arch					6	3	3	13	23	16	19	10	3	3																																	
3rd arch						10		10	39	16	19	6																																			
4th arch	3	6	6	26	29	19	6	3																																						
Total																								6	6	6		16	19	10	10	3	13	3	3		3							

[a]N=37. [b]N=16. [c]N=31.

showed higher gill raker counts for bonytail. However, these data were not reported by Snyder (1981), and Rosenfeld's information probably came from presentations of preliminary results from my study given at professional meetings. Rosenfeld further stated that the observed difference in gill-raker number between cultured bonytail and humpback chub juveniles resulted from local environmental factors acting on their parents, which had been collected from different localities and habitats. He suggested that, because cultured bonytail progeny came from parents collected from Lake Mohave (in his words "lake-dwelling parents") and cultured humpback chub progeny came from parents collected from riverine habitats, comparably higher gill-raker counts would be expected in bonytail young. This thinking calls to mind the archaic "ecotype" concept that was coined by botanists (Grant 1963) and has been used variously by different authors. Use of the term ecotype infers either slight genetic differentiation, caused by environmentally induced mutations, among conspecific local populations having rapid turnover of generations (e.g., DDT-resistant insect populations) or no genetic differentiation, where variation within certain morphological characters among conspecific local populations is explained by the direct selective influence of local habitat-based, abiotic or biotic, factors on individuals and subsequent expression of this variation in the local population's phenotype. Mayr (1977, 1982) rejected the validity of the ecotype concept because of its typological connotation (i.e., among individuals of a population, stability within morphological characters is expected and variability is unrealistic) and favored population thinking (i.e., among individuals of a population, variability within morphological characters is expected and stability is unrealistic).

Rosenfeld's reasoning is flawed in several ways. Bonytail in Lake Mohave represent a relict group of adults from a population that occurred in the lower Colorado River prior to closure of Lake Mohave. Successful reproduction by bonytail in Lake Mohave has never been documented (Jonez and Sumner 1954; Bozek et al. 1984). Following Rosenfeld's rationale, this would mean that bonytail adults remaining in Lake Mohave somehow developed additional gill rakers in response to local environmental conditions during the period from closure of Lake Mohave in 1954 to collection of brood stock in 1979-1981, and that this acquired trait was passed on to their cultured progeny. This Lamarckian scenario is obviously absurd.

If gill-raker counts observed in this study for bonytail juveniles were indeed an aberration, a plausible explanation might be that, in Lake Mohave, those bonytail adults with higher gill-raker counts had better survival than those with lower gill-raker counts. Adults with higher gill-raker counts may then have occurred in comparably greater numbers and had an increased chance of being captured for brood stock. However, gill-raker counts observed in this study for YOY juveniles showed closed agreement with gill-raker counts reported by Holden (1968, Table 6) and Smith et al. (1979) for adults of these fishes collected from a variety of localities and habitats. Also, gill-raker counts for the three hatchery-cultured bonytail adults examined in this study closely agreed with those observed for YOY juvenile bonytail. Total counts for the adults were: 30-32, first gill arch; 38-40, second gill arch; 38-39, third gill arch; 30-32, fourth gill arch; and 137-144, all gill arches combined. These data further support the observation that the full complement of gill rakers was present early in the juvenile

TABLE 6. Frequency distribution of gill-raker counts for adult *Gila cypha*, *G. elegans*, and *G. robusta robusta*. Data are from Holden (1968). Number of gill rakers are total counts for the first gill arch, left side. Values in the table are number of specimens having a particular gill-raker count.

Taxon and location	Number of gill rakers															
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
G. cypha																	
Upper Green R., UT						1											
Lake Powell, UT-AZ				1		2		1	1								
Lee Ferry, AZ			1		2	1	2	3	1								
G. elegans																	
Upper Green R.				1	1	1	5	7	12	16	13	23	10	3			
Lake Powell													1				
Lake Mohave, AZ-NV										1	1		1		1	1	1
G. robusta																	
Upper Green R.	2	2	6	20	17	6	3	2	2								
White R., CO			1	4	4	3	5	1									
Colorado R., CO		1		3	5	4	2	1	1								
San Juan R., NM		3	3	7	8	2											
Black R., AZ			1	6		1	2										

period. Holden's (1968) data on gill-raker number (and other meristic data given in his work) show the normal morphological variability among conspecific local populations and within a character state. Holden attributed the slightly higher gill-raker counts for bonytail from Lake Mohave to their larger size compared to bonytail from other localities. However, his reported gill-raker counts for bonytail were made on one specimen from Lake Powell and six specimens from Lake Mohave compared to 92 specimens from the upper Green River. If more bonytail specimens from Lake Powell and Lake Mohave had been available for Holden's study, it is possible that greater overlap in gill-raker number among the three populations would have been observed. Smith et al. (1970) reported modal gill-raker counts on the second gill arch, external row, of 15 for humpback chub, 17 for bonytail, and 14 for Colorado roundtail chub.

Young from the bonytail X Colorado roundtail chub cross typically had 17 postvent myomeres and 19 postvent vertebrae, 47 total myomeres and vertebrae, 9 dorsal fin principal rays, 10 anal fin principal rays, and 112 total gill rakers. Bonytail X humpback chub young typically had 17 postvent myomeres and 19 postvent vertebrae, 46 total myomeres and 47 total vertebrae, 9 dorsal fin principal rays, 9-10 anal fin principal rays, and 105-117 total gill rakers (Tables D-1, D-2).

Morphometrics: Regressions of log-log plots of body-part measurements against a standard measure showed allometric growth in nearly all taxa and body parts (Figures B-1 to B-42; Table C-1). Most k values (i.e., growth coefficient constants) were less than 1.0, indicating negative allometry. Only ΣF plotted against SL, P2 plotted against PFO, and OAPHP plotted against OAPOP (CPLR) had k values that

approximated isometry (k equal to 1.0). In some instances, k values for these measurements exceeded 1.0, indicating positive allometry.

Multiple growth stanzas were exhibited by most characters, with bonytail usually having comparably more growth stanzas per character. Martin (1949) stated that growth stanzas may result from physiological changes in the organism (e.g., changing from an endogenous to an exogenous food source). Observed discontinuities in growth may also be the result of changes in how a particular body part or standard is measured. In this study, SL was measured to the posterior margin of the notochord until the adult complement of principal caudal fin rays was observed. Thereafter, SL was measured to the posterior margin of the hypural plates. Points at which criteria for measuring SL changed (indicated by arrow on graphs) roughly corresponded to growth changes in many of the characters.

Six morphometrics were diagnostically useful in taxon separation of metalarvae or juveniles (Figures 8-12; Tables 7, 8, A-3 to A-5, A-10, A-15 to A-7). Bonytail juveniles tended to have a considerably narrower caudal peduncle than juvenile humpback and Colorado roundtail chubs. The mean value of body depth at APM expressed as % HL (D:APM/HL) for bonytail was lower than mean D:APM/HL values for humpback and Colorado roundtail chub. No notable difference in this morphometric was observed between humpback and Colorado roundtail chub juveniles. There was overlap between the higher D:APM/HL values for bonytail and the lower D:APM/HL values for humpback and Colorado roundtail chub. In larval phases, ranges of this morphometric showed overlap among all fishes, but mean values were generally lower for metalarval bonytail and Colorado roundtail chub than for humpback chub metalarvae.

FIGURE 8. Log-log plot of selected, diagnostically useful measurements (**D:APM** against **HL**) for *Gila cypha* (●), *G. elegans* (♦), and *G. robusta robusta* (□) metalarvae and young-of-the-year juveniles (sensu Snyder and Muth 1988, in press, see Methods). Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. See Methods for capture locations of brood stocks and young. See Figure 4 for definitions of character abbreviations and methods of measurement.

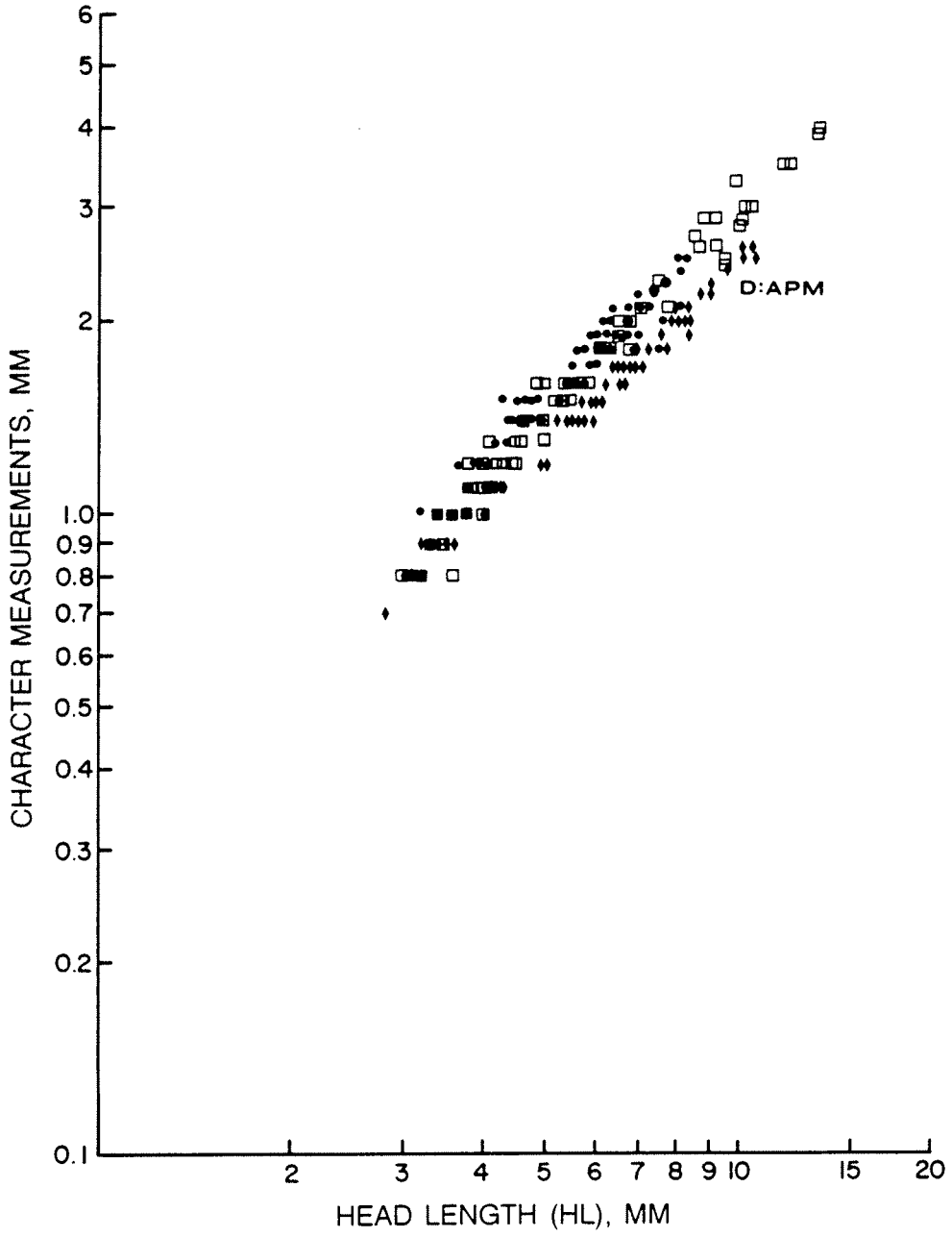

CHARACTER MEASUREMENTS, MM
6
5
4
3
2
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
D:APM
2
3
4
5
6
7
8
9
10
15
20
HEAD LENGTH (HL), MM

FIGURE 9. Log-log plots of selected, diagnostically useful measurements (ΣFL and DB against SL) for *Gila cypha* (●), *G. elegans* (◆), and *G. robusta robusta* (□) metalarvae and young-of-the-year juveniles (sensu Snyder and Muth 1988, in press, see Methods). Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. See Methods for capture locations of brood stocks and young. See Figure 4 for definitions of character abbreviations and methods of measurement.

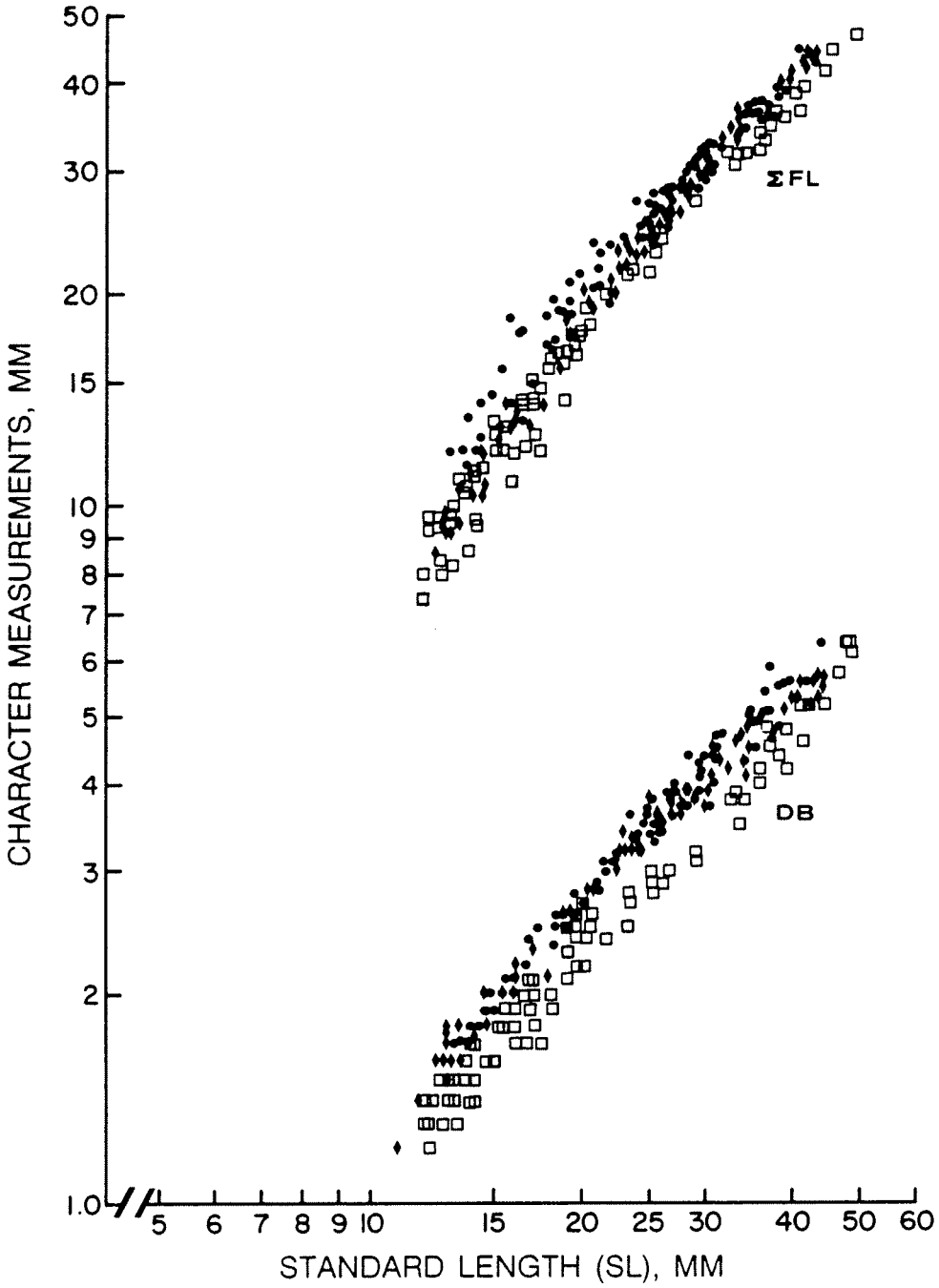

CHARACTER MEASUREMENTS, MM
50
40
30
20
15
10
9
8
7
6
5
4
3
2
1.0
ΣFL
DB
5
6
7
8
9
10
15
20
25
30
40
50
60
STANDARD LENGTH (SL), MM

FIGURE 10. Log-log plot of selected, diagnostically useful measurements (**OAPHP** against **OAPOP**) for *Gila cypha* (●), *G. elegans* (♦), and *G. robusta robusta* (□) metalarvae and young-of-the-year juveniles (sensu Snyder and Muth 1988, in press, see Methods). Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. See Methods for capture locations of brood stocks and young. See Figure 5 for definitions of character abbreviations and methods of measurement.

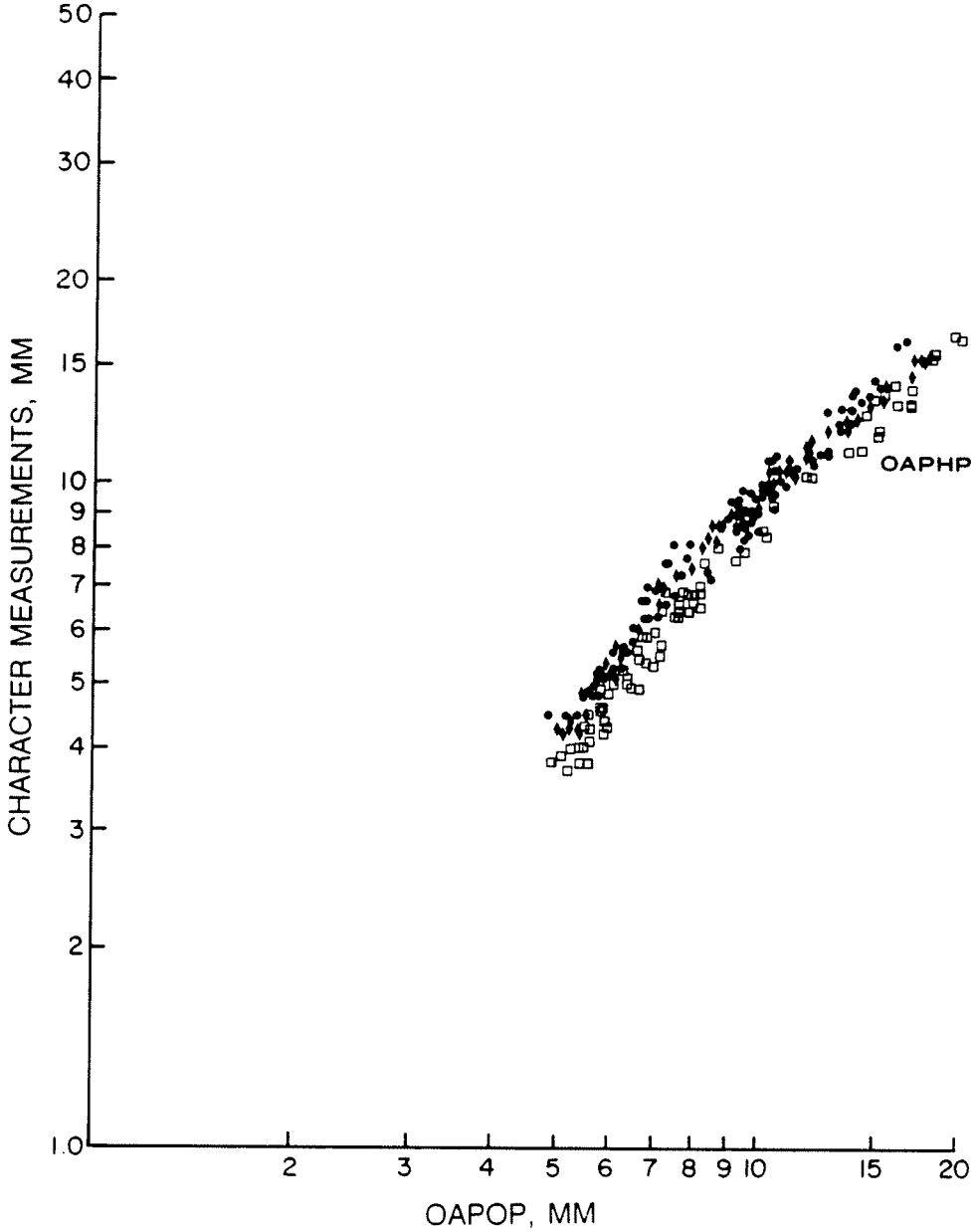

CHARACTER MEASUREMENTS, MM
50
40
30
20
15
10
9
8
7
6
5
4
3
2
1.0
2
3
4
5
6
7
8
9
10
15
20
OAPOP, MM
OAPHP

FIGURE 11. Log-log plot of selected, diagnostically useful measurements (**P1** against **PFO**) for *Gila cypha* (●), *G. elegans* (♦), and *G. robusta robusta* (□) metalarvae and young-of-the-year juveniles (sensu Snyder and Muth 1988, in press, see Methods). Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. See Methods for capture locations of brood stocks and young. See Figure 4 for definitions of character abbreviations and methods of measurement.

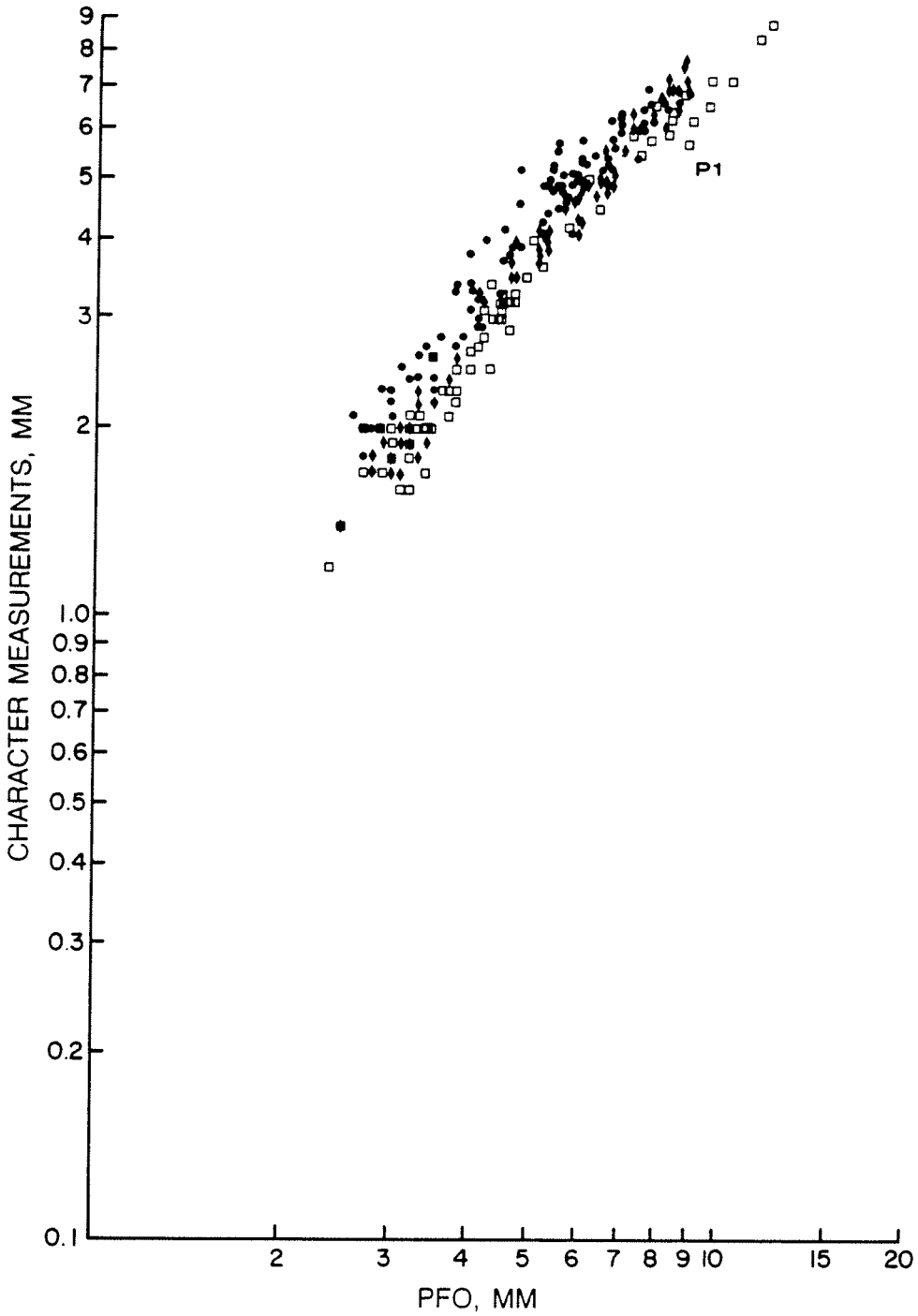

CHARACTER MEASUREMENTS, MM
9
8
7
6
5
4
3
2
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
P1
2
3
4
5
6
7
8
9
10
15
20
PFO, MM

FIGURE 12. Log-log plot of selected, diagnostically useful measurements (P2 against PFO) for *Gila cypha* (●), *G. elegans* (◆), and *G. robusta robusta* (□) metalarvae and young-of-the-year juveniles (sensu Snyder and Muth 1988, in press, see Methods). Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. See Methods for capture locations of brood stocks and young. See Figure 4 for definitions of character abbreviations and methods of measurement.

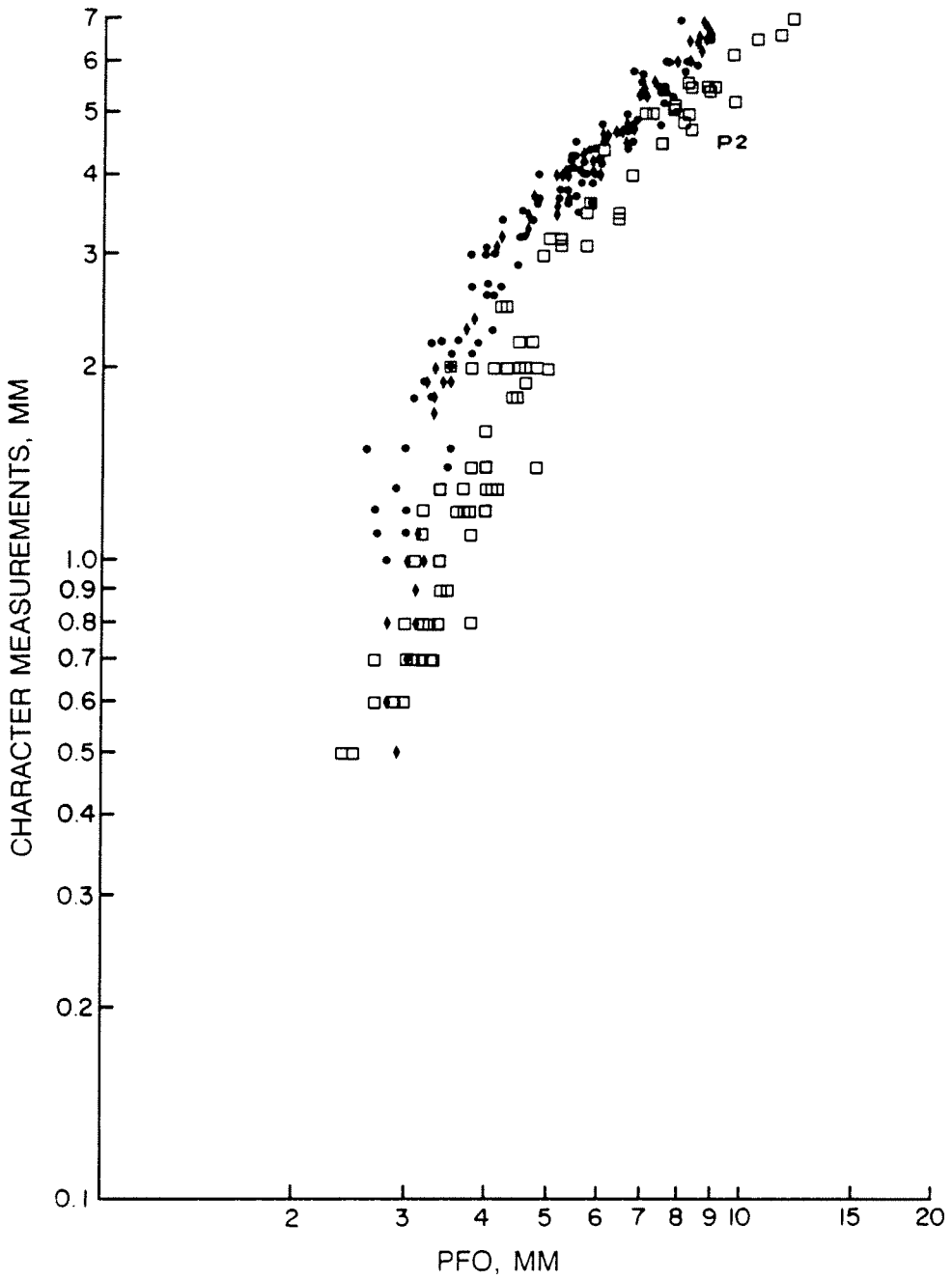

CHARACTER MEASUREMENTS, MM
PFO, MM
P2
7
6
5
4
3
2
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
2
3
4
5
6
7
8
9
10
15
20

TABLE 7. Means and ranges of selected, diagnostically useful morphometrics for *Gila cypha*, *G. elegans*, and *G. robusta robusta* metalarvae and young-of-the-year (YOY) juveniles (sensu Snyder and Muth 1988, in press, see Methods). Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. Juveniles examined were less than 50 mm in standard length. See Methods for capture locations of brood stocks and young. See Figures 4-6 for definitions of abbreviations and methods of measurement.

Morphometric and developmental and standard length interval	*G. cypha* Mean	*G. cypha* Range	*G. elegans* Mean	*G. elegans* Range	*G. robusta* Mean	*G. robusta* Range
Depth at APM as % HL:						
Juveniles	30	24-34	25	23-27	29	25-34
DB as % SL:						
Metalarvae						
≤ 15 mm SL	13	13-14	13	11-14	11	10-12
> 15 - ≤ 17 mm SL	13	13-15	13	13-14	11	10-13
> 17 - ≤ 19 mm SL	14	14-15	14	14-14	11	10-12
> 19 mm SL	14	13-15	14	14-14		11-12
CPLR[a]:						
Metalarvae						
≤ 15 mm SL	87	83-92	84	78-92	75	70-86
> 15 - ≤ 17 mm SL	89	84-94	91	89-93	80	70-88
> 17 - ≤ 19 mm SL	95	89-104	95	93-97	84	76-89
> 19 mm SL	96	84-103	97	94-100		90-92
Juveniles	95	86-112	94	87-102	85	78-95
ΣF[b] as % SL:						
Metalarvae						
≤ 15 mm SL	92	85-102	76	71-85	74	62-85
> 15 - ≤ 17 mm SL	99	81-118	83	77-89	80	68-91
> 17 - ≤ 19 mm SL	101	92-109	89	84-97	81	68-92
> 19 mm SL	105	93-116	94	90-101		83-93
Juveniles	104	92-118	100	94-109	91	86-100
P1 as % PFO:						
Metalarvae						
≤ 15 mm SL	74	61-81	60	55-66	61	50-73
> 15 - ≤ 17 mm SL	74	63-79	62	55-70	64	57-73
> 17 - ≤ 19 mm SL	79	69-89	64	63-65	66	60-73
> 19 mm SL	81	71-95	75	68-80		68-74
Juveniles	88	71-110	80	70-90	72	63-85

TABLE 7. Continued.

Morphometric and developmental and standard length interval	*G. cypha* Mean	*G. cypha* Range	*G. elegans* Mean	*G. elegans* Range	*G. robusta* Mean	*G. robusta* Range
P2 as % PFO:						
Metalarvae						
≤ 15 mm SL	44	36-58	29	17-35	25	20-38
> 15 - ≤ 17 mm SL	59	43-67	56	52-61	34	21-57
> 17 - ≤ 19 mm SL	64	55-79	59	54-62	41	30-55
> 19 mm SL	69	62-77	73	63-76		45-62
Juveniles	74	62-91	74	68-80	54	40-72

[a]CPLR (caudal peduncle length ratio) is OAPHP expressed as % OAPOP. [b]ΣF is the sum of lengths of all fins (i.e., P1+P2+D+A+C = ΣF).

TABLE 8. Frequency distribution of selected, diagnostically useful morphometrics for *Gila cypha*, *G. elegans*, and *G. robusta robusta* metalarvae and young-of-the-year (YOY) juveniles (sensu Snyder and Muth 1988, in press, see Methods). Data for *G. cypha* and *G. r. robusta* are from cultured and field-collected wild young. Data for *G. elegans* are from cultured young. Juveniles examined were less than 50 mm in standard length. See Methods for capture locations of brood stocks and young. See Figures 4-6 for definitions of abbreviations and methods of measurement.

Morphometric and developmental and standard length interval	*G. cypha* N	*G. cypha* % of N	*G. elegans* N	*G. elegans* % of N	*G. robusta* N	*G. robusta* % of N
Depth at APM as % HL:						
Juveniles	83		52		53	
23				3		
24		1		15		
25-27		15		82		18
≥ 28		84				82
DB as % SL:						
Metalarvae						
≤ 15 mm SL	11		17		32	
≤ 12				53		100
13		82		35		
≥ 14		18		12		
> 15 - ≤ 17 mm SL	8		7		14	
≤ 12						86
13		75		71		14
≥ 14		25		29		
> 17 - ≤ 19 mm SL	8		3		7	
≤ 12						100
13		37				
≥ 14		63		100		
> 19 mm SL	6		7		2	
≤ 12						100
13		33				
≥ 14		67		100		
CPLR[a]						
Metalarvae						
≤ 15 mm SL	11		17		32	
≤ 82				30		97
83-86		27		35		3
≥ 87		73		35		
> 15 - ≤ 17 mm SL	8		7		14	
≤ 83						79
84-88		37				21
≥ 89		63		100		

TABLE 8. Continued.

Morphometric and developmental and standard length interval	*G. cypha* N	*G. cypha* % of N	*G. elegans* N	*G. elegans* % of N	*G. robusta* N	*G. robusta* % of N
> 17 - ≤ 19 mm SL	8		3		7	
≤ 88						86
89		25				14
≥ 90		75		100		
> 19 mm SL	5		7		2	
≤ 92		40				100
≥ 93		60		100		
Juveniles	83		52		53	
≤ 85						62
86-95		55		69		38
96-102		29		31		
≥ 103		16				
ΣF^b as % SL:						
Metalarvae						
≤ 15 mm SL	11		17		32	
≤ 84				94		97
85		9		6		3
≥ 86		91				
> 15 - ≤ 17 mm SL	8		7		14	
≤ 80				14		36
81-91		37		86		64
≥ 92		63				
> 17 - ≤ 19 mm SL	8		3		7	
≤ 91				67		86
92		13				14
≥ 93		87		33		
> 19 mm SL	4		7		2	
≤ 92				57		50
93		25				50
≥ 94		75		43		
Juveniles	83		52		53	
≤ 91						49
92-100		24		63		51
101-109		65		37		
≥ 110		11				
P1 as % PFO:						
Metalarvae						
≤ 15 mm SL	11		17		32	
≤ 60				41		41
61-73		55		59		59
≥ 74		45				

TABLE 8. Continued.

Morphometric and developmental and standard length interval	*G. cypha* N	*G. cypha* % of N	*G. elegans* N	*G. elegans* % of N	*G. robusta* N	*G. robusta* % of N
> 15 - ≤ 17 mm SL	8		7		14	
≤ 62				43		43
63-73		37		57		57
≥ 74		63				
> 17 - ≤ 19 mm SL	8		3		7	
≤ 68				100		57
69-73		25				43
≥ 74		75				
> 19 mm SL	6		7		2	
≤ 74		50		29		100
≥ 75		50		71		
Juveniles	83		52		53	
≤ 69						28
70-85		42		77		72
86-90		20		23		
≥ 91		38				
P2 as % PFO:						
Metalarvae						
≤ 15 mm SL	11		17		32	
≤ 35				100		94
36-38		27				6
≥ 39		73				
> 15 - ≤ 17 mm SL	7		7		14	
≤ 42				14		93
43-57		29		57		7
≥ 58		71		29		
> 17 - ≤ 19 mm SL	8		3		7	
≤ 54				33		86
55		13				14
≥ 56		87		67		
> 19 mm SL	6		7		2	
≤ 61						50
62		17				50
≥ 63		83		100		
Juveniles	83		52		53	
≤ 61						74
62-72		43		29		26
73-80		43		71		
≥ 81		14				

[a]CPLR (caudal peduncle length ratio) is OAPHP expressed as % OAPOP. [b]ΣF is the sum of lengths of all fins (i.e., P1+P2+D+A+C = ΣF).

Length of dorsal fin base (DB) was similar between humpback chub and bonytail, and mean DB values (expressed as % SL) were greater for metalarvae of these fishes than for metalarval Colorado roundtail chub. Juvenile humpback chub and bonytail tended to have a longer dorsal fin base than Colorado roundtail chub juveniles, but DB ranges were similar among juveniles of all fishes.

Mean values of the caudal peduncle length ratio (CPLR) were similar between humpback chub and bonytail and were notably higher in these fishes than in Colorado roundtail chub. Of humpback chub and bonytail specimens, 80-100% had individual CPLR values greater than mean CPLR values for Colorado roundtail chub. There was overlap between lower CPLR values for humpback chub and bonytail and higher CPLR values for Colorado roundtail chub. A similar morphometric was used by Smith et al. (1979) to help distinguish humpback chub and bonytail from *G. robusta*.

All fins tended to be longest in humpback chub and shortest in Colorado roundtail chub. Combined lengths of all fins expressed as % SL (ΣF) provided the best separation between humpback and Colorado roundtail chub. All humpback chub specimens had individual ΣF values greater than mean values for Colorado roundtail chub. Metalarval bonytail and Colorado roundtail chub less than or equal to 17 mm SL had similar mean ΣF values. Bonytail juveniles and metalarvae over 17 mm SL had mean ΣF values close to those for humpback chub and higher than those for Colorado roundtail chub juveniles and metalarvae longer than 17 mm SL. There was overlap between the lower ΣF values for humpback chub and larger bonytail and higher ΣF values for Colorado roundtail chub.

Mean values of lengths of the paired fins expressed as % PFO (P1/PFO and P2/PFO) were higher for humpback chub than for Colorado roundtail chub. There was overlap in these morphometrics between the lower values for humpback chub and higher values for Colorado roundtail chub. Metalarval bonytail and Colorado roundtail chub less than or equal to 19 mm SL had similar mean P1/PFO values. Bonytail juveniles and metalarvae longer than 19 mm SL had mean P1/PFO values that were close to those for humpback chub and higher than those for Colorado roundtail chub juveniles and metalarvae greater than 19 SL. The mean value of P2/PFO for bonytail metalarvae less than or equal to 15 mm SL was slightly higher than that for Colorado roundtail chub less than or equal to 15 mm SL. Bonytail juveniles and metalarvae over 15 mm SL had mean P2/PFO values that were close to those for humpback chub and higher than those for Colorado roundtail chub juveniles and metalarvae greater than 15 mm SL.

Suttkus and Clemmer (1977) and Smith et al. (1979) considered eye diameter to be diagnostically useful in distinguishing young humpback chub, bonytail, and Colorado roundtail chub. For specimens examined in my study, eye diameter was not notably different among the three fishes. Distance from the anterior margin of the snout to origins of the paired fins, origins and insertions of the dorsal and anal fins, and the posterior margin of the vent tended to be slightly greater in Colorado roundtail chub than in humpback chub and bonytail.

Preliminary diagnostic characters developed early in this study for larval and YOY juvenile humpback chub, bonytail, and Colorado roundtail chub were applied to young *Gila* collected by Richard A. Valdez, BIO/WEST, Inc., Logan, Utah, from the Cataract Canyon Region,

Colorado River, Utah, in 1986-1988. Of the 274 *Gila* metalarvae and YOY juveniles analyzed for diagnostic morphometrics and meristics, 230 were identified as Colorado roundtail chub, 13 as humpback chub, 19 as questionable humpback chub, and 12 as possible humpback X Colorado roundtail chub hybrids. Fish identified as questionable humpback chub had morphometric values within the discrete portion of the humpback chub range and 9 principal anal fin rays or a terminal mouth. Mouth position is not a primary character in the final diagnostics, and an anal fin principal-ray count of 9 is not uncommon for humpback chub. Accordingly, the questionable humpback chub specimens would now be identified as humpback chub. Most morphometric values for specimens identified as possible humpback X Colorado roundtail chub hybrids fell within the observed range of overlap between the two taxa. These fish had 9 principal anal fin rays and a terminal or subterminal mouth.

Keys

Powles and Markle (1984) stated that keys have not generally been used in identification of fish larvae because anatomical characters are dynamic, it is difficult to adequately cover a specific region or taxonomic group, and summarizing the typically large amount of information required to identify fish larvae has been impractical (but use of computers may help in organizing diagnostic information). In this study, the dynamic nature of diagnostic characters during early ontogeny was accommodated by keys for each of the three larval phases (i.e., protolarva, mesolarva, and metalarva) and the YOY portion of the juvenile period. Humpback chub and Colorado roundtail chub larvae and juveniles examined represented several local populations and included

known-identity wild and cultured specimens. DELTA-based computer programs for key generation facilitated development of the keys.

To use the keys, a low-power microscope and some means of measuring to the nearest 0.1 mm are required. It is important to calibrate the measuring device before making observations; when taking measurements on a group of specimens, it is best to check calibration periodically. Except for fin lengths, OAPOP, and OAPHP, measurements are made parallel or perpendicular to the body axis. Specimens must be completely submerged in fluid (usually water) and positioned such that their body axis is horizontal. Pieces of glass can be used to prop up or hold down a specimen. Curved or bent specimens that cannot be gently straightened or flattened can be measured in sections. Specimens larger than the range of the measuring device also can be measured in sections. Measurement units are the nearest whole or tenth of a millimeter.

Keys for larval fish require myomere counts. For accurate counts, the first and last myomeres must be identified and included. The first myomere is partial (apparent only in the dorsal half of the body), deltoid in shape, and located immediately behind the occiput. The most-posterior (last) myomere is defined as lying anterior to the most-posterior complete myoseptum. Difficulty in discerning the last myomere is often increased by the presence of a partial "false" myoseptum posterior to the last complete myoseptum (Siefert 1969). Early in the larval period, myomeres are most readily observed using transmitted light. Polarizing filters can be used and often dramatically increase contrast between myomeres and the separating myosepta. Myomeres of some metalarvae and most YOY juveniles are difficult to observe even with

polarized light; reflected light at a low angle and higher magnification may facilitate observations.

Principal fin-ray counts on the dorsal and anal fins are used in the metalarva and juvenile keys. Developing fin rays must not be confused with folds or creases in the finfold. Because pterygiophores appear before the principal fin rays they support and because there is an one-to-one correspondence between pterygiophores and principal fin rays, pterygiophore counts can usually substitute for dorsal fin and anal fin principal-ray counts in postflexion mesolarvae. It is also important to distinguish principal fin rays from rudimentary fin rays. Dorsal fin and anal fin principal rays include all branched fin rays and the long unbranched fin ray preceding them. Terminal branching for some principal fin rays might not be evident until late in the metalarval phase, but the association of principal fin rays with pterygiophores immediately below and anterior to them is obvious on close examination. The most posterior principal fin ray for the dorsal and anal fins consists of two elements that articulate with the last pterygiophore. These elements are counted together as one principal fin ray. The association between dorsal fin and anal fin principal rays and their pterygiophores is used to confirm principal fin-ray counts. Transmitted and polarized light are useful in observing pterygiophores and fin rays. Clearing and staining specimens can facilitate counting of fin-ray meristics, especially pterygiophores on postflexion mesolarvae.

Vertebra and gill-raker counts are used in the juvenile key. Counts can be readily made on cleared and stained specimens. To facilitate counting of gill rakers, individual gill arches should be carefully excised from the left side of the specimen. Both external and

internal rows of gill rakers are counted. Longwave (soft) x-raying of specimens may be used to observe vertebrae (Tucker and Laroche 1984). The four Weberian-complex vertebrae and the urostylar vertebra are included in counts.

Keys are seldom perfect and by convention do not cover all possible character extremes. Even though over 750 specimens were analyzed in this study, there undoubtedly will be specimens with character extremes beyond those observed for a given taxon. Some specimens may be hybrids, especially specimens from areas of syntopy (Rivas 1964). A hybrid specimen might exhibit intermediacy over all morphological characters examined, but it may more closely resemble one of the two parental taxa for a specific character (Campton 1988). The comparative summary and species accounts must be used to confirm or refine conclusions reached through the keys. Data on collection date and location can be cautiously used to delimit possible taxa. Because humpback chub and bonytail are endangered, accurate and confident identification of their young is critical. Accordingly, the keys are somewhat conservative. When a specimen is near the boundary between developmental intervals, the adjacent key should be used to help confirm results of the proper key. Similarly, within keys, if a character state is nearly borderline or if criteria the specimens meet are unclear, both branches of the key should be tried. In either of these situations, if the conclusions are different, then the specimen's identity should be left tentative or questionable. If available, diagnostic meristic values are included as supplementary information to help confirm conclusions reached through morphometric character sets. Positive diagnosis is not always possible when character states are very similar

or have areas of overlap between taxa. In these cases, the keys conclude with *Gila* sp. and a footnote. Wild *Gila* specimens taken through the keys and identified as humpback chub or bonytail should be submitted to an expert for verification. Notification of additional information, errors, misleading criteria, or problems uncovered by users, and suggestions for revisions, will be appreciated.

Key to protolarvae of *G. cypha*, *G. elegans*, and *G. r. robusta*

1. Myomeres
   a. ≥ 20 postvent; ≥ 49 total.....*G. elegans*
   b. ≤ 19 postvent; ≤ 48 total.....2
2. Standard length (SL)
   a. 6 mm.....*G. cypha*
   b. ≥ 7 mm.....*Gila* sp.*

Key to flexion mesolarvae of *G. cypha*, *G. elegans*, and *G. r. robusta*

1. Myomeres
   a. ≥ 19 postvent; ≥ 50 total.....*G. elegans*
   b. ≤ 19 postvent; ≤ 48 total .....*Gila* sp.*

Key to postflexion mesolarvae of *G. cypha*, *G. elegans*, and *G. r. robusta*

1. Myomeres
   a. ≥ 21 postvent; ≥ 50 total.....*G. elegans*
      (≥ 10 dorsal fin pterygiphores; ≥ 10 anal fin pterygiophores)
   b. ≤ 19 postvent; ≤ 48 total.....2
2. Dorsal fin pterygiophores
   a. 10.....*G. cypha*
   b. 9.....3

* *G. cypha*, *G. r. robusta*, or hybrid.

3. Standard length

   a. 10 mm.....4

   b. ≥ 11 mm.....5

4. Pectoral fin rays

   a. Present, incomplete complement.....*G. cypha*

   b. Absent.....*G. r. robusta*

5. Standard length

   a. 11 mm.....6

   b. 12 mm.....7

6. Pelvic fin rays

   a. Present, incomplete complement.....*G. cypha*

   b. Absent.....*G. r. robusta*

7. Anal fin pterygiophores

   a. ≥ 10.....*Gila* sp.*

   b. ≤ 9.....*Gila* sp.**

Key to metalarvae of *G. cypha*, *G. elegans*, and *G. r. robusta*

1. Myomeres

   a. ≥ 19 postvent; ≥ 49 total.....*G. elegans*

      (≥ 10 dorsal fin principal rays; ≥ 10 anal fin principal rays)

   b. ≤ 19 postvent; ≤ 48 total.....2

2. Dorsal fin principal rays

   a. 10.....*G. cypha*

   b. 9.....3

*Probably *G. cypha*, possibility of *G. r. robusta*.

**Probably *G. r. robusta*, possibility of *G. cypha*.

3. Standard length

   a. ≤ 15 mm.....4

   b. > 15 mm.....9

4. CPLR (OAPHP as % OAPOP)

   a. ≥ 87.....*G. cypha*

   (anal fin principal rays typically 10)

   b. 83-86.....5

   c. ≤ 82.....*G. r. robusta*

   (anal fin principal rays typically 9)

5. ΣF (sum of lengths of all fins, i.e., P1+P2+D+A+C=ΣF) as % SL

   a. ≥ 86.....*G. cypha*

   b. 85.....6

   c. ≤ 84.....*G. r. robusta*

6. P2 (length of pelvic fin) as % PFO (distance between origins of pectoral and pelvic fins)

   a. ≥ 39.....*G. cypha*

   b. 36-38.....7

   c. ≤ 35.....*G. r. robusta*

7. P1 (length of pectoral fin) as % PFO

   a. ≥ 74.....*G. cypha*

   b. 61-73.....8

   c. ≤ 60.....*G. r. robusta*

8. DB (distance between origin and insertion of dorsal fin) as % SL

   a. ≥ 13.....*G. cypha*

   b. ≤ 12.....*G. r. robusta*

9. Standard length

   a. ≤ 17 mm.....10

   b. > 17 mm.....15

10. CPLR (%)

   a. ≥ 89.....*G. cypha*
   (anal fin principal rays typically 10; mouth may be somewhat subterminal and overhung by snout)

   b. 83-86.....11

   c. ≤ 82.....*G. r. robusta*
   (anal fin principal rays typically 9; mouth terminal, not overhung by snout)

11. ΣF as % SL

   a. ≥ 92.....*G. cypha*

   b. 81-91.....12

   c. ≤ 80.....*G. r. robusta*

12. P2 as % PFO

   a. ≥ 58.....*G. cypha*

   b. 43-57.....13

   c. ≤ 42.....*G. r. robusta*

13. P1 as % PFO

   a. ≥ 74.....*G. cypha*

   b. 63-73.....14

   c. ≤ 62.....*G. r. robusta*

14. DB as % SL

    a. ≥ 14.....*G. cypha*

    b. 13.....*Gila* sp.*

    c. ≤ 12.....*G. r. robusta*

15. Standard length

    a. ≤ 19 mm.....16

    b. > 19 mm.....21

16. CPLR (%)

    a. ≥ 90.....*G. cypha*

    (anal fin principal rays typically 10; mouth may be somewhat subterminal and overhung by snout)

    b. 89.....17

    c. ≤ 88.....*G. r. robusta*

    (anal fin principal rays typically 9; mouth terminal, not overhung by snout)

17. ΣF as % SL

    a. ≥ 93.....*G. cypha*

    b. 92.....18

    c. ≤ 91.....*G. r. robusta*

18. P2 as % PFO

    a. ≥ 56.....*G. cypha*

    b. 55.....19

    c. ≤ 54.....*G. r. robusta*

**G. cypha*, *G. r. robusta*, or hybrid.

19. P1 as % PFO

    a. ≥ 75.....*G. cypha*

    b. 69-73.....20

    c. ≤ 68.....*G. r. robusta*

20. DB as % SL

    a. ≥ 13.....*G. cypha*

    c. ≤ 12.....*G. r. robusta*

21. CPLR (%)

    a. ≥ 93.....*G. cypha*

    (anal fin principal rays typically 10; mouth may be somewhat subterminal and overhung by snout)

    b. ≤ 92.....22

22. ΣF as % SL

    a. ≥ 94.....*G. cypha*

    b. 93.....23

    c. ≤ 92.....*G. r. robusta*

    (anal fin principal rays typically 9; mouth terminal, not overhung by snout)

23. P2 as % PFO

    a. ≥ 63.....*G. cypha*

    b. 62.....24

    c. ≤ 61.....*G. r. robusta*

24. P1 as % PFO

    a. ≥ 75.....*G. cypha*

    b. ≤ 74.....25

25. DB as % SL

a. ≥ 13.....*G. cypha*

c. ≤ 12.....*G. r. robusta*

Key to juveniles (≤ 50 mm SL) of *G. cypha*, *G. elegans*, and *G. r. robusta*

1. Dorsal fin principal rays

a. ≥ 10.....2

b. 9.....8

2. Depth at APM (anterior margin of most posterior myomere) as % HL (head length, OP1)

a. 23.....*G. elegans*
(mouth terminal to subterminal, slightly oblique to nearly horizontal, not overhung by snout; ≥ 21 postvent vertebrae; ≥ 49 total vertebrae; ≥ 133 total gill rakers)

b. 24-27.....3

b. ≥ 28.....*G. cypha*
(especially in specimens ≥ 30 mm SL, mouth subterminal to inferior, nearly horizontal, overhung by snout; ≤ 20 postvent vertebrae; ≤ 48 total vertebrae; ≤ 109 total gill rakers).

3. CPLR (%)

a. ≥ 103.....*G. cypha*

b. 86-102.....4

4. ΣF as % SL

a. ≥ 110.....*G. cypha*

b. 92-109.....5

5. P2 as % PFO

a. ≥ 81.....*G. cypha*

b. 62-80.....6

6. Pl as % PFO

   a. ≥ 91.....*G. cypha*

   b. 70-90.....7

7. Vertebrae and gill rakers

   a. ≤ 20 postvent vertebrae; ≤ 48 total vertebrae; ≤ 109 total gill rakers.....*G. cypha*
   (especially in specimens ≥ 30 mm SL, mouth subterminal to inferior, nearly horizontal, overhung by snout).

   b. ≥ 21 postvent vertebrae; ≥ 49 total vertebrae; ≥ 133 total gill rakers.....*G. elegans*
   (mouth terminal to subterminal, slightly oblique to nearly horizontal, not overhung by snout)

8. CPLR (%)

   a. ≥ 96.....*G. cypha*
   (anal fin principal rays typically 10; especially in specimens ≥ 30 mm SL, mouth subterminal to inferior, nearly horizontal, overhung by snout)

   b. 86-95.....9

   c. ≤ 85.....*G. r. robusta*
   (anal fin principal rays typically 9; mouth terminal to subterminal, slightly oblique to nearly horizontal, not overhung by snout)

9. ΣF as % SL

   a. > 101.....*G. cypha*

   c. 92-100.....10

   b. ≤ 91.....*G. r. robusta*

10. P2 as % PFO

    a. ≥ 73.....*G. cypha*

    b. 62-72.....11

    c. ≤ 61.....*G. r. robusta*

11. P1 as % PFO

    a. ≥ 75.....*G. cypha*

    b. ≤ 74.....*G. r. robusta*

CONCLUSIONS

Known-identity humpback chub, bonytail, and Colorado roundtail chub larvae and YOY juveniles examined in this study were characterized by several taxon-specific developmental and morpho-meristic features. Bonytail were readily separated from humpback and Colorado roundtail chub by several meristics, including postvent and total myomeres or vertebrae, gill rakers, and modal number of dorsal fin principal rays. Counts of most meristic series, except for anal fin principal rays, were very similar between humpback and Colorado roundtail chub and had limited value in distinguishing young of these two fishes. Early in development, onset of some developmental events occurred at a smaller size in humpback chub than in Colorado roundtail chub, but for all practical purposes, protolarvae and flexion mesolarvae cannot be distinguished. Metalarval and YOY juvenile humpback and Colorado roundtail chub were separated to taxon by several morphometrics based on length of the caudal peduncle relative to trunk length and on fin morphology. Problems associated with using morphometry in larval-fish taxonomy were discussed earlier (i.e., dynamic nature of growth and development and non-genetic phenotypic variability). Field identification of wild young *Gila* using these diagnostic criteria is not realistic.

The keys presented here are not intended to be a panacea for all the difficulties surrounding identification of wild, field-collected young *Gila*. If taken too literally, keys can be a misleading illusion rather than a helpful tool. Descriptive information presented in this work should be considered a framework on which new data can be hung as knowledge of natural, intra- or inter-populational morphological variability increases. Accordingly, additional taxonomic studies are needed and require a broad-based, population-by-population geographical perspective. All members of the *G. robusta* superspecies complex should be studied, especially for examination of systematic relationships. For future taxonomic studies on young *Gila*, complete developmental series of all fishes of concern will need to be prepared. Known-identity specimens should be studied initially to establish base sets of taxon-specific characters. After these characters have been established, specimens of questionable identity (e.g., hybrids or fish collected from areas of syntopy) can then be studied. Because of the possible occurrence of morphological or physiological artifacts in artificially cultured specimens, it is best to complement study of cultured specimens with study of field-collected wild fish. Existing curated collections of young *Gila* may be used to some extent, but additional field collections, with measurement of selected habitat parameters (e.g., water temperature and clarity and substrate), will be necessary. Successful field collection of young fish will depend on the state of knowledge of spawning seasons, dispersal patterns of larvae, and nursery requirements. Hatchery or laboratory culture of these fishes will be needed to provide complete developmental series. Culture

efforts should include artificial production of hybrids and experiments on rearing embryos and larvae under different environmental conditions.

The U.S. Fish and Wildlife Service has contracted the Smithsonian Institution to investigate, in cooperation with outside researchers, questions and issues related to taxonomy of native *Gila* spp. in the Colorado River Basin and having implications to management and recovery of threatened or endangered forms. The initial research plan proposed by the Smithsonian Institution calls for concomitant studies on morphological, biochemical, molecular, and cytological attributes of adult and immature stages of all *G. robusta* complex members. Relationships among the *G. robusta* subspecies might be of particular interest. Results of preliminary electrophoretic analyses recently conducted by D. Buth (University of California, Los Angeles), W. L. Minckley (Arizona State University), and R. L. Mayden (University of Alabama, Tusculoosa) have shown that, biochemically, subspecies of *G. robusta* are very similar and that humpback chub and bonytail are two distinct forms (paper given at the 21st Annual Meeting of the Desert Fishes Council, 1989, Albuquerque, New Mexico). Perhaps these techniques, accompanied by morphological analyses, can be applied to larvae and YOY juveniles of these fishes.

With initiation of the *Gila* taxonomy project (Smithsonian Institution), a few basic questions come to mind. What is the expected outcome of this work, and how will it benefit management and recovery? Several issues have been proposed with no initial mention of objectives and goals. Will a revision of the taxonomic status of humpback chub, bonytail, and roundtail chub be a result? Probably not. Most experts will probably agree that these fishes are distinct forms, deserving of

specific status. Should identification of *Gila* in the field be left in the hands of experienced field researchers as it has been in the past, or must additional taxonomic criteria be applied to assure more accurate identification? Has the sudden push to resolve questions on *Gila* taxonomy relative to management and recovery come too late? Because of man-induced habitat alterations, have reproductive barriers between syntopic populations been reduced to a point where, at least for some populations, a significant number of the fish are hybrids? If this is shown to be the case, what can realistically be done to alleviate this potential problem? Can habitats be restored to more pristine conditions to salvage the remaining "pure" forms (if they can be adequately identified)? Members of the *G. robusta* superspecies complex are either rare or declining in abundance. Would a solution to the taxonomic questions be to place the entire complex on the federal list of threatened or endangered species? The 1973 Endangered Species Act as amended in 1978 defines the term species as "any subspecies of fish or wildlife or plants, and distinct population segments of any species of vertebrate fish or wildlife which interbreeds when mature". Efforts to achieve this type of listing would be monumental and would certainly be strongly opposed by water developers and users.

REFERENCES

Abbott, L. A., F. A. Bisby, and D. J. Rogers. 1985. Taxonomic analysis in biology: computers, models, and databases. Columbia University Press, New York.

Ahlstrom, E. H., J. L. Butler, and B. Y. Sumida. 1976. Pelagic Stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories from the northwest Atlantic. Bulletin of Marine Science 26:285-402.

Ahlstrom, E. H., and H. G. Moser. 1981. Systematics and development of early life history stages of marine fishes: achievements during the past century, present status and suggestions for the future. Rapports et Proces-Verbaux des Reunions Conseil International Pour l'Exploration de la Mer 178:541-546.

Allendorf, F. W., N. Ryman, and F. M. Utter. 1988. Genetics and fishery management: past, present, and future. Pages 1-19 *in* N. Ryman and F. Utter, editors. Population genetics and fishery management. University of Washington Press, Seattle.

Atchley, W. R., C. T. Gaskins, and D. Anderson. 1976. Statistical properties of ratios: empirical results. Systematic Zoology 26:211-214.

Baird, S. F., and C. Girard. 1953a. Descriptions of some new fishes from the River Zuni. Proceedings of the Academy of Natural Sciences of Philadelphia 6:368-369.

Baird, S. F., and C. Girard. 1953b. Fishes. Pages 148-152 *in* Captain L. Sitgreave's report of an expedition down the Zuni and Colorado rivers. 32nd Congress, 2nd Session, Executive Report 59.

Balinsky, B. I. 1948. On the development of specific characters in cyprinid fishes. Proceedings of the Zoological Society of London 118:335-344.

Ball, R. C, and E. H. Bacon. 1954. Use of pituitary material in the propagation of minnows. Progressive Fish-Culturist 16:108-113.

Balon, E. K. 1981a. Saltatory processes and altricial to precocial forms in the ontogeny of fishes. American Zoologist 21:573-596.

Balon, E. K. 1981b. Additions and amendments to the classification of reproductive styles in fishes. Environmental Biology of Fishes 6:377-389.

Balon, E. K. 1985a. The theory of saltatory ontogeny and life history models revisited. Pages 13-30 *in* E. K. Balon, editor. Early life histories of fishes: new developmental, ecological and evolutionary perspectives. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Balon, E. K. 1985b. Reflections on epigenetic mechanisms: hypotheses and case histories. Pages 239-270 *in* E. K. Balon, editor. Early life histories of fishes: new developmental, ecological and evolutionary perspectives. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Bartlett, M. S. 1949. Fitting a straight line when both variables are subject to error. Biometrics 5:207-212.

Baxter, G. T., and J. R. Simon. 1970. Wyoming fishes (revised edition). Wyoming Game and Fish Department Bulletin 4, Cheyenne.

Beckman, W. C. 1952. Guide to the fishes of Colorado. University of Colorado Museum Leaflet Number 11, Boulder.

Behnke, R. J., C. A. Carlson, D. L. Miller, D. E. Snyder, E. J. Wick, L. D. Zuckerman. 1982. A survey and analysis of existing information on fishes in northwest Colorado. Volume 6 *in* D. W. Crumpacker, editor. Wildlife conservation and energy development in northwest Colorado, 14 volume series. Colorado Division of Wildlife, Denver.

Behnke, R. J., and D. E. Benson. 1983. Endangered and threatened fishes of the Upper Colorado River Basin. Colorado State University Cooperative Extension Service Bulletin 503A, Fort Collins.

Bestgen, K. R., and D. L. Propst. 1989. Distribution, status, and notes on the ecology of *Gila robusta* (Cyprinidae) in the Gila River Drainage, New Mexico. The Southwestern Naturalist 34:402-412.

Blair, W. F., A. P. Blair, P. Bradkorb, F. R. Cagle, and G. A. Moore. 1968. Vertebrates of the United States. McGraw Hill, New York.

Blaxter, J. H. S. 1984. Ontogeny, systematics, and fisheries. Pages 1-6 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, S. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication Number 1.

Boehlert, G. W. 1984. Scanning electron microscopy. Pages 43-48 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication 1.

Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. Humphries, Jr., G. R. Smith, R. E. Strauss. 1985. Morphometrics in evolutionary biology: the geometry of size and shape change, with examples from fishes. The Academy of Natural Sciences of Philadelphia Special Publication 15.

Bozek, M. A., J. Paulson, and J. E. Deacon. 1984. Factors affecting reproductive success of bonytail chubs and razorback suckers in Lake Mohave. U.S. Department of the Interior Technical Report Number 12, Albuquerque, New Mexico.

Brothers, E. B. 1984. Otolith studies. Pages 50-57 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication 1.

Bulkey, R. V., C. R. Berry, R. Pimentel, and T. Black. 1982. Tolerance and preferences of Colorado River endangered fishes to selected habitat parameters. Pages 185-241 *in* Final report, contracted studies, part 3. Colorado River Fishery Project. U.S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah.

Campton, D. E. 1988. Natural hybridization and introgression in fishes: methods of detection and genetic interpretations. Pages 161-192 *in* N. Ryman and F. Utter, editors. Population genetics & fishery management. University of Washington Press, Seattle.

Carlson, C. A., C. G. Prewitt, D. E. Snyder, E. J. Wick, E. L. Ames, and W. D. Fronk. 1979. Fishes and macroinvertebrates of the White and Yampa Rivers. U.S. Bureau of Land Management Biological Sciences Series 1, Denver, Colorado.

Carlson, C. A., and R. T. Muth. 1989. The Colorado River: lifeline of the American Southwest. Canadian Special Publications in Fisheries and Aquatic Sciences 106:220-239.

Carlson, C. A., and R. T. Muth. In press. Endangered species management. *In* C. Kohler and W. Hubert, editors. Inland fisheries management in North America. American Fisheries Society, Bethesda, Maryland.

Chart, T. E., and J. S. Cranney 1989. Radio telemetry monitoring of stocked *Gila elegans* in the Green River, Utah. Annual progress report. Utah Division of Wildlife Resources, Salt Lake City.

Cohen, D. M. 1984. Ontogeny, taxonomy, and phylogeny. Pages 7-11 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, S. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication Number 1.

CRFRT (Colorado River Fishes Recovery Team). 1989a. Humpback chub (*Gila cypha*) recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado.

CRFRT. 1989b. Bonytail chub (*Gila elegans*) recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado.

Dallwitz, M. J. 1980. A general system for coding taxonomic descriptions. Taxon 29:41-46.

Dallwitz, M. J., and T. A. Paine. 1986. User's guide to the DELTA system--a general system for processing taxonomic descriptions. CSIRO Australian Division of Entomology Report Number 13.

Douglas, M. E., W. L. Minckley, and H. M. Tyus. 1989. Qualitative characters, identification of Colorado River chubs (Cyprinidae: genus *Gila*), and the "art of seeing well". Copeia 1989:653-662.

Dunn, J. R. 1983. The utility of developmental osteology in taxonomic and systematic studies of teleost larvae: a review. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service Circular 450.

Dunn, J. R. 1984. Developmental osteology. Pages 48-50 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication 1.

Fahay, W. E. 1981. The influence of temperature change on number of dorsal fin rays developing in *Fundulus majalis* (Walbaum). Rapports et Proces-Verbaux des Reunions Conseil International Pour l'Exploration de la Mer 178:567.

Fuiman, L. A. 1979. Descriptions and comparisons of catostomid fish larvae: Northern Atlantic Drainage species. Transactions of the American Fisheries Society 108:560-603.

Fuiman, L. A. 1982. Correspondence of myomeres and vertebrae and their natural variability during the first year of life in yellow perch. Pages 56-59 *in* C. F. Bryan, J. V. Conner, and F. M. Truesdale, editors. Proceedings of the fifth annual larval fish conference. Louisiana Cooperative Fishery Research Unit, Louisiana State University, Baton Rouge.

Fuiman, L. A. 1983. Growth gradients in fish larvae. Journal of Fish Biology 23:117-123.

Fuiman, L. A. and L. Corazza. 1979. Morphometry and allometry: implications for larval fish taxonomy. Pages 1-18 *in* R. Wallus and C. W. Voigtlander, editors. Proceedings of a workshop on freshwater larval fishes. Tennessee Valley Authority, Norris, Tennessee.

Fuiman, L. A., J. V. Conner, B. F. Lathrop, G. L. Buynak, D. E. Snyder, and J. L. Loos. 1983. State of the art identification for cyprinid fish larvae from eastern North America. Transactions of the American Fisheries Society 112:319-332.

Fujii, R. 1969. Chromatophores and pigments. Pages 307-354 *in* W. S. Hoar and D. J. Randall. Fish physiology -- reproduction and growth, bioluminescence, pigments, and poisons. Volume III. Academic Press, New York.

Futuyma, D. J. 1986. Evolutionary biology. Sinauer Associates, Inc., Sunderland, Massachusetts.

Gaufin, A. R., C. R. Smith, and P. Dotson. 1960. Aquatic survey of the Green River and tributaries with Flaming Gorge basin. Pages 139-169 *in* C. E. Dibble, editor. Ecological studies of the flora and fauna of Flaming Gorge Reservoir basin, Utah and Wyoming. University of Utah Anthropological Paper 48.

Govoni, J. J. 1984. Histology. Pages 40-42 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication 1.

Grant, V. 1963. The origin of adaptations. Columbia University Press, New York.

Hamman, R. L. 1981a. Hybridization of three species of chub in a hatchery. Progressive Fish-Culturist 43:140-141.

Hamman, R. L. 1981b. Spawning and culture of Colorado squawfish in raceways. Progressive Fish-Culturist 43:173-177.

Hamman, R. L. 1982a. Induced spawning and culture of bonytail chub. Progressive Fish-Culturist 44:201-203.

Hamman, R. L. 1982b. Spawning and culture of humpback chub. Progressive Fish-Culturist 44:213-216.

Hamman, R. L. 1985. Induced spawning of the hatchery-reared bonytail. Progressive Fish-Culturist 47:239-241.

Hardy, J. D., Jr., G. E. Drewry, R. S. Fritzsche, G. D. Johnson, P. W. Jones, and F. D. Martin. 1978. Development of fishes of the Mid-Atlantic Bight: an atlas of egg, larval and juvenile stages. U.S. Fish and Wildlife Service Biological Services Program FWS/OBS-78/12.

Hay, D. E. 1981. Effects of capture and fixation on gut contents and body size of Pacific herring larvae. Rapports et Proces-Verbaux des Reunions Conseil International Pour l'Exploration de la Mer 178:395-400.

Haynes, C. M. 1980. Endangered humpback chub range extension documented. U.S. Fish and Wildlife Service Endangered Species Technical Bulletin 5(10):3.

Haynes, C. M., R. T. Muth, and T. P. Nesler. 1985. Identification of habitat requirements and limiting factors for Colorado squawfish and humpback chub. Job final report SE-3-4. Colorado Division of Wildlife, Fort Collins.

Holden, P. B. 1968. Systematic studies of the genus *Gila* (Cyprinidae) of the Colorado River Basin. Masters thesis. Utah State University, Logan.

Holden, P. B., and C. B. Stalnaker. 1970. Systematic studies of the cyprinid genus *Gila*, in the Upper Colorado River Basin. Copeia 1970:409-420.

Holden, P. B., and C. B. Stalnaker. 1975. Distribution and abundance of mainstream fishes of the middle and upper Colorado River Basin, 1967-1973. Transactions of the American Fisheries Society 104:217-231.

Hubbs, C. L. 1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of the water during development. American Naturalist 56:360-372.

Hubbs, C. L. 1924. Seasonal variation in the number of vertebrae of fishes. Papers of the Michigan Academy of Sciences, Arts, and Letters 2:207-214.

Humphries, J. M., F. L. Bookstein, B. Chernoff, G. R. Smith, R. L. Elder, and S. G. Poss. 1981. Multivariate discrimination by shape in relation to size. Systematic Zoology 30:291-308.

Huxley, J. S. 1932. Problems of relative growth. Methuen and Company, London.

Johnson, J. E. 1987. Protected fishes of the United States and Canada. American Fisheries Society, Bethesda, Maryland.

Jonez, A., and R. C. Sumner. 1954. Lakes Mead and Mohave investigations: a comparative study of an established reservoir as related to a newly created impoundment. Final report, federal aid project F-1-R. Nevada Fish and Game Commission, Reno.

Jordan, D. S., and B. W. Evermann. 1896. The fishes of North and Middle America. Bulletin of the U.S. National Museum 47:1-1240.

Joseph, T. W., J. A. Sinning, R. J. Behnke, and P. B. Holden 1977. An evaluation of the status, life history, and habitat requirements of endangered and threatened fishes of the Upper Colorado River System. U.S. Fish and Wildlife Service FWS/OBS-77/62, Fort Collins, Colorado.

Kaeding, L. R., and M. A. Zimmerman. 1983. Life history and ecology of the humpback chub in the Little Colorado and Colorado rivers of the Grand Canyon. Transactions of the American Fisheries Society 112:577-594.

Kaeding, L. R., B. D. Burdick, P. A. Schrader, and W. R. Noonan, 1986. Recent capture of a bonytail (*Gila elegans*) and observations on this nearly extinct cyprinid from the Colorado River. Copeia 1986:1021-1023.

Kaeding, L. R., and C. McAda. In press. Temporal and spatial relations between the spawning of humpback chub and roundtail chub in the Upper Colorado River. Transactions of the American Fisheries Society.

Karp, C. A., and H. M Tyus. 1989. Reproduction ecology of *Gila* spp. in Yampa and Green rivers, Dinosaur National Monument, Colorado and Utah. Final report. U.S. Fish and Wildlife Service, Vernal, Utah.

Kendall, A. W., Jr., E. H. Ahlstrom, and H. G. Moser. 1984. Early life history stages of fishes and their characters. Pages 11-22 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, S. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication Number 1.

Kidwell, J. F., and H. B. Chase. 1967. Fitting the allometric equation: a comparison of ten methods by computer simulation. Growth 31:165-179.

Kuhry, B., and L. F. Marcus. 1977. Bivariate linear models in biometry. Systematic Zoology 26:201-209.

LaRivers, I. 1962. Fishes and fisheries of Nevada. Nevada State Printing Office, Carson City.

Lee, S. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh.

Lindsey, C. C. 1988. Factors controlling meristic variation. Pages 197-274 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology -- the physiology of developing fish: viviparity and posthatching juveniles. Volume XI, Part B. Academic Press, Inc., San Diego, California.

Mabee, P. M. 1989. Assumptions underlying the use of ontogenetic sequences for determining character state order. Transactions of the American Fisheries Society 118:151-158.

Maddux, H. R., D. M. Kubly, J. C. deVos, Jr., W. K. Persons, R. Staedicke, and R. L. Wright. 1987. Effects of varied flow regimes on aquatic resources of Glen and Grand canyons. Final report. Arizona Game and Fish Department, Phoenix.

Mansfield, P. J., A. H. Mansfield. 1981. Influence of background color and intensity of illumination on melanophore expansion in larval fish. Pages 60-62 *in* C. F. Bryan, J. V. Conner, and F. M. Truesdale, editors. Proceedings of the fifth annual larval fish conference. Louisiana Cooperative Fishery Research Unit, Louisiana State University, Baton Rouge.

Markle, D. F. 1984. Phosphate buffered formalin for long term preservation of formalin fixed ichthyoplankton. Copeia 1984: 525-527.

Marliave, J. B. 1988. Variation in pigment and nape morphology of larval tidepool sculpin. American Fisheries Society Symposium 5:80-88.

Marr, J. C. 1955. The use of morphometric data in systematics, racial and relative growth studies in fishes. Copeia 1955:23-31.

Marsh, P. C. 1985. Effect of incubation temperature on survival of embryos of native Colorado River fishes. The Southwestern Naturalist 30:129-140

Martin, W. R. 1949. The mechanics of environmental control of body form in fishes. University of Toronto Studies Biological Series No. 58, The University of Toronto Press, Canada.

Mayr, E. 1977. Populations, species, and evolution: an abridgement of Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts.

Mayr, E. 1982. The growth of biological thought: diversity, evolution, and inheritance. Harvard University Press, Cambridge, Massachusetts.

Miller, R. R. 1946. *Gila cypha*, a remarkable new species of cyprinid fish from the Colorado River in Grand Canyon, Arizona. Journal of the Washington Academy of Sciences 36:409-415.

Miller, R. R., and C. H. Lowe. 1964. An annotated checklist of the fishes of Arizona. Pages 133-151 *in* C. H. Lowe, editor. The vertebrates of Arizona. University of Arizona Press, Tucson.

Minckley, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix.

Minckley, C. O., S. W. Carothers, J. W. Jordan, H. D. Usher. 1981. Observations on the humpback chub, *Gila cypha*, within the Colorado and Little Colorado rivers, Grand Canyon National Park, Arizona. U.S. Department of the Interior, National Park Service, Transactions and proceedings Series 7.

Minckley, W. L., and E. S. Gustafson. 1982. Early development of the razorback sucker, *Xyrauchen texanus* (Abbott). Great Basin Naturalist 42:553-561.

Minckley, W. L., D. A. Hendricks, and C. E. Bond. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. Pages 519-614 *in* C. H. Hocutt and E. O. Wiley, editors. The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Minckley, W. L., D. G. Buth, and R. L. Mayden. 1989. Origin of brood stock and allozyme variation in hatchery-reared bonytail, an endangered North American cyprinid fish. Transactions of the American Fisheries Society 118:131-137.

Moyle, P. B. 1976. Inland fishes of California. University of California Press, Berkeley.

Muth, R. T., and C. M. Haynes. 1984. Plexiglas light-trap for collecting small fishes in low-velocity riverine habitats. Progressive Fish-Culturist 46:59-62.

Muth, R. T., C. M. Haynes, and C. A. Carlson. 1985. Culture of roundtail chub, *Gila robusta robusta* (Cyprinidae), through the larval period. The Southwestern Naturalist 30:152-154.

Nesler, T. P., R. T. Muth, and A. F. Wasowicz. 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. American Fisheries Society Symposium 5:68-79.

Ohmart, R. S., B. W. Anderson, and W. C. Hunter. 1988. The ecology of the lower Colorado River from Davis Dam to the Mexico-United States international boundary: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7):1-296.

Osmundson, D. B., and L. R. Kaeding. 1989. Studies of Colorado squawfish and razorback sucker use of the "15-mile reach" of the Upper Colorado River as part of conservation measures for the Green Mountain and Ruedi Reservoir water sales. Final report. U. S. Fish and Wildlife Service, Grand Junction, Colorado.

Pothoff, T. 1984. Clearing and staining techniques. Pages 35-37 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, S. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication 1.

Powles, H, and D. F. Markle. 1984. Identification of larvae. Pages 31-33 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, S. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication 1.

Rinne, J. N. 1976. Cyprinid fishes of the genus *Gila* from the lower Colorado River Basin. The Wasmann Journal of Biology 34:65-107.

Rivas, L. R. 1964. A reinterpretation of the concepts "sympatric" and "allopatric" with proposal of the additional terms "syntopic" and "allotopic". Systematic Zoology 13:42-43

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the U.S. and Canada, fourth edition. American Fisheries Society Special Publication 12.

Rosenfeld, M. J. 1986a. Morphometry in chubs of the genus *Gila* from the Green and Colorado rivers, Colorado-Utah: principal component analysis. Utah Museum of Natural History, University of Utah, Salt Lake City.

Rosenfeld, M. J. 1986b. A preliminary electrophoresis study of the Colorado River chub (Pisces: Cyprinidae, genus *Gila*) complex. Department of Biology, University of Utah, Salt Lake City.

Rosenfeld, M. J., and J. A. Wilkinson. 1989. Biochemical genetics of the Colorado River *Gila* complex (Pisces: Cyprinidae). The Southwestern Naturalist 34:232-244.

Sandknop, E. M., B. Y. Sumida, and H. G. Moser. 1984. Early life history descriptions. Pages 23-24 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, S. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication Number 1.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184, Ottawa.

Seim, E., and B. E. Saether. 1983. On rethinking allometry: which regression model to use? Journal of Theoretical Biology 104:161-168.

Siefert, R. E. 1969. Characteristics for separation of white and black crappie larvae. Transactions of the American Fisheries Society 98:326-328.

Sigler, W. F., and R. R. Miller. 1963. Fishes of Utah. Utah Department of Fish and Game, Salt Lake City.

Simpson, G. G., A. Roe, and R. C. Lewontin. 1960. Quantitative zoology. Harcourt, Brace, & World, Inc., New York.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company, New York.

Smith, G. R. 1978. Biogeography of intermountain fishes. Pages 17-42 *in* K. T. Harper and J. L. Reveal, editors. Intermountain biogeography: a symposium. Great Basin Naturalist Memoirs 2.

Smith, G. R., R. R. Miller, and W. D. Sable. 1979. Species relationships among fishes of the genus *Gila* in the Upper Colorado River Drainage. Pages 613-623 *in* R. M. Linn, editor. Proceedings of the first conference on scientific research in the national parks. U.S. Department of the Interior, National Park Service, Transactions and Proceedings Series Number 5.

Smith, R. J. 1980. Rethinking allometry. Journal of Theoretical Biology 87:97-111.

Snyder, D. E. 1976. Terminologies for intervals of larval fish development. Pages 41-60 *in* J. Boreman, editor. Proceedings of a workshop on Great Lakes fish egg and larvae identification. U.S. Fish and Wildlife Service, FWS/OBS-76/23, Ann Arbor, Michigan.

Snyder, D. E. 1981. Contributions to a guide to the cypriniform fish larvae of the Upper Colorado River System in Colorado. U.S. Bureau of Land Management Biological Sciences Series 3, Denver, Colorado.

Snyder, D. E. 1983. Fish eggs and larvae. Pages 165-197 *in* L. Nielsen and D. Johnson, editors. Fishery techniques. American Fisheries Society, Bethesda, Maryland.

Snyder, D. E., and R. T. Muth. 1988. Description and identification of June, Utah, and mountain sucker larvae and early juveniles. Utah State Division of Wildlife Resources Publication 88-8, Salt Lake City.

Snyder, D. E., and R. T. Muth. In press. Descriptions and identification of razorback, flannelmouth, white, Utah, bluehead, and mountain sucker larvae and early juveniles. Colorado Division of Wildlife Technical Publication, Fort Collins.

Stanford, J. A., and J. V. Ward. 1986a. The Colorado River System. Pages 353-374 *in* B. R. Davies and K. F. Walker, editors. The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

Stanford, J. A., and J. V. Ward. 1986b. Reservoirs of the Colorado system. Pages 375-383 *in* B. R. Davies and K. F. Walker, editors. The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

Stanford, J. A., and J. V. Ward. 1986c. Fishes of the Colorado system. Pages 385-402 *in* B. R. Davies and K. F. Walker, editors. The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

Starnes, W. C. 1990. Colorado River Basin *Gila* taxonomy project phase 1 report, part 2 (draft). U. S. Fish and Wildlife Service, Denver, Colorado.

Strauss, R. E., and F. L. Bookstein. 1982. The truss: body form reconstruction in morphometrics. Systematic Zoology 31:113-135.

Strauss, R. E., and L. A. Fuiman. 1985. Quantitative comparisons of body form and allometry in larval and adult Pacific sculpins (Teleostei: Cottidae). Canadian Journal of Zoology 63:1582-1589.

Suttkus, R. D., and G. H. Clemmer. 1977. The humpback chub, *Gila cypha*, in the Grand Canyon area of the Colorado River. Occasional Papers of the Tulane University Museum of Natural History 1:1-30.

Taylor, W. R., and C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9:107-119.

Tucker, J. W., and J. L. Laroche. 1984. Radiographic techniques in studies of young fish. Pages 37-39 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, S. W. Kendall, Jr., and S. L. Richardson, editors. Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication 1.

Tyus, H. M., B. D. Burdick, R. A. Valdez, C. M. Haynes, T. A. Lytle, and C. R. Berry. 1982a. Fishes of the Upper Colorado River Basin: distribution, abundance, and status. Pages 12-70 *in* W. H. Miller, H. M. Tyus, and C. A. Carlson, editors. Fishes of the Upper Colorado River System: present and future. American Fisheries Society, Bethesda, Maryland.

Tyus, H. M., C. W. McAda, and B. D. Burdick. 1982b. Green River fishery investigations: 1979-1981. Pages 1-99 *in* W. H. Miller, J. J. Valentine, D. L. Archer, H. M. Tyus, R. A. Valdez, and L. R. Kaeding, editors. Final report, field investigations, part 2. Colorado River Fishery Project. U.S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah.

Tyus, H. M., R. L. Jones, and L. A. Trinca. 1987. Colorado River fishes monitoring project, 1982-1985. Final report. U.S. Fish and Wildlife Service, Vernal, Utah.

Tyus, H. M., and C. A. Karp. 1989. Habitat use and streamflow needs of rare and endangered fishes, Yampa River, Colorado. U.S. Fish and Wildlife Service Biological Report 89(14):1-27.

USDI (U.S. Department of the Interior). 1989. Endangered and threatened wildlife and plants. 50 CFR 17.11 and 17.12. U.S. Government Printing Office, Washington, D. C.

USFWS (U.S. Fish and Wildlife Service). 1987. List of approved recovery plans. Endangered Species Technical Bulletin 12(1): 10-14.

USFWS. 1988. Endangered Species Technical Bulletin 13(6-7):1-8.

Uyeno, T. 1961. Osteology and phylogeny of the American cyprinid fishes allied to the genus *Gila*. Ph.D. dissertation. University of Michigan, Ann Arbor.

Valdez, R. A. 1985. Cataract Canyon fish study. Final report. Contract number S-CS-40-02820. U.S. Bureau of Reclamation, Salt Lake City, Utah.

Valdez, R. A. 1987. Fisheries biology and rafting. Annual summary report--1986, Contract Number 6-CS-40-03980, conducted by Bio/West, Inc. U.S. Bureau of Reclamation, Salt Lake City, Utah.

Valdez, R. A. 1988. Fisheries biology and rafting. Annual summary report--1987, Contract Number 6-CS-40-03980, conducted by Bio/West, Inc. U.S. Bureau of Reclamation, Salt Lake City, Utah.

Valdez, R. A. 1989. Informal larval/YOY humpback chub survey: field notes and observations. BIO/WEST, Inc., Logan, Utah.

Valdez, R. A., and G. H. Clemmer. 1982. Life history and prospects for recovery of the humpback chub and bonytail chub. Pages 109-119 *in* W. H. Miller, H. M. Tyus, and C. A. Carlson, editors. Fishes of the Upper Colorado River System: present and future. American Fisheries Society, Bethesda, Maryland.

Valdez, R. A., R. G. Mangan, R. P. Smith, and B. Nilson. 1982. Upper Colorado River fisheries investigation (Rifle, Colorado, to Lake Powell, Utah). Pages 101-279 *in* W. H. Miller, J. J. Valentine, D. L. Archer, H. M. Tyus, R. A. Valdez, and L. R. Kaeding, editors. Final report, field investigations, part 2. Colorado River Fishery Project. U.S. Fish and Wildlife Service and Bureau of Reclamation, Salt Lake City, Utah.

Vanicek, C. D., and R. H. Kramer. 1969. Life history of the Colorado squawfish, *Ptychocheilus lucius*, and the Colorado chub, *Gila robusta*, in the Green River in Dinosaur National Monument, 1964-1966. Transactions of the American Fisheries Society 98: 193-208.

Weil, W. B., Jr. 1962. Adjustment for size: a possible misuse of ratios. American Journal of Clinical Nutrition 11:249-252.

Williams, J. E., D. B. Bowman, J. E. Brooks, A. A. Echelle, R. J. Edwards, D. A. Hendrickson, and J. L. Landye. 1985. Endangered aquatic ecosystems in North American deserts with a list of vanishing fishes of the region. Journal of the Arizona-Nevada Academy of Science 20:1-62.

Winn, H. E., and R. R. Miller. 1954. Native postlarval fishes of the lower Colorado River Basin, with a key to their identification. California Fish and Game 40:273-285.

Yeager, B. L., and R. Wallus. 1982. Development of larval *Polyodon spathula* (Walbaum) form the Cumberland River in Tennessee. Pages 73-77 *in* C. F. Bryan, J. V. Conner, and F. M. Truesdale, editors. Proceedings of the fifth annual larval fish conference. Louisiana Cooperative Fishery Research Unit, Louisiana State University, Baton Rouge.

Youson, J. H. 1988. First metamorphosis. Pages 135-196 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology -- the physiology of developing fish: viviparity and posthatching juveniles. Volume XI, Part B. Academic Press, Inc., San Diego, California.

APPENDIX A

TAXON ACCOUNTS FOR *GILA CYPHA*, *G. ELEGANS*, AND *G. ROBUSTA ROBUSTA*

Humpback chub, Gila cypha

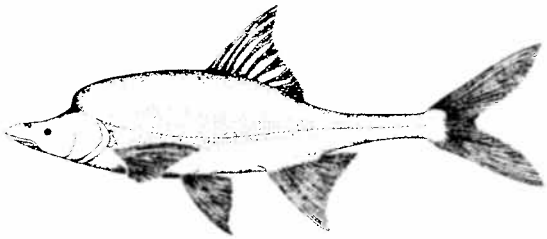


FIGURE A-1. Gila cypha adult (from Behnke and Benson 1983).

Status, Distribution, and Habitat. Species was described by Miller (1946). Endangered on federal list of threatened and endangered species; recovery plan has been approved. Listed as protected by Arizona, Colorado, and Utah. Endemic to the Colorado River Basin. Historic distribution is not known with certainty because of the relatively recent discovery of the species. Because of its habitat requirements, probably never widespread or common in the basin. Present distribution restricted; rare or incidental where found. Occurs primarily in canyon-bound segments of larger rivers. Adults typically found in habitats with swift, deep water and rock substrate or cover. Young mostly found in near-shore, low-velocity habitats (e.g., eddies, backwaters, or embayments) with silt, sand, or rock substrate. In laboratory tests, preferred water temperature was 24°C.

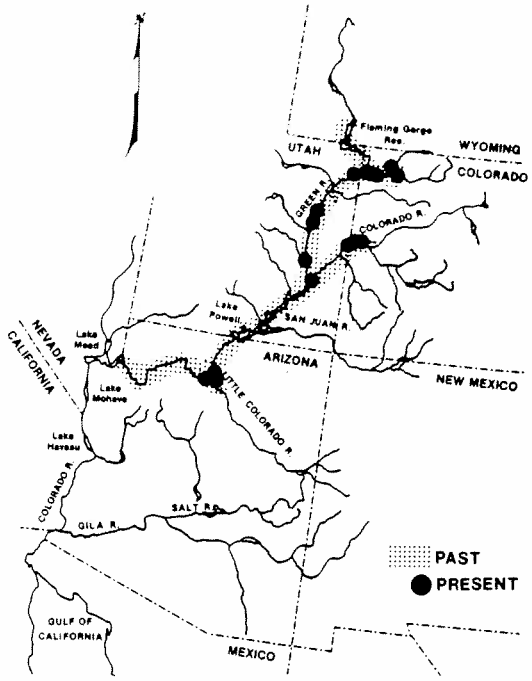


FIGURE A-2. Distribution of Gila cypha.

References: Minckley 1973; Holden and Stalnaker 1975; Joseph et al. 1977; Smith et al. 1979; Lee et al. 1980; Minckley et al. 1981; Behnke et al. 1982; Bulkley et al. 1982; Tyus et al. 1982, 1987; Valdez and Clemmer 1982; Behnke and Benson 1983; Kaeding and Zimmerman 1983; Stanford and Ward 1986c; Johnson 1987; USDI 1987; USFWS 1987, 1988; Valdez 1987, 1988, 1989; Carlson and Muth 1989, in press; CRFRT 1989a.

Adult Diagnosis. Morphology: Gray or olivaceous on dorsal surface, silvery on ventrolateral surfaces. Skull flattened or concave on dorsal surface. Mouth subterminal to inferior, nearly horizontal. Snout long, fleshy, overhangs mouth. Eyes very small (eye diameter about 13.0 in head length). Body streamlined, compressed. Anterodorsal nuchal hump prominent, abrupt over occiput, truncate anteriorly (shape and prominence variable). Caudal peduncle thin, moderately slender, somewhat pencil-like (least depth of caudal peduncle about 4.8 in head length). Fins large, expansive, falcate; caudal fin lobes moderately long and pointed. Squamation incomplete; body and caudal peduncle almost scaleless except for lateral line scales (scales have basal radii). Total length to 35-45 cm. Meristics*: Dorsal fin principal rays = (8)-9-10; anal fin principal rays = (9)-10-11; caudal fin principal rays = (18)-19-(20); pectoral fin rays = (15)-16-17-18-(19); pelvic fin rays = 8-9-10; lateral line scales = (73-75)-76-80-82-87-(90); pharyngeal teeth = 2,5-4,2(1); gill rakers = 22-25-26-28 [13-15-17]; total vertebrae = 45-46-47-48-(49).

Reproduction. Mature at 3-5 years of age. Non-guarding, open-substrate lithophils. Spawn shortly after peak spring flows during late April-early July at water temperatures of 12-21°C (typically 16-19°C). Under hatchery conditions, percent egg hatch was highest at water temperatures of 19-22°C. In laboratory tests, percent egg hatch was highest and incidence of abnormal larvae was lowest at a water temperature of 20°C. Probably spawn in near-shore areas of moderate water velocity and depth over sand, gravel, or cobble substrate. Breeding males have orange-red coloration along ventrolateral surfaces and small tubercles on anterior portion of the body. Breeding colors and tubercles are less pronounced in females. Reported mean fecundity of females injected with a preparation of carp pituitary was about 5,200 eggs/kg body weight. Prefertilization egg diameter ranges from 0.9 mm (immature eggs) to 2.2 mm (mature eggs). Egg diameter after fertilization and water hardening ranges from 2.3 to 3.3 mm with a mean of 2.7 mm. Eggs are demersal and adhesive. Young hatch in about 3-7 d after fertilization and swim up in about 3-4 d after hatching at water temperatures of 19-20°C.

*Mean or modal values are underlined, and rare or questionable extremes are enclosed by parentheses. Gill-raker counts are for the first gill arch, both external and internal rows of gill rakers, or for the second gill arch, external row of gill rakers only (enclosed in brackets [ ]). Reported vertebrae counts were adjusted (if needed) to include the four vertebrae of the Weberian complex.

References: Miller 1946; Gaufin et al. 1960; Sigler and Miller 1963; Miller and Lowe 1964; Blair et al. 1968; Holden 1968; Holden and Stalnaker 1970; Minckley 1973; Suttkus and Clemmer 1977; Smith et al. 1979; Balon 1981b; Hamman 1982b; Valdez and Clemmer 1982; Behnke and Benson 1983; Kaeding and Zimmerman 1983; Marsh 1985; CRFRT 1989a; Tyus and Karp 1989; original data from this study.

TABLE A-1. Size or age at onset of selected developmental events for Gila cypha as observed under low-power magnification. Fish examined were cultured from brood stock collected from the Little Colorado River, Arizona (Figure 1, Methods). Fish were reared in 18-23-°C water. Age is days after hatching. P = principal rays; R = rudimentary rays; scales are lateral series. See Figure 4 for definitions of other abbreviations and methods of measuring standard and total length (SL and TL). Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

Event or structure	SL (mm)	TL (mm)	Age
Hatched	6-7	7	
Eyes pigmented	prior to hatching		
Yolk assimilated	10	11	11
Gut looped, 90° bend	13	16	22
Finfold absorbed	21	24-25	
P1 buds formed	6-7	7	
P2 buds formed	<13	<16	22
Transition to:			
Flexion mesolarva	9	9-10	7
Postflexion mesolarva	10-11	12	16
Metalarva	<13	<16	20
Juvenile	21	27	<36

Fin rays or scales	First Formed SL (mm)	First Formed TL (mm)	Last Formed SL (mm)	Last Formed TL (mm)
Dorsal - P	10	11	<13	<16
Dorsal - R	<13	<16	15	20
Anal - P	10	11	<13	<16
Anal - R	<13	<16	15	20
Caudal - P	9	9-10	10-11	12
Caudal - R	<11	<12	21	27
Pectoral	10-11	12-13	14-15	20
Pelvic	11-12	13-14	15	20
Scales	<25	<32	50[a]	

[a]Data from Suttkus and Clemmer (1977).

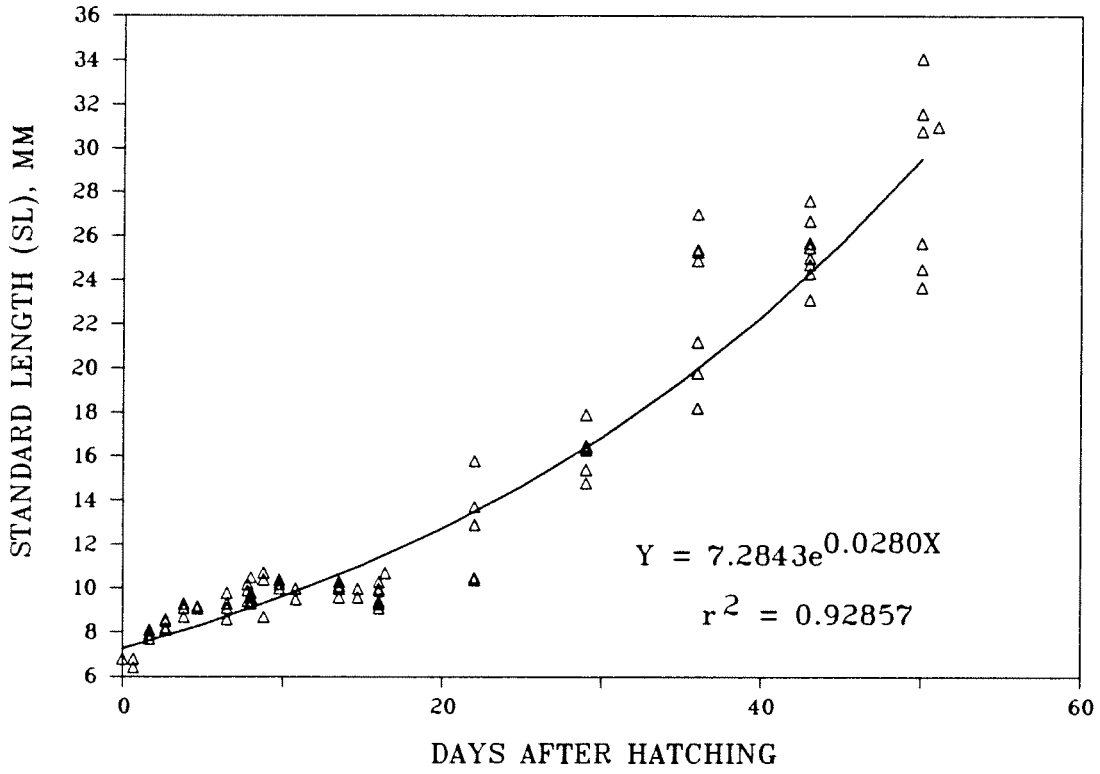


FIGURE A-3. Exponential growth curve for Gila cypha larvae and young-of-the-year juveniles cultured from brood stock collected from the Little Colorado River, Arizona (Figure 1, Methods). Fish were reared in 18-23-°C water. See Figure 4 for methods of measuring SL.

TABLE A-2. Size or age at onset of selected developmental events for Gila cypha as observed under low-power magnification. Fish examined were cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods). Fish were reared in 18-23-°C water. Age is days after hatching. P = principal rays; R = rudimentary rays; scales are lateral series. See Figure 4 for definitions of other abbreviations and methods of measuring standard and total length (SL and TL). Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

Event or structure	SL (mm)	TL (mm)	Age
Hatched	6-7	7	
Eyes pigmented	prior to hatching		
Yolk assimilated	9-10	10-11	10
Gut looped, 90° bend	15	16	19
Finfold absorbed	22	26	
P1 buds formed	6	7	
P2 buds formed	11	13	19
Transition to:			
Flexion mesolarva	9-10	10-11	6
Postflexion mesolarva	10	11-12	16
Metalarva	<13	<16	15
Juvenile	22	27	<32

Fin rays or scales	First Formed SL (mm)	First Formed TL (mm)	Last Formed SL (mm)	Last Formed TL (mm)
Dorsal - P	10	11	<13	<16
Dorsal - R	11	13	14	18
Anal - P	10	11	<13	<16
Anal - R	<12	<15	14	18
Caudal - P	9-10	10-11	10	11-12
Caudal - R	<12	<14	22	27
Pectoral	10-11	11-13	13-15	19
Pelvic	11-12	13-14	14-15	20
Scales	<26	<34		

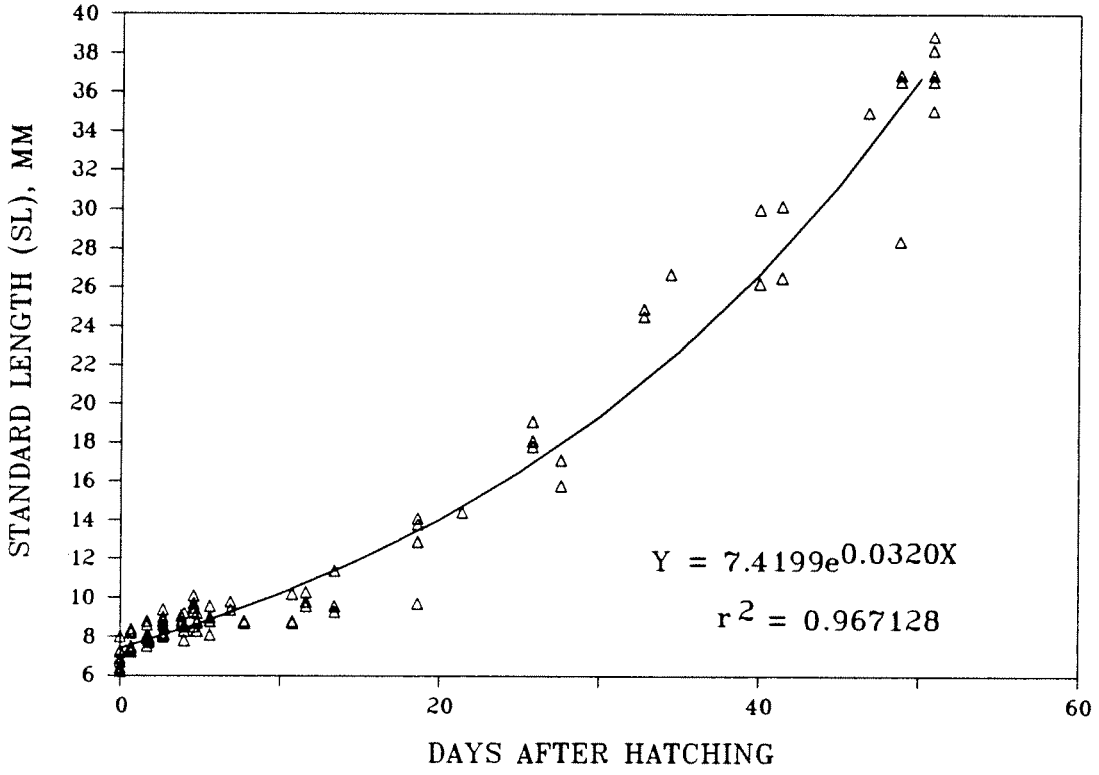


FIGURE A-4. Exponential growth curve for Gila cypha larvae and young-of-the-year juveniles cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods). Fish were reared in 18-23-°C water. See Figure 4 for methods of measuring SL.

TABLE A-3. Summary of selected morphometrics by developmental phase for Gila cypha cultured from brood stock collected from the Little Colorado River, Arizona (Figure 1, Methods). See Figures 4, 5 for definitions of abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Protolarvae (N=16)				Flexion Mesolarvae (N=31)				Postflexion Mesolarvae (N=10)				Metalarvae (N=13)				Juveniles (N=26)			
			Range				Range				Range				Range				Range	
	Mean	±SD	Min	Max	Mean	±SD	Min	Max	Mean	±SD	Min	Max	Mean	±SD	Min	Max	Mean	±SD	Min	Max
SL,mm	8	1	6	9	10	0	9	10	11	1	10	12	16	2	13	20	27	3	21	34
TL,mm	9	1	7	10	11	1	10	12	12	1	12	14	21	3	16	25	34	4	27	44
Lengths %SL:																				
AS to AE	3	0	2	3	3	1	2	4	4	0	4	4	5	0	5	6	6	1	5	7
PE	9	1	7	10	10	1	8	11	11	1	10	11	13	1	12	14	13	1	12	14
OP1	19	1	17	20	21	1	18	22	21	1	19	22	27	1	26	28	25	1	23	28
OP2													48	1	47	50	48	1	45	50
OPAF			30	52			28	36			34	40			42	61				
ODF			28	41			36	42			45	49			.50	53[b]				
OD													53	1	51	54	51	1	49	53
ID													66	1	65	68	66	1	64	68
PV	66	2	63	69	67	2	64	70	67	1	65	70	66	2	64	69	64	1	62	67
OA													67	1	65	69	65	1	63	67
IA													78	1	77	79	77	1	75	80
ED	6	0	6	7	7	1	6	8	7	0	7	7	8	0	7	8	7	0	6	7
PFO													21	1	20	23	22	1	20	24
DB													14	0	13	15	14	1	13	16
AB													11	1	10	12	12	1	11	14
CP													34	1	33	35	35	1	33	37
CL							2	4[a]	5	1	4	6	15	1	14	17	15	1	14	18
P1			5	12			10	15			12	15	17	1	16	19	18	1	17	21
P2													14	1	14	16	15	1	14	17
D													23	1	22	25	24	1	22	25
A													19	1	18	20	20	1	18	21
C			3	9			4	13	14	1	12	16	29	2	27	31	28	1	26	31
ΣF[c]													104	6	93	118	105	4	93	115
LDR													20	1	18	22	21	1	18	23
LAR													17	1	16	19	17	1	16	20
Depths %SL:																				
at ME	11	1	10	12	12	1	11	14	12	1	11	13	15	1	15	16	14	1	14	16
BPE	12	1	11	14	13	1	12	15	14	1	12	15	17	1	16	18	17	1	16	19
APM	3	0	3	4	5	1	3	6	5	1	5	6	8	0	8	9	8	0	7	8
Widths %SL:																				
at BPE	11	1	9	12	13	1	11	14	14	1	12	15	17	1	15	20	17	1	16	19
APM	2	0	2	3	2	0	2	3	3	0	2	3	5	0	4	5	4	0	4	5
% HL:																				
ED	34	2	29	38	33	3	27	39	34	2	30	38	29	1	27	31	26	2	23	30
Depth at APM	18	2	15	20	22	3	15	26	24	1	22	26	30	1	28	32	30	1	28	32
%PFO:																				
P1																	85	5	73	94
≤17mm SL													77	3[d]	73	81				
>17mm SL													87	3[e]	83	90				
P2																	71	3	64	77
≤17mm SL													56	8[d]	44	67				
>17mm SL													73	4[e]	70	79				
CPLR[f]													88	3	83	92	92	3	85	97

[a]N=10. [b]N=2. [c]ΣF is the sum of lengths of all fins (i.e., P1+P2+D+A+C = ΣF). [d]N=9. [e]N=4. [f]CPLR (caudal peduncle length ratio) is OAPHP expressed as % OAPOP.

TABLE A-4. Summary of selected morphometrics by developmental phase for Gila cypha cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods). See Figures 4, 5 for definitions of abbreviations and methods of measurement. Developmental-interval terminology as defined by Snyder and Muth (1988, in press, see Methods).

	Protolarvae (N=51)				Flexion Mesolarvae (N=25)				Postflexion Mesolarvae (N=6)				Metalarvae (N=12)				Juveniles (N=38)			
	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max
SL,mm	8	1	6	9	10	1	9	10	12	1	10	14	16	2	14	19	31	6	22	43
TL,mm	9	1	7	10	10	1	9	11	13	2	11	17	21	3	17	25	39	7	27	54
Lengths %SL:																				
AS to AE	3	1	2	5	4	1	2	5	4	0	3	4	6	1	5	6	6	1	5	7
PE	9	1	8	11	10	1	8	12	11	0	11	12	12	1	11	14	12	1	11	14
OP1	18	2[a]	13	20	21	2	18	24	23	2	21	27	26	1	25	28	25	1	21	28
OP2									46	1[b]	45	46	47	1	45	48	46	1	42	48
OPAF			30	55			28	33			33	36			36	53				
ODF			31	46			40	42			42	47								
OD													51	2	48	53	49	1	46	51
ID													65	2	62	67	63	1	60	67
PV	65	2	61	69	66	2	63	70	67	2	66	70	66	1	65	68	64	1	60	67
OA													65	1	63	68	64	1	61	66
IA													76	1	74	78	75	1	72	78
ED	6	1	5	7	6	1	5	6	7	0	7	8	7	0	7	8				
≤25mm SL																	7	1[c]	7	8
>25mm SL																	6	1[d]	5	7
PFO									20	2[b]	18	23	21	1	19	23	21	1	18	23
DB													14	1	13	15	14	1	12	16
AB													11	1	9	13	11	1	10	13
CP													35	1	32	37	36	1	34	39
CL							1	4[e]	7	1	6	9					14	1	13	16
≤15mm SL													9	1[f]	7	10				
>15mm SL													13	1[g]	12	16				
P1			3	13[a]			11	15			11	16	15	1	14	17	17	1	15	19
P2											5	7[b]					15	1	14	17
≤15mm SL													8	0[f]	7	8				
>15mm SL													13	1[g]	13	14				
D													21	1	20	23	23	1	21	25
A													17	1	16	19	19	1	17	21
C			2	7			4	14	16	3	10	23	26	2	23	28	27	2	21	32
ΣF[h]													90	5	85	98	101	5	90	109
LDR													18	1	17	19	21	1	19	23
LAR													15	1	14	16	17	1	14	19
Depths %SL:																				
at ME	11	1	10	15	12	1	10	14					14	1	14	16	14	1	12	17
≤12mm SL									13	0[c]	12	13								
>12mm SL											15	15[i]								
BPE	12	1	10	14	14	1	12	15					16	1	15	18	16	1	14	19
≤12mm SL									14	1[c]	14	15								
>12mm SL											17	17[i]								
APM	4	1	3	5	5	1	3	5					8	1	7	9	8	1	6	9
≤12mm SL									5	0[c]	5	5								
>12mm SL											7	8[i]								
Widths %SL:																				
at BPE	12	1	10	14	12	1	11	14	14	1	12	15	16	1	15	18	16	1	14	18
APM	3	0	2	3	2	0	2	3	3	0	3	3	4	0	3	5	4	0	3	5
% HL:																				
ED	34	3	29	42	31	2	27	37	31	3	27	36	27	1	26	30	24	2	20	29
Depth at APM	21	2[a]	18	25	22	2	18	24					31	2	29	35	31	2	28	34
≤12mm SL									22	0[c]	22	23								
>12mm SL											28	35[i]								
% PFO:																				
P1											59	61[b]	70	4	61	75	85	6	71	97
P2											29	32[b]					74	6	62	88
≤17mm SL													47	9[j]	36	59				
>17mm SL															63	64[i]				
CPLR[k]													92	5	87	104	95	5	87	108

[a]N=47. [b]N=3. [c]N=4. [d]N=34. [e]N=6. [f]N=5. [g]N=7. [h]ΣF is the sum of lengths of all fins (i.e., P1+P2+D+A+C = ΣF).
[i]N=2. [j]N=10. [k]CPLR (caudal peduncle length ratio) is OAPHP expressed as % OAPOP.

TABLE A-5. Summary of selected morphometrics by developmental phase for Gila cypha collected from the Little Colorado River, Arizona (Figure 1, Methods). See Figures 4, 5 for definitions of abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Metalarvae (N=8)				Juveniles (N=18)			
	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max
SL,mm	17	3	13	21	32	7	21	45
TL,mm	22	4[a]	15	27	42	10[b]	28	59
Lengths %SL:								
AS to AE	6	1	5	7	7	1	6	8
PE	13	1	12	14	13	1	12	14
OP1	26	2	24	29	26	1	25	29
OP2	48	1	46	50	46	1	45	48
OD	52	1	50	54	50	1	48	53
ID	65	1	63	67	65	1	62	68
PV	65	2	62	68	62	1	59	65
OA	65	2	63	68	63	1	61	66
IA	77	1	76	79	76	1	74	78
ED	7	1	6	8	6	1	5	7
PFO	22	2	20	26	20	1	19	22
DB	13	1	13	14	14	1	13	16
AB	12	1	9	13	13	1	11	14
CP	35	2	32	37	37	1	34	39
CL	13	2[c]	10	16	15[b]	1	13	18
P1	17	2	13	20	19	1	18	20
P2					16	1	15	18
≤17mm SL	10	1[d]	9	11				
>17mm SL	16	1[e]	15	17				
D	23	3	19	27	24	1	23	26
A	19	2	17	22	21	1	19	23
C	27	3[c]	21	31	28	2[b]	26	32
ΣF[f]	100	12[a]	81	116	109	4[b]	103	118
LDR	20	2[a]	16	22	21	1	19	24
LAR	16	2[a]	12	19	18	1	16	20
Depths %SL:								
at ME	15	1	13	16	13	1[b]	12	15
BPE	16	1	15	17	15	1[b]	14	17
APM	7	1	6	8	7	0	6	8
Widths %SL:								
at BPE	16	1	15	17	16	1	14	17
APM	3	0	2	4	3	0	3	4
% HL:								
ED	27	2	25	31	23	2	20	27
Depth at APM	28	2	26	31	27	1	24	30
%PFO:								
P1	77	11	63	95	98	7	83	110
P2					80	5	72	91
≤17mm SL	47	8[d]	40	58				
>17mm SL	71	5[e]	64	77				
CPLR[f]	97	6[a]	87	103	103	3	99	112

[a]N=7. [b]N=17. [c]N=6. [d]N=3. [e]N=4. [f]ΣF is the sum of lengths of all fins (i.e., P1+P2+D+A+C = ΣF).

[g]CPLR (caudal peduncle length ratio) is OAPHP expressed as % OAPOP.

TABLE A-6. Summary of selected meristics by developmental phase for Gila cypha cultured from brood stock collected from the Little Colorado River, Arizona (Figure 1, Methods). See Figures 4-6 for definitions of abbreviations and methods of counting. N_i is number of specimens out of the total number (N) having modal count. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Protolarvae (N=16)				Flexion Mesolarvae (N=31)				Postflexion Mesolarvae (N=10)				Metalarvae (N=13)				Juveniles (N=26)			
	Mode	N_i	Range Min	Max	Mode	N_i	Range Min	Max	Mode	N_i	Range Min	Max	Mode	N_i	Range Min	Max	Mode	N_i	Range Min	Max
SL,mm			6	9			9	10			10	12			13	20			21	34
TL,mm			7	10			10	12			12	14			16	25			27	44
Myomeres or vertebrae[a]:																				
to OP2													16	8	15	17	15	14	15	16
OD													19	7	18	20	18	8	17	19
PV	29	9	28	30	29	17	28	30	29	7	27	30	28	8	28	29	27	10	26	28
Postvent	18	10	16	18	17	18	16	19	18	5	16	18	17	12	16	17	20	10	19	20
Total	46	9	45	47	46	11	45	48	47	5	45	47	45	7	44	46	47	12	46	47
Principal fin rays:																				
P1													16	5[b]	14	16	16	17	14	16
P2													9	5[b]	9	9	9	26	9	9
D[c]									9	10	9	9	9	13	9	9	9	25	9	10
A[c]									10	8	9	10	10	9	9	10	10	23	9	10
C									19	9	18	19	19	13	19	19	19	26	19	19
Gill rakers[d]:																				
1st gill arch																				
External row																	11	11	9	11
Internal row																	14	11	13	15
Total																	26	8	23	26
2nd gill arch																				
External row																	12	10	12	15
Internal row																	14	12	12	15
Total																	27	9	24	30
3rd gill arch																				
External row																	13	11	11	14
Internal row																	13	12	11	14
Total																	26	11	22	27
4th gill arch																				
External row																	10	10	9	12
Internal row																	8	9	8	12
Total																	21	9	18	24
Total																				
External row																	46	9	43	51
Internal row																	47	9	47	56
Total																	96	9	90	107

[a]For juveniles, vertebra counts on 16 cleared and stained specimens; counts include the four vertebrae of the Weberian complex and the urostylar vertebra. [b]N=8. [c]For postflexion mesolarvae, counts were based on pterygiophores using whole specimens examined with polarized light or cleared and stained specimens. [d]Counts were made on gill arches excised from the left side of 16 cleared and stained specimens (four gill arches per specimen).

TABLE A-7. Summary of selected meristics by developmental phase for Gila cypha cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods). See Figures 4-6 for definitions of abbreviations and methods of counting. N_i is number specimens out of the total number (N) having modal count. Developmental-interval terminology as defined by Snyder and Muth (1988, in press, see Methods).

	Flexion						Postflexion									
	Protolarvae (N=51)		Range		Mesolarvae (N=25)		Range		Mesolarvae (N=6)		Range		Metalarvae (N=12)		Range		Juveniles (N=38)		Range	
	Mode	N_i	Min	Max	Mode	N_i	Min	Max	Mode	N_i	Min	Max	Mode	N_i	Min	Max	Mode	N_i	Min	Max
SL,mm			6	9			9	10			10	14			14	19			22	43
TL,mm			7	10			9	11			11	17			17	25			27	54
Myomeres or vertebrae[a]:																				
to OP2									16	3[b]	16	16	17	7	15	17	15	10	14	16
OD													19	8	17	20	17	9	16	18
PV	29	29	28	30	29	18	28	30	30	3	28	30	29	7	28	30	26	11	25	28
Postvent	17	30	16	19	17	14	17	19	17	5	17	18	17	8	16	19	19	10	19	20
Total	46	26	45	48	46,47	11	45	48	47	4	45	47	46	6	45	47	46	10	44	46
Principal fin rays:																				
P1													16	2[b]	15	16	16	28	15	17
P2													9	3[b]	9	9	9	38	9	9
D[c]									9	6	9	9	9	11	9	10	9	30	9	10
A[c]									10	5	9	10	10	10	9	10	10	30	9	10
C									19	6	19	19	19	12	19	19	19	38	19	19
Gill rakers[d]:																				
1st gill arch																				
External row																	11	9	9	13
Internal row																	13	10	12	16
Total																	24	5	22	29
2nd gill arch																				
External row																	14	6	11	14
Internal row																	13	9	13	16
Total																	27	7	25	29
3rd gill arch																				
External row																	13	7	12	16
Internal row																	13	8	12	15
Total																	25	5	25	30
4th gill arch																				
External row																	12	8	9	15
Internal row																	9	8	9	11
Total																	21	7	18	26
Total																				
External row																	48,51	4	43	55
Internal row																	48	4	47	56
Total																	101	4	90	109

[a]For juveniles, vertebra counts on 14 cleared and stained specimens; counts include the four vertebrae of the Weberian complex and the urostylar vertebra. [b]N=3. [c]For postflexion mesolarvae, counts were based on pterygiophores using whole specimens examined with polarized light or cleared and stained specimens. [d]Counts were made on gill arches excised from the left side of 14 cleared and stained specimens (four gill arches per specimen).

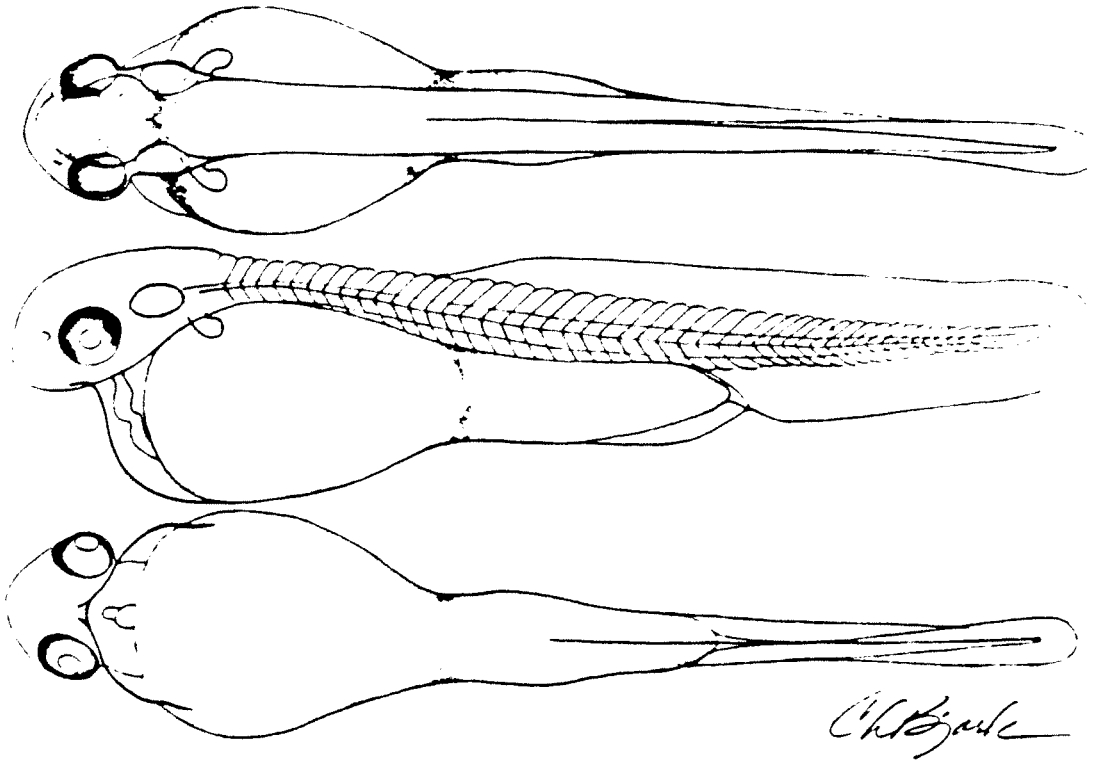
TABLE A-8. Summary of selected meristics by developmental phase for Gila cypha collected from the Little Colorado River, Arizona (Figure 1, Methods). See Figures 4-6 for definitions of abbreviations and methods of counting. N_i is number of specimens out of the total number (N) having modal count. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Metalarvae (N=8)				Juveniles (N=21)			
			Range				Range	
	Mode	N_i	Min	Max	Mode	N_i	Min	Max
SL,mm			13	21			21	45
TL,mm			15	27[a]			28	59[b]
Myomeres or vertebrae[c]:								
to OP2	16	6	15	16	16	3	15	17
OD	17,18	3	17	19	18,19	3	17	19
PV	28	4	26	28	28	4	26	28
Postvent	17,18	3	16	19	18	3	18	20
Total	45	4	44	46	47	4	44	48
Principal fin rays:								
P1	15[d]	3	15	16	16	14	14	17
P2	9[e]	4	8	9	9	19	9	10
D	9	8	9	9	9	17	9	10
A	10	7	10	11	10	16	9	11
C	19	7	18	19	19	20	19	20
Gill rakers[f]:								
1st gill arch								
External row					11,12	2	9	12
Internal row					14	4	14	16
Total					26	3	23	27
2nd gill arch								
External row					13	4	13	14
Internal row					13	3	11	14
Total					26	3	24	28
3rd gill arch								
External row					14,15	2	13	17
Internal row					11	4	12	13
Total					28	3	24	28
4th gill arch								
External row					13	3	12	14
Internal row					10	4	8	10
Total					23	3	20	24
Total								
External row					55	2	49	55
Internal row					46,48	2	46	51
Total					102	2	96	106

[a]N=7. [b]N=17. [c]For juveniles, vertebra counts on 7 cleared and stained specimens; counts include the four vertebrae of the Weberian complex and the urostylar vertebra. [d]N=4. [e]N=5. [f]Counts were made on gill arches excised from the left side of 7 cleared and stained specimens (four gill arches per specimen).

FIGURE A-5. Gila cypha protolarva (sensu Snyder and Muth 1988, in press, see Methods), recently hatched, 6.3 mm standard length, 6.6 mm total length. Cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods).

FIGURE A-6. Gila cypha protolarva (sensu Snyder and Muth 1988, in press, see Methods), 8.4 mm standard length, 8.7 mm total length. Cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods).



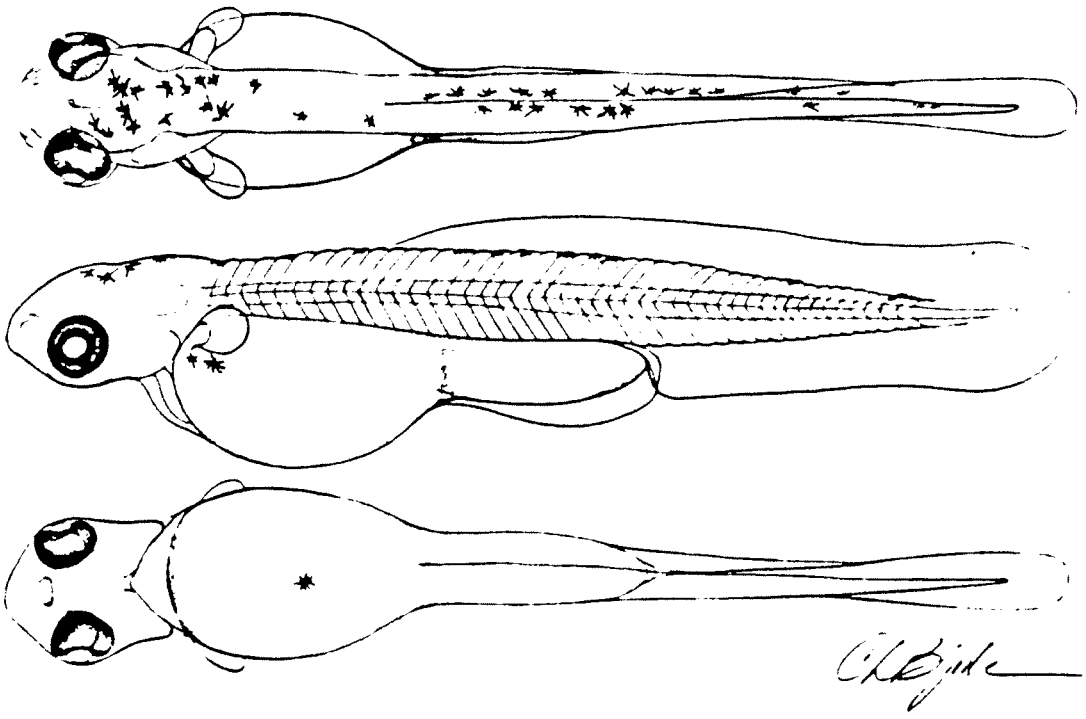
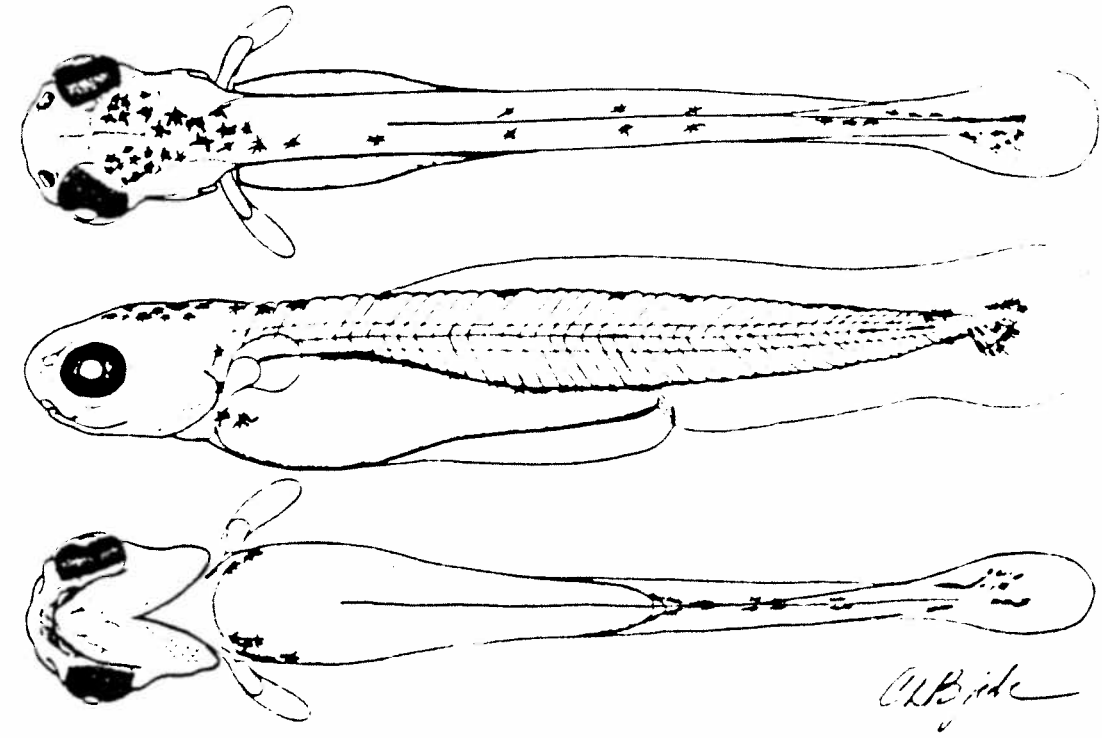


FIGURE A-7. Gila cypha flexion mesolarva (sensu Snyder and Muth 1988, in press, see Methods), recently transformed, 8.9 mm standard length, 9.3 mm total length. Cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods).

FIGURE A-8. Gila cypha postflexion mesolarva (sensu Snyder and Muth 1988, in press, see Methods), 10.6 mm standard length, 11.7 mm total length. Cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods).



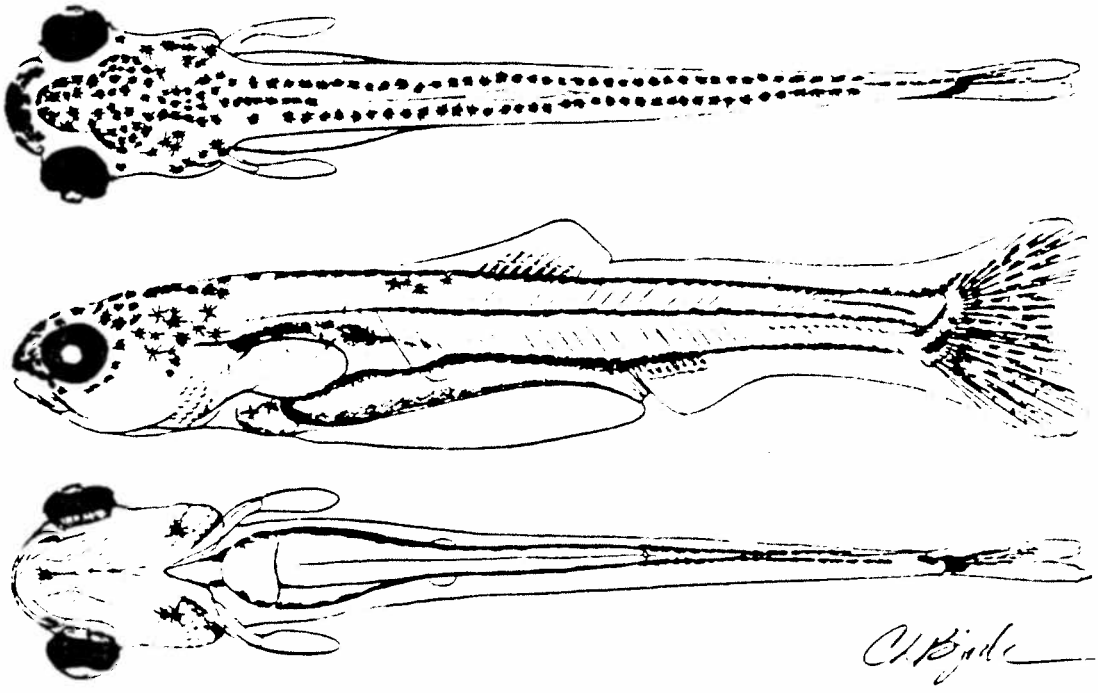
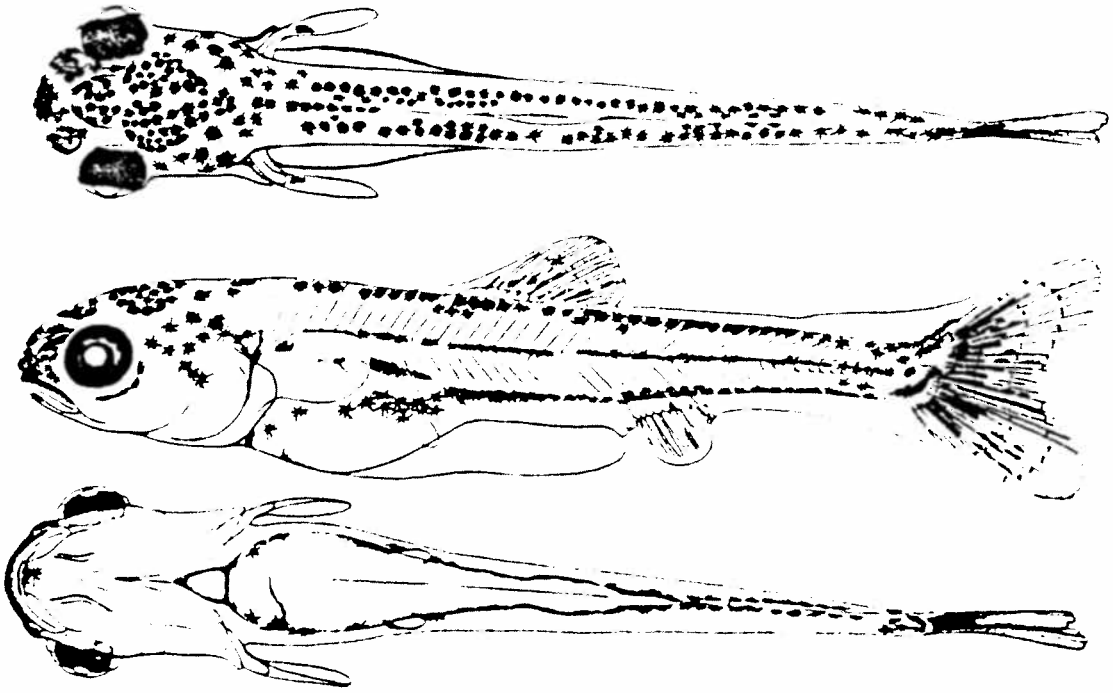


FIGURE A-9. Gila cypha metalarva (sensu Snyder and Muth 1988, in press, see Methods), recently transformed, 12.2 mm standard length, 14.1 mm total length. Cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods).

FIGURE A-10. Gila cypha metalarva (sensu Snyder and Muth 1988, in press, see Methods), 14.8 mm standard length, 18.4 mm total length. Cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods).



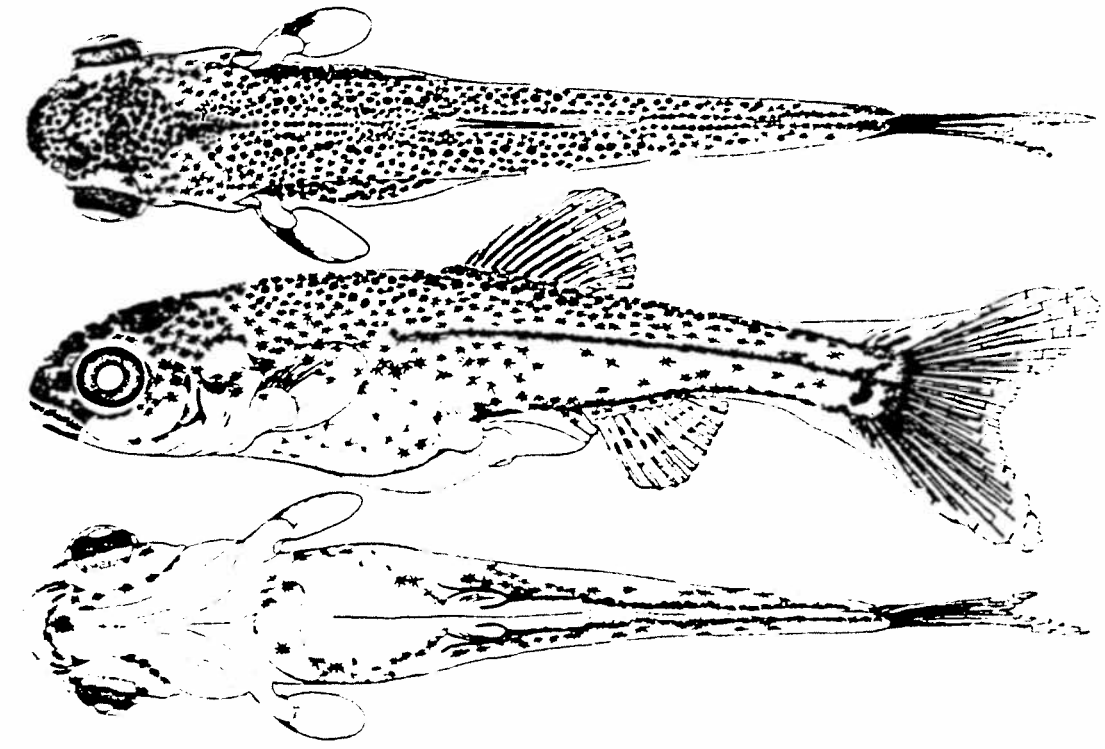
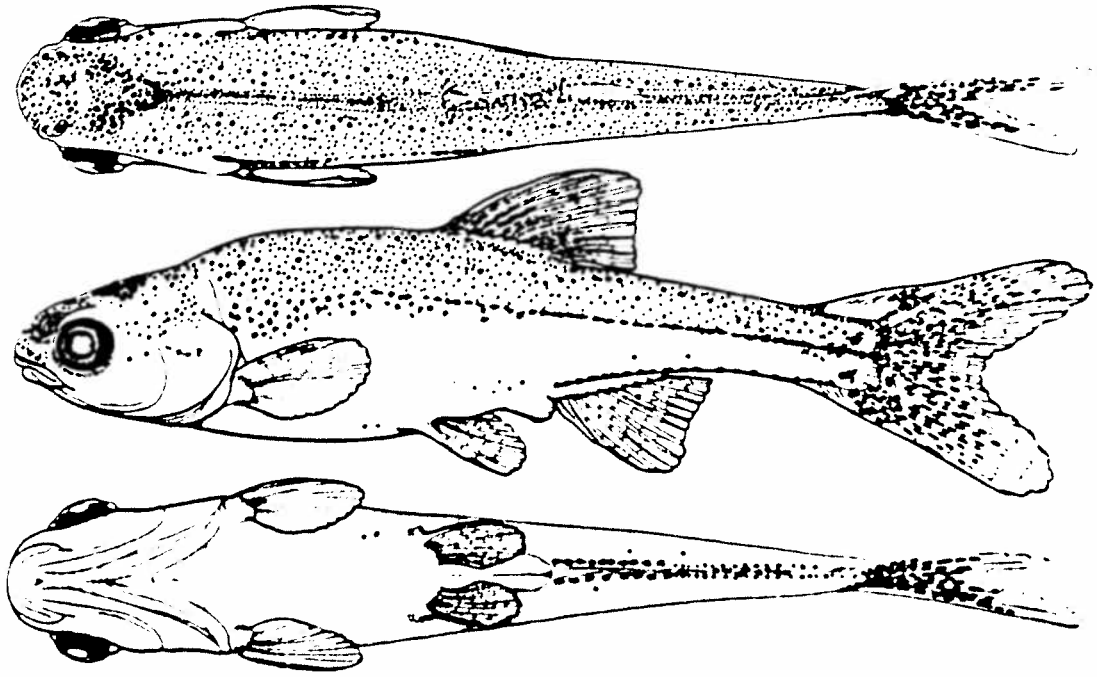


FIGURE A-11. Gila cypha juvenile (sensu Snyder and Muth 1988, in press, see Methods), recently transformed, 20.8 mm standard length, 25.0 mm total length. Cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods).

FIGURE A-12. Gila cypha juvenile (sensu Snyder and Muth 1988, in press, see Methods), 33.6 mm standard length, 44.2 mm total length. Cultured from brood stock collected from the Colorado River, Colorado (Figure 1, Methods).



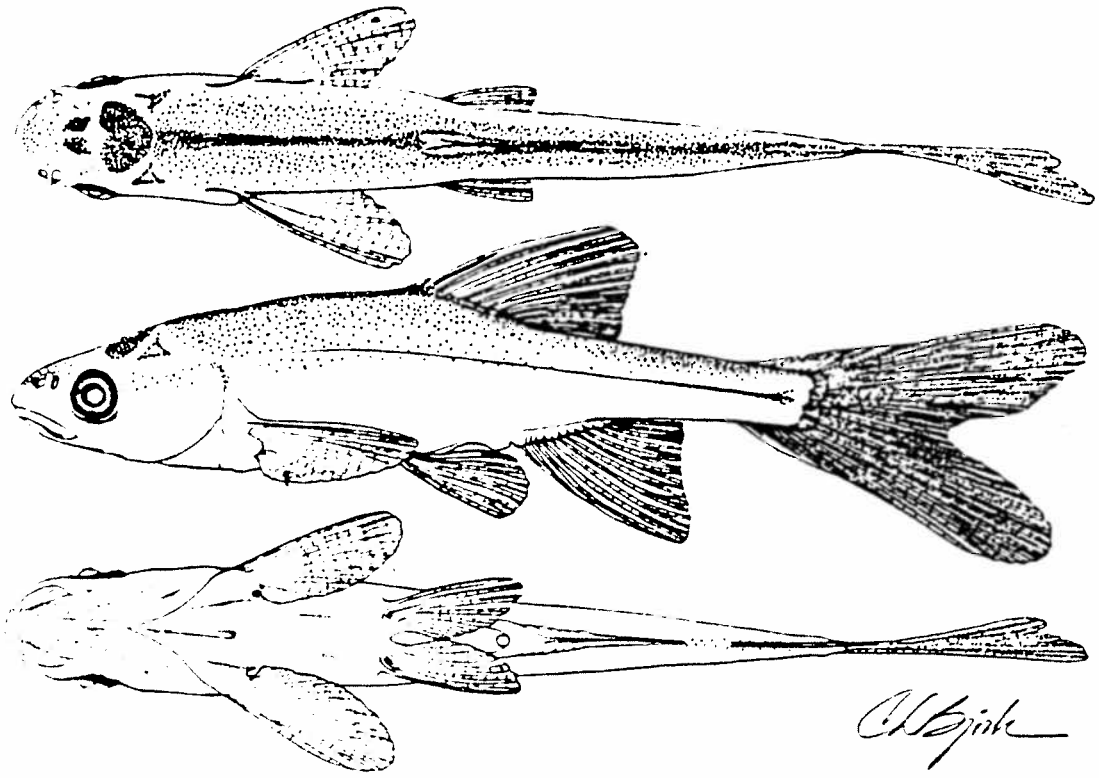
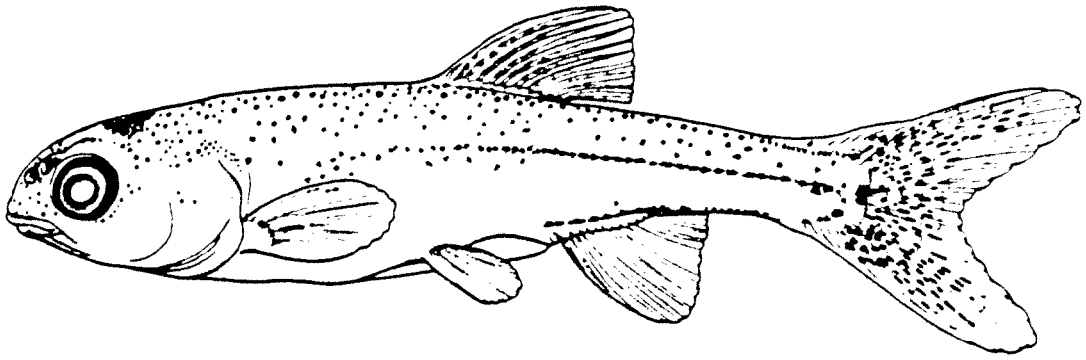


FIGURE A-13. Gila cypha metalarva (sensu Snyder and Muth 1988, in press, see Methods), 14.7 standard length, 19.0 total length. Cultured from brood stock collected from the Little Colorado River, Arizona (Figure 1, Methods).

FIGURE A-14. Gila cypha juvenile (sensu Snyder and Muth 1988, in press, see Methods), recently transformed, 18.3 standard length, 23.3 total length. Cultured from brood stock collected from the Little Colorado River, Arizona (Figure 1, Methods).



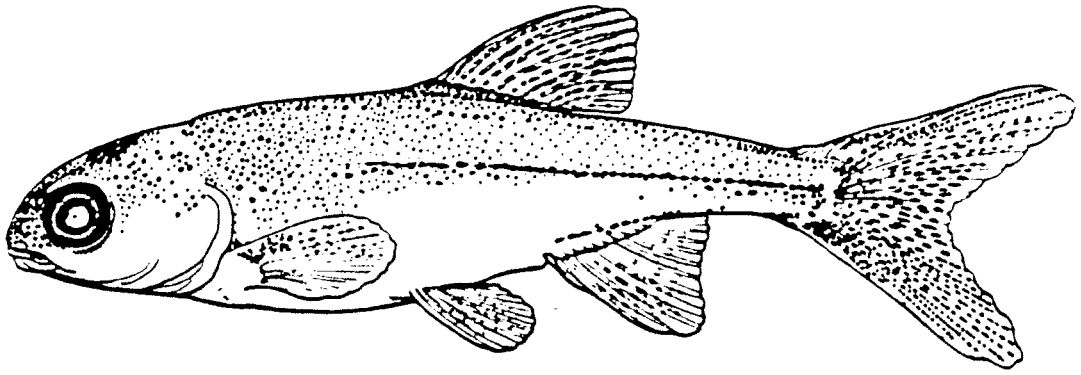
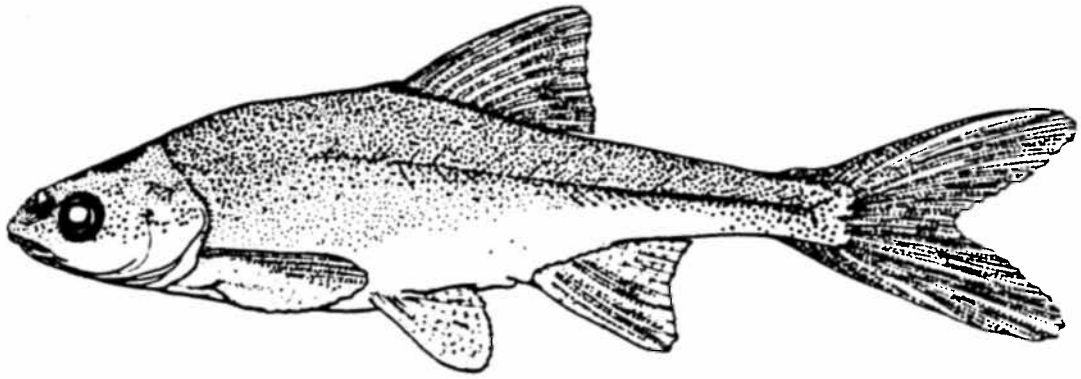


FIGURE A-15. Gila cypha juvenile (sensu Snyder and Muth 1988, in press, see Methods), 37.0 standard length, 46.3 total length. Cultured from brood stock collected from the Little Colorado River, Arizona (Figure 1, Methods).



Bonytail, Gila elegans

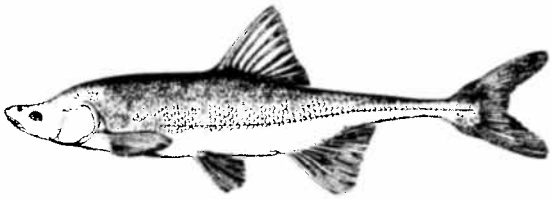


FIGURE A-16. Gila elegans adult (from Behnke and Benson 1983).

Status, Distribution, and Habitat. Species was described by Baird and Girard (1953a). Endangered on federal list of threatened and endangered species; recovery plan has been approved. Listed as protected by Arizona, California, Colorado, Nevada, and Utah. Endemic to the Colorado River Basin. Historically, probably one of the most abundant species in the basin. Past distribution is not known with certainty because of the species' rapid decline prior to extensive fish surveys in the basin. Present distribution extremely restricted. Rarest of the basin's native fishes; probably functionally extinct in the wild. Occurred in main channels of large rivers. Adults have been found in open-river habitats with low to moderate water velocity (e.g., runs, pools, or eddies) and rocky substrate. Young were mostly found in near-shore, low-velocity habitats (e.g., backwaters) with silt, sand, or gravel substrate. In laboratory tests, preferred water temperature was about 24°C.

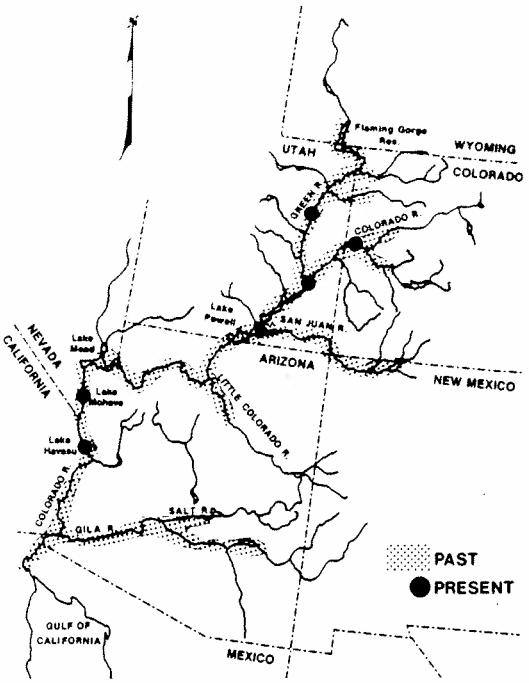


FIGURE A-17. Distribution of Gila elegans

References: Vanicek and Kramer 1969; Minckley 1973; Holden and Stalnaker 1975; Rinne 1976; Joseph et al. 1977; Smith et al. 1979; Behnke et al. 1982; Bulkley et al. 1982; Tyus et al. 1982, 1987; Valdez and Clemmer 1982; Behnke and Benson 1983; Valdez 1985, 1987; Kaeding et al. 1986; Stanford and Ward 1986c; Johnson 1987; USDI 1987; USFWS 1987; Ohmart et al. 1988; Carlson and Muth 1989, in press; CRFRT 1989b.

Adult Diagnosis. Morphology: Gray or olivaceous on dorsal surface, silvery on ventrolateral surfaces. Skull concave anteriorly on dorsal surface arching gradually posteriorly. Mouth terminal to subterminal, (larger specimens) slightly oblique to nearly horizontal, not overhung by snout. Eyes small (eye diameter about 7.0 in head length). Body extremely streamlined, slender, elongate, somewhat compressed. Anterodorsal nuchal hump moderate-high (especially in larger specimens), uniformly arched from head to back. Caudal peduncle extremely slender, long, pencil-like (least depth of caudal peduncle about 5.0-6.5 in head length). Fins large, well-developed, long, falcate; caudal fin deeply forked, extremely long caudal fin lobes. Squamation often incomplete; dorsal and ventral surfaces of body and caudal peduncle scaleless or with minute, deeply embedded scales that lack basal radii. Total length to 35-50 cm. Meristics*: Dorsal fin principal rays = (9)-10-11; anal fin principal rays = (9)-10-11; caudal fin principal rays = (18)-19; pectoral fin rays = 16; pelvic fin rays = 9-10; lateral line scales = 75-88-90-(99); pharyngeal teeth = 2,5-4,2; gill rakers = 23-29-33-36 [(15)-16-18-(21)]; total vertebrae = (46-47)-49-51.

Reproduction: Mature at 4-7 (maybe as young as 2 or 3) years of age. Non-guarding, open-substrate lithophils. Probably spawned during May-early July at water temperatures of 17-21°C. Under hatchery conditions, percent egg hatch was highest at water temperatures of 20-22°C. In laboratory tests, percent egg hatch was highest at water temperatures of 15 and 20°C. Believed to have spawned in eddies or pools over cobble or boulder substrate. Jones and Sumner (1954) observed bonytails spawning over a gravel shelf in Lake Mohave in May. Breeding males have orange-red coloration along ventrolateral surfaces and small tubercles on anterior portion of the body. Breeding colors and tubercles are less pronounced in females. Reported mean fecundity of females injected with a preparation of carp pituitary was about 21,500-52,670 eggs/kg body weight. Egg diameter after fertilization and water hardening ranges from 2.0 to 2.4 mm with a mean of 2.2 mm. Eggs are demersal and adhesive. Young hatch in about 4-7 d after fertilization and swim up in about 2-3 d after hatching at water temperatures of 20-21°C.

*Mean or modal values are underlined, and rare or questionable extremes are enclosed by parentheses. Gill-raker counts are for the first gill arch, both external and internal rows of gill rakers, or for the second gill arch, external row of gill rakers only (enclosed in brackets [ ]). Reported vertebrae counts were adjusted (if needed) to include the four vertebrae of the Weberian complex.

References: Baird and Girard 1853a, 1853b; Miller 1946; Beckman 1952; LaRivers 1962; Sigler and Miller 1963; Holden 1968; Vanicek and Kramer 1969; Baxter and Simon 1970; Holden and Stalnaker 1970; Minckley 1973; Moyle 1976; Rinne 1976; Smith et al. 1979; Balon 1981b; Hamman 1982a, 1985; Valdez and Clemmer 1982; Behnke and Benson 1983; Bosek et al. 1984; Marsh 1985; CRFRT 1989b; original data from this study.

TABLE A-9. Size or age at onset of selected developmental events for Gila elegans as observed under low-power magnification. Fish examined were cultured from brood stock collected from Lake Mohave, Nevada side (Figure 1, Methods). Fish were reared in 18-23-°C water. Age is days after hatching. P = principal rays; R = rudimentary rays; scales are lateral series. See Figure 4 for definitions of other abbreviations and methods of measuring standard and total length (SL and TL). Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

Event or structure	SL (mm)	TL (mm)	Age
Hatched	5-6	7	
Eyes pigmented	prior to hatching		
Yolk assimilated	8-9	9	7-8
Gut looped, 90° bend	14-15	16	24
Finfold absorbed	22	28	
P1 buds formed	6	7	
P2 buds formed	11	12	17
Transition to:			
Flexion mesolarva	8	9	8
Postflexion mesolarva	9	11	17
Metalarva	11	13	<20
Juvenile	22	28	<38

Fin rays or scales	First Formed SL (mm)	First Formed TL (mm)	Last Formed SL (mm)	Last Formed TL (mm)
Dorsal - P	9	10	11	13
Dorsal - R	11	13	13	16
Anal - P	9	10	11	13
Anal - R	12	13	13	16
Caudal - P	8	9	9	11
Caudal - R	9-10	10-11	<23	<29
Pectoral	9-10	11-12	14	17
Pelvic	10-11	11-13	15	18
Scales	<26	<32		

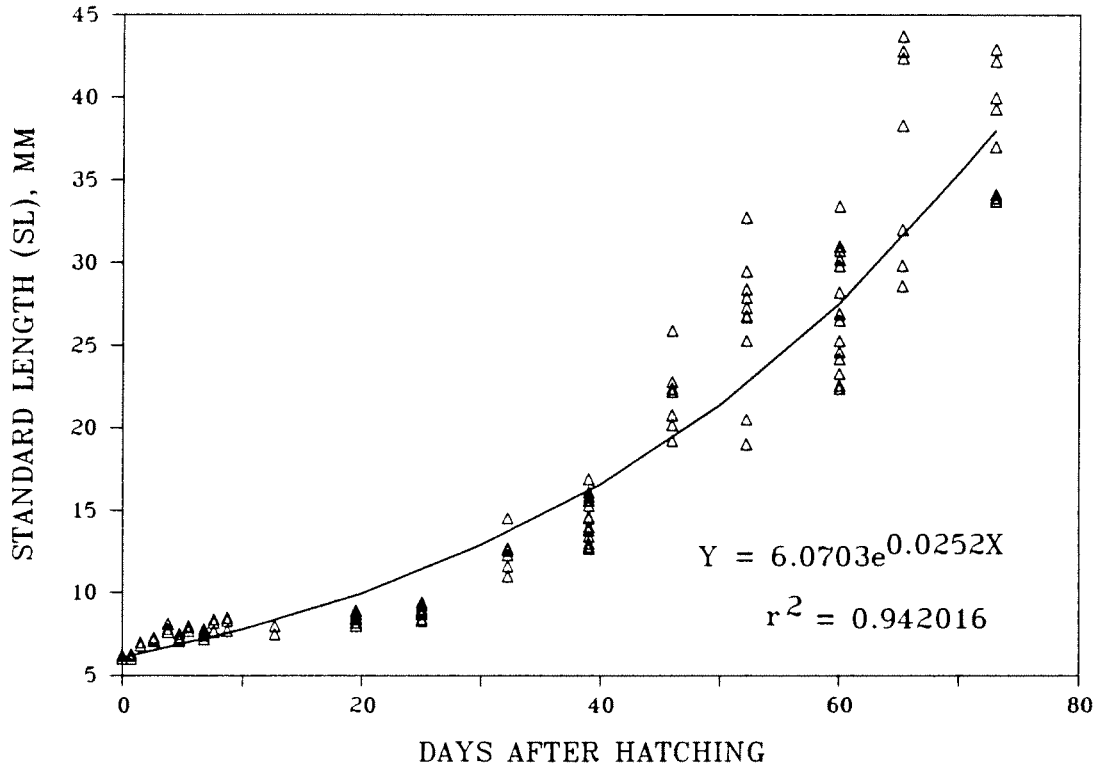


FIGURE A-18. Exponential growth curve for Gila elegans larvae and young-of-the-year juveniles cultured from brood stock collected from Lake Mohave, Nevada side (Figure 1, Methods). Fish were reared in 18-23-°C water. See Figure 4 for methods of measuring SL.

TABLE A-10. Summary of selected morphometrics by developmental phase for Gila elegans cultured from brood stock collected from Lake Mohave, Nevada side (Figure 1, Methods). See Figures 4, 5 for definitions of abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Protolarvae (N=37)				Flexion Mesolarvae (N=20)				Postflexion Mesolarvae (N=4)				Metalarvae (N=34)				Juveniles (N=52)			
	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max
SL,mm	7	0	7	8	9	1	8	9	10	1	9	11	16	3	11	22	31	6	22	44
TL,mm	8	0	7	9	9	1	9	11	12	1	11	13	19	4	13	28	39	8	28	54
Lengths %SL:																				
AS to AE	3	0	2	3	3	0	2	4			3	4[a]					5	0	5	6
≤17mm SL													4	1[b]	3	5				
>17mm SL													5	0[c]	5	6				
PE	9	1	7	10	9	1	8	10	11	0	11	11					12	1	11	13
≤17mm SL													12	1[b]	11	13				
>17mm SL													13	1[c]	12	14				
OP1	18	1	16	21	21	1	19	24	22	0	22	24					24	1	22	26
≤17mm SL													25	1[b]	23	27				
>17mm SL													26	1[c]	24	28				
OP2											44	46[a]	47	1	44	49	45	1	44	47
OPAF			28	38			29	32			29	31			31	55				
ODF			39	42			42	45			43	46			46	48[a]				
OD													52	2	50	57	51	1	49	54
ID													65	2	62	69	65	1	62	66
PV	65	2	62	70	67	2	63	70	67	1	66	69	65	2	62	70				
≤32mm SL																	63	1[d]	61	64
>32mm SL																	63	1[e]	60	65
OA													65	2	63	69	64	1	62	67
IA													77	2	75	85	76	1	74	78
ED	7	0	6	7	7	1	6	8			7	8[a]	8	1	7	9	7	1	6	7
PFO											22	23[a]					21	1	19	23
≤13mm SL													23	0[f]	22	24				
>13mm SL													21	1[g]	19	22				
DB																	14	1	12	15
≤17mm SL													13	1[b]	11	14				
>17mm SL													14	0[c]	14	14				
AB													12	1	10	13	12	1	10	14
CP													35	1	33	38	36	1	34	38
CL							3	4[h]	4	1	3	4					13	1	11	15
≤14mm SL													9	1[i]	7	9				
>14mm SL													12	1[j]	10	14				
P1			4	12			12	13			12	13	14	1	12	15	17	1	15	19
P2											2	3[a]					16	1	15	18
≤13mm SL													6	1[f]	5	8				
>13-≤19mm SL													11	1[k]	10	12				
>19mm SL													15	1[j]	13	16				
D																	22	1	20	24
≤17mm SL													18	1[b]	15	21				
>17mm SL													21	1[c]	20	23				
A																	20	1	18	22
≤17mm SL													16	1[b]	14	17				
>17mm SL													19	0[c]	18	20				
C			4	7			5	15	14	0	14	14					25	1	23	28
≤17mm SL													22	1[b]	19	24				
>17mm SL													25	1[c]	24	26				
ΣF^m																	100	3	94	109
≤17mm SL													78	5[b]	71	89				
>17mm SL													92	5[c]	84	101				
LDR																	19	1	17	21
≤17mm SL													15	1[b]	13	17				
>17mm SL													18	1[c]	17	20				
LAR																	16	1	15	18
≤17mm SL													12	1[b]	10	14				
>17mm SL													15	1[c]	15	16				

TABLE A-10. Continued.

	Protolarvae (N=37) Mean±SD		Range Min	Max	Flexion Mesolarvae (N=20) Mean±SD		Range Min	Max	Postflexion Mesolarvae (N=4) Mean±SD		Range Min	Max	Metalarvae (N=34) Mean±SD		Range Min	Max	Juveniles (N=52) Mean±SD		Range Min	Max
Depths %SL:																				
at ME	11	1	10	12	12	1	10	13	13	0	13	13	14	1	12	16	13	1	12	15
BPE	12	1	10	13	13	1	12	14	14	0	14	14	16	1	15	17	16	1	15	17
APM	4	0	4	4	4	1	3	5	5	0	5	6					6	0	6	7
≤13mm SL													6	0[h]	6	7				
>13mm SL													7	0[n]	6	7				
Widths %SL:																				
at BPE	12	1	11	14	13	1	11	14	13	1	13	14	15	1	14	16	15	1	14	16
APM	3	0	2	3	2	0	2	3	3	1	2	3					4	0	3	4
≤17mm SL													3	0[b]	2	4				
>17mm SL													3	0[c]	3	4				
% HL:																				
ED	36	3	31	42	34	3	29	39	31	1	31	33	31	2	27	34	27	2	23	31
Depth at APM	21	2	17	25	20	2	17	23	23	1	21	24	26	1	23	29	25	1	23	27
% PFO:																				
P1											56	58[a]					80	5	70	90
≤19mm SL													61	4[o]	55	70				
>19mm SL													75	3[p]	68	80				
P2											8	13[a]					74	4	69	80
≤15mm SL													29	6[q]	17	35				
>15-≤19mm SL													58	4[f]	52	62				
>19mm SL													73	2[h]	63	76				
CPLR[r]																	94	4	87	102
≤17mm SL													86	4[b]	78	93				
>17mm SL													97	2[c]	93	100				

[a]N=2. [b]N=24. [c]N=10. [d]N=32. [e]N=19. [f]N=11. [g]N=23. [h]N=7. [i]N=14. [j]N=20. [k]N=15. [l]N=8. [m]ΣF is the sum of lengths of all fins (i.e., P1+P2+D+A+C = ΣF). [n]N=27. [o]N=28. [p]N=6. [q]N=16. [r]CPLR (caudal peduncle length ratio) is OAPHP expressed as % OAPOP.

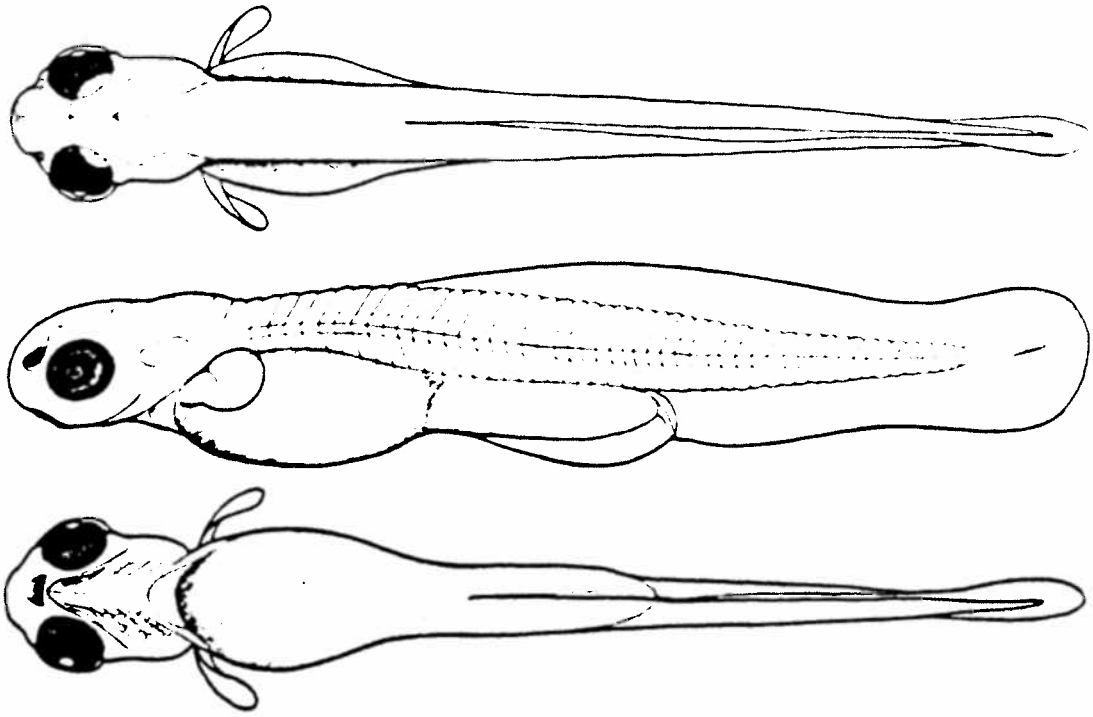
TABLE A-11. Summary of selected meristics by developmental phase for Gila elegans cultured from brood stock collected from Lake Mohave, Nevada side (Figure 1, Methods). See Figures 4-6 for definitions of abbreviations and methods of counting. N_i is number of specimens out of the total number (N) having modal count. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Protolarvae (N=37)				Flexion Mesolarvae (N=20)				Postflexion Mesolarvae (N=4)				Metalarvae (N=34)				Juveniles (N=52)			
			Range				Range				Range				Range				Range	
	Mode	N_i	Min	Max	Mode	N_i	Min	Max	Mode	N_i	Min	Max	Mode	N_i	Min	Max	Mode	N_i	Min	Max
SL,mm			7	8			8	9			9	11			11	22			22	44
TL,mm			7	9			9	11			11	13			13	28			28	54
Myomeres or vertebrae[a]:																				
to OP2									17	2[b]	17	17	17	26	16	18	16	10	15	17
OD													20	17	19	22	20	9	19	20
PV	30	35	29	31	30	15	30	32	30	4	30	30	30	23	29	32	28	9	27	29
Postvent	21	23	20	21	21	12	19	21	21	3	20	21	20	23	19	21	22	9	21	23
Total	51	24	49	51	51	13	50	52	51	3	50	51	50	25	49	52	50	10	49	51
Principal fin rays:																				
P1													16	10[c]	14	17	16	35	14	17
P2													9	15[c]	9	9	9	51	8	9
D[d]									10	4	10	10	10	34	10	10	10	51	10	11
A[d]									10	4	10	10	10	27	10	11	10	31	10	11
C									19	2	16	19	19	28	17	20	19	50	18	19
Gill rakers[e]:																				
1st gill arch																				
External row																	13	10	13	15
Internal row																	19	8	18	20
Total																	31,33	5	31	34
2nd gill arch																				
External row																	18	15	18	19
Internal row																	19	10	18	21
Total																	37	9	34	39
3rd gill arch																				
External row																	19	12	18	20
Internal row																	19	7	16	20
Total																	38	6	35	39
4th gill arch																				
External row																	18	6	15	20
Internal row																	13	16	13	13
Total																	31	6	28	33
Total																				
External row																	68,70	4	65	72
Internal row																	69,70	5	66	73
Total																	133	5	133	143

[a]For juveniles, vertebra counts on 16 cleared and stained specimens; counts include the four vertebrae of the Weberian complex and the urostylar vertebra. [b]N=2. [c]N=15. [d]For postflexion mesolarvae, counts were based on pterygiophores using whole specimens examined with polarized light or cleared and stained specimens. [e]Counts were made on gill arches excised from the left side of 16 cleared and stained specimens (four gill arches per specimen).

FIGURE A-19. Gila elegans protolarva (sensu Snyder and Muth 1988, in press, see Methods), 7.0 mm standard length, 7.5 mm total length. Cultured from brood stock collected from Lake Mohave, Nevada side (Figure 1, Methods).

FIGURE A-20. Gila elegans mesolarva (sensu Snyder and Muth 1988, in press, see Methods), 9.4 mm standard length, 10.7 mm total length. Cultured from brood stock collected from Lake Mohave, Nevada side (Figure 1, Methods).



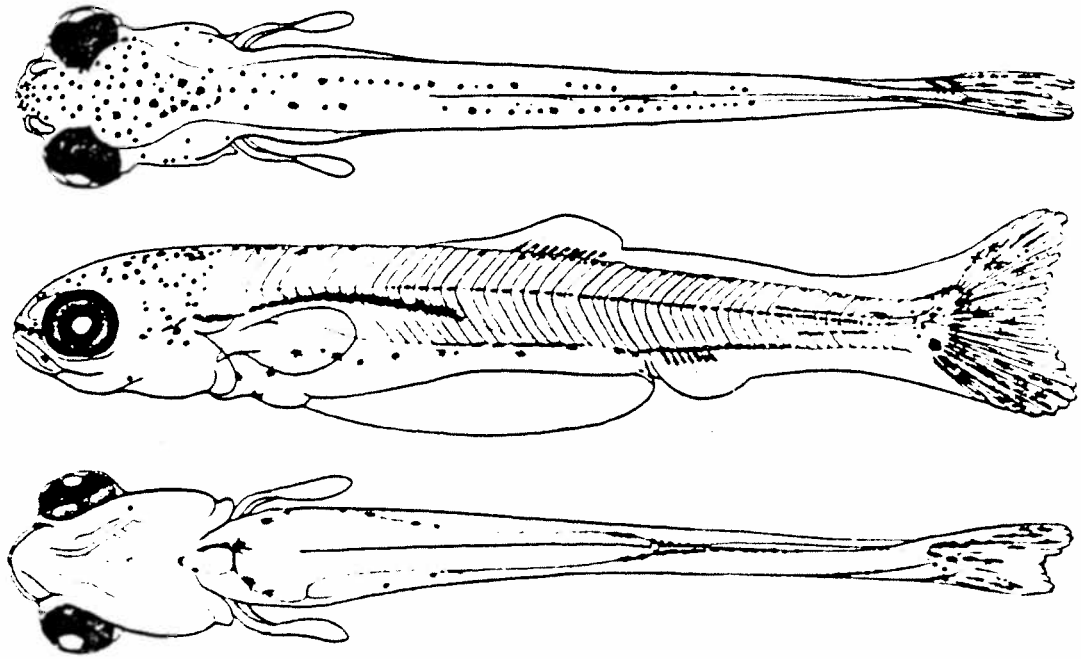
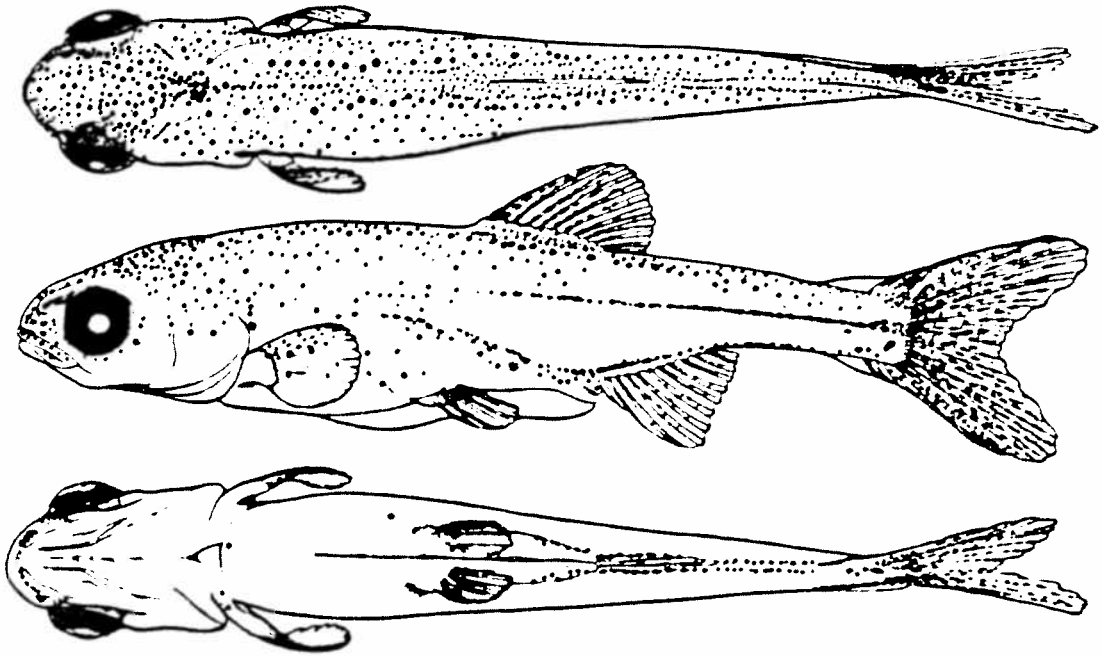
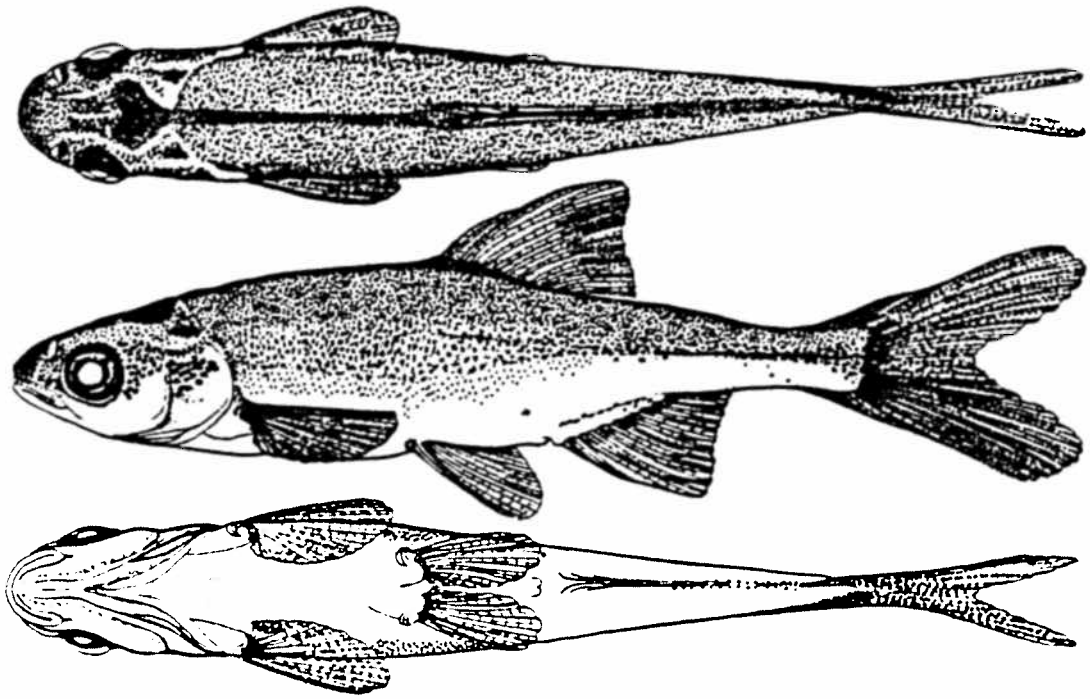


FIGURE A-21. Gila elegans metalarva (sensu Snyder and Muth 1988, in press, see Methods), 15.0 mm standard length, 18.2 mm total length. Cultured from brood stock collected from Lake Mohave, Nevada side (Figure 1, Methods).

FIGURE A-22. Gila elegans juvenile (sensu Snyder and Muth 1988, in press, see Methods), 34.0 mm standard length, 42.7 mm total length. Cultured from brood stock collected from Lake Mohave, Nevada side (Figure 1, Methods).





Colorado Roundtail Chub, Gila robusta robusta

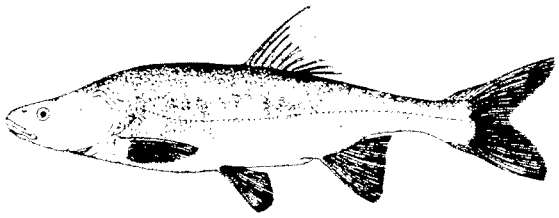


FIGURE A-23. Gila robusta robusta adult (from Behnke and Benson 1983).

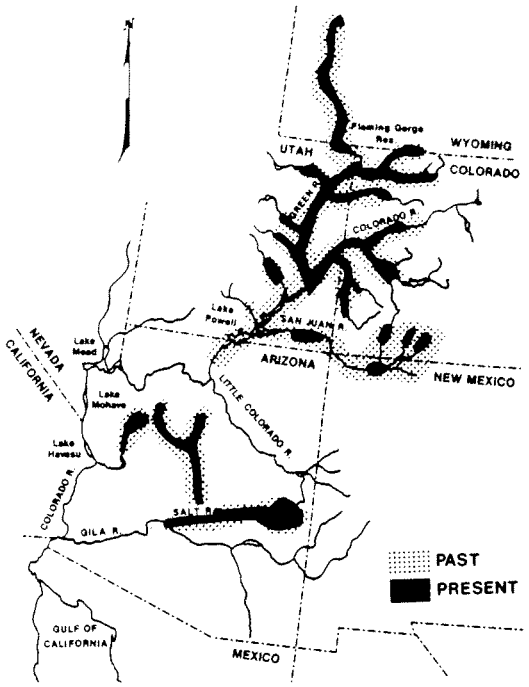


FIGURE A-24. Distribution of Gila robusta robusta.

Status, Distribution, and Habitat. Species was described by Baird and Girard (1953a). The robusta subspecies is one of at least four recognized subspecies of Gila robusta. Listed as protected by New Mexico and Utah, and listed as a fish of special concern by Arizona and Wyoming. Endemic to the Colorado River Basin. Widespread, rare to abundant where found. Occurs in warm streams and larger rivers. Adults have been collected in various habitats, from riffles to pools to backwaters. Typically found in pools, eddies, or shallow runs with silt-cobble substrate and adjacent to moderate- to high-velocity areas; often in association with boulders, overhanging cliffs, or vegetation in smaller streams. Young mostly found in near-shore, low-velocity habitats (e.g., eddies, backwaters, or embayments) with silt, sand, gravel, or boulder substrate.

References: Vanicek and Kramer 1969; Minckley 1973; Holden and Stalnaker 1975; Rinne 1976; Joseph et al. 1977; Carlson et al. 1979; Smith et al. 1979; Lee et al. 1980; Behnke et al. 1982; Tyus et al. 1982; Stanford and Ward 1986c; Johnson 1987; Carlson and Muth 1989.

Adult Diagnosis. Morphology: Gray or olivaceous on dorsal surface, silvery on ventrolateral surfaces. Skull may be slightly depressed, flattened, or rounded on dorsal surface. Mouth terminal to subterminal, slightly oblique to nearly horizontal, not overhung by snout. Eyes small (eye diameter about 8.0 in head length). Body moderately streamlined, elongate, rounded, somewhat compressed; back may be slightly arched in large specimens. Caudal peduncle moderately robust, relatively deep; least depth of caudal peduncle about 3.0-4.3 (perhaps 4.9) in head length. Fins small to moderately large, rounded, slightly falcate. Squamation complete; scales small, basal radii (if present) poorly developed. Total length to 25-50 cm. Meristics*: Dorsal fin principal rays = (8)-9-(10); anal fin principal rays = (7)-8-9-(10); caudal fin principal rays = 19; pectoral fin rays = 15; pelvic fin rays = 9-10; lateral line scales = (73)-75-79-86; pharyngeal teeth = 2,5-4,2; gill rakers = 20-23-25-28 [12-13-15]; total vertebrae = (43)-45-46-(48-49).

Reproduction. Mature at 4-5 years of age. Non-guarding, open-substrate lithophils. Spawn during late May-late July at water temperatures of 16-20°C (typically 18°C or higher). Under laboratory conditions, egg hatching success exceeded 90% at a water temperature of 19°C. Spawn in shallow pools or eddies over gravel or cobble substrate. Breeding males have orange-red coloration along ventrolateral surfaces and small tubercles on anterior portion of body. Breeding colors and tubercles are less pronounced in females. Reported fecundity of manually stripped females ranged from about 39,500 to 41,350 eggs/kg body weight. Diameter of mature eggs before fertilization ranges from 1.6 to 2.4 mm with a mean of 2.2 mm. Egg diameter after fertilization and water hardening ranges from 2.7 to 3.1 mm with a mean of 2.8 mm. Eggs are demersal and adhesive. Young hatch in about 5-6 d after fertilization and swim up in about 3-5 d after hatching at water temperatures of 19-20°C.

*Mean or modal values are underlined, and rare or questionable extremes are enclosed by parentheses. Gill-raker counts are for the first gill arch, both external and internal rows of gill rakers, or for the second gill arch, external row of gill rakers only (enclosed in brackets [ ]). Reported vertebrae counts were adjusted (if needed) to include the four vertebrae of the Weberian complex.

References: Baird and Girard 1853a, 1853b; Jordan and Evermann 1896; Miller 1946; Beckman 1952; Gaufin et al. 1960; Uyeno 1961; LaRivers 1962; Sigler and Miller 1963; Holden 1968; Vanicek and Kramer 1969; Baxter and Simon 1970; Holden and Stalnaker 1970; Minckley 1973; Rinne 1976; Joseph et al. 1977; Carlson et al. 1979; Smith et al. 1979; Balon 1981b; Behnke et al. 1982; Behnke and Benson 1983; Muth et al. 1985.

TABLE A-12. Size or age at onset of selected developmental events for Gila robusta robusta as observed under low-power magnification. Fish examined were cultured from brood stock collected from the Yampa River, Colorado (Figure 1, Methods). Eggs were incubated and fish were reared in 19-20-°C water. Embryological developmental stages conform to the convention of Balinsky (1948). Age is hours after fertilization for embryos and days after hatching for larvae. P = principal rays; R = rudimentary rays. See Figure 4 for definitions of other abbreviations and methods of measuring standard and total length (SL and TL). Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods). Rare or questionable extremes in parentheses. Some of these data were first reported by Muth et al. (1985).

Event or structure	Age	Stage	SL (mm)	TL (mm)
Embryology:				
Cleavage	4	3		
Blastula	20	11		
Late gastrula	36	14		
Late neurula	44	16		
Oval eyes	56	19		
Early tail-bud	60	20		
Finfold	92	23		
Pigmented eyes	108	24		
Hatched			7(8)	8(9)
Yolk assimilated	9		10	11
Gut looped, 90° bend	26		12-13	15-16
Finfold absorbed			19	24
P1 buds formed			7	8
P2 buds formed	17		11	13

Event or structure	SL (mm)	TL (mm)	Age	SL (mm)	TL (mm)
Transition to:					
Flexion mesolarva	9-10	11	9		
Postflexion mesolarva	11	12-13	15		
Metalarva	12	15	18		
Juvenile	19	24	<50		
Fin rays:	First formed			Last formed	
Dorsal - P	10	11-12		12	15
Dorsal - R	12	14		13	16
Anal - P	10	12		12	15
Anal - R	13	15		<14	<18
Caudal - P	9-10	11		11	12-13
Caudal - R	11	12		<20	<25
Pectoral	11	13		14-15	18-19
Pelvic	12	14		14-15	18-19

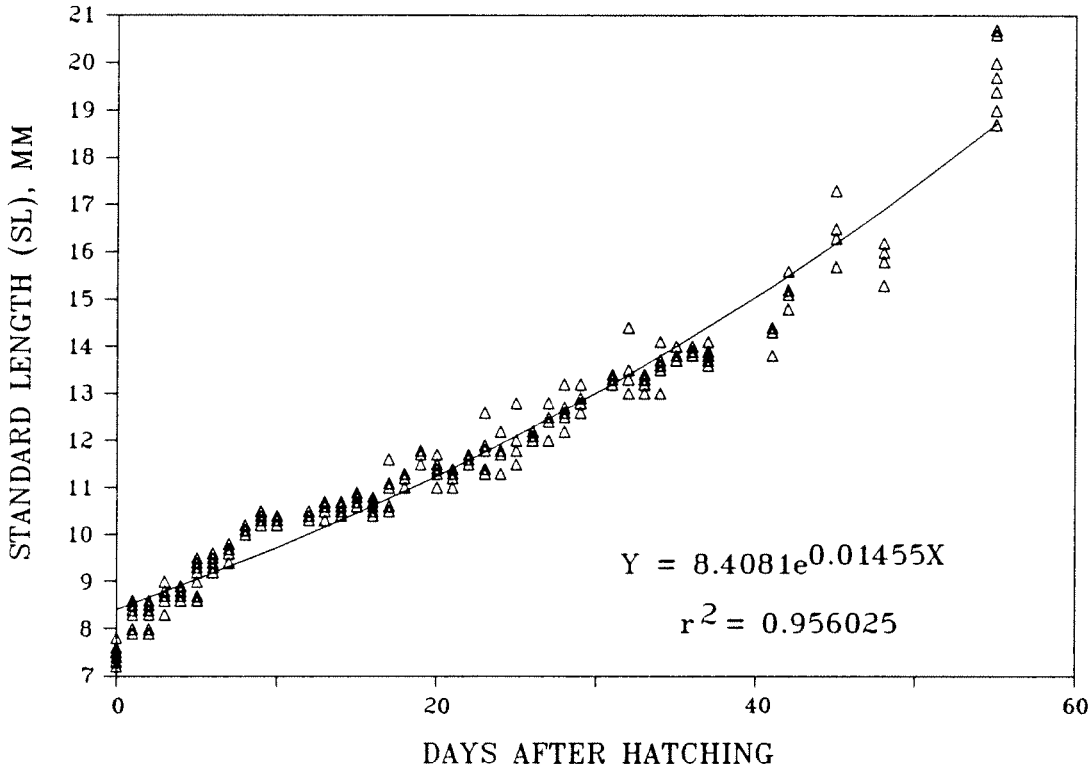


FIGURE A-25. Exponential growth curve for Gila robusta robusta larvae and young-of-the-year juveniles cultured from brood stock collected from the Yampa River, Colorado (Figure 1, Methods). Fish were reared in 19-20-°C water. See Figure 4 for methods of measuring SL.

TABLE A-13. Size at onset of selected developmental events for Gila robusta robusta as observed under low-power magnification. Fish examined were collected from the Yampa River, Colorado (Figure 1, Methods). Fish were sampled in near-shore, low-velocity habitats with 18-24-°C water. P = principal rays; R = rudimentary rays; scales are lateral series. See Figure 4 for definitions of other abbreviations and methods of measuring standard and total length (SL and TL). Developmental interval-terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods). Rare or questionable extremes in parentheses.

Event or structure	SL (mm)	TL (mm)	Fin rays or scales	First Formed SL (mm)	First Formed TL (mm)	Last Formed SL (mm)	Last Formed TL (mm)
Yolk assimilated	9	11	Dorsal - P	10	11	13	15
Gut looped, 90° bend	13	15	Dorsal - R	12	14	14	17-18
Finfold absorbed	20	25	Anal - P	10	12	13	15
P2 buds formed	12	13	Anal - R	<13	<16	<16	<19
Transition to:			Caudal - P	(8)9	(9)11	11	12
Flexion mesolarva	(8)9	(9)11	Caudal - R	11	12-13	<22	<27
Postflexion mesolarva	11	12	Pectoral	11-12	13-14	14	17
Metalarva	13	15	Pelvic	13	15	16	19
Juvenile	20	26	Scales	<25	<30		

TABLE A-14. Size at onset of selected developmental events for Gila robusta robusta as observed under low-power magnification. Fish examined were collected from the White River, Colorado (Figure 1, Methods). Fish were sampled in near-shore, low-velocity habitats with 17-24-°C water. P = principal rays; R = rudimentary rays; scales in lateral series. See Figure 4 for definitions of other abbreviations and methods of measuring standard and total length (SL and TL). Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

Event or Structure	SL (mm)	TL (mm)	Fin rays or scales	First Formed SL (mm)	First Formed TL (mm)	Last Formed SL (mm)	Last Formed TL (mm)
Yolk assimilated	10	11	Dorsal - P	10	11	12	14
Gut looped, 90° bend	12	15	Dorsal - R	<12	<15	14	17
Finfold absorbed	20	26	Anal - P	10	12	12	14
P2 buds formed	<12	<14	Anal - R	<12	<15	<15	<18
Transition to:			Caudal - P	9	10	10-11	12
Flexion mesolarva	9	10	Caudal - R	11	13	<22	<27
Postflexion mesolarva	10-11	12	Pectoral	12-13	14-15	15	18
Metalarva	13	14	Pelvic	13	15	17	21
Juvenile	20	26	Scales	<25	<30		

TABLE A-15. Summary of selected morphometrics by developmental phase for Gila robusta robusta cultured from brood stock collected from the Yampa River, Colorado (Figure 1, Methods). See Figures 4, 5 for definitions of abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Protolarvae (N=20)		Range		Flexion Mesolarvae (N=8)		Range		Postflexion Mesolarvae (N=12)		Range		Metalarvae (N=20)		Range		Juveniles (N=20)		Range	
	Mean	±SD	Min	Max	Mean	±SD	Min	Max	Mean	±SD	Min	Max	Mean	±SD	Min	Max	Mean	±SD	Min	Max
SL,mm	8	1	7	10	10	0	10	11	11	0	11	12	14	2	12	17	20	1	19	21
TL,mm	9	1	8	10	11	0	11	12	13	1	12	14	18	3	15	22	25	1	24	26
Lengths %SL:																				
AS to AE	3	0	2	3	4	0	3	4	4	0	4	5	5	0	4	6	5	1	5	6
PE	9	1	8	10	11	1	11	12	12	1	11	13	13	1	11	15	14	1	13	16
OP1	18	1	17	20	22	1	19	23	25	1	22	26	27	1	25	28	27	1	25	28
OP2									48	1[a]	47	50	52	1	49	54	50	1	49	52
OPAF			29	55			29	37			33	41			39	59				
ODF			26	39			40	45			43	47			50	53[a]				
OD													54	1	52	55	53	1	52	55
ID													66	1	63	68	66	1	64	69
PV	69	1	67	72	68	1	67	69	70	1	69	72	69	2	67	73	66	2	64	68
OA													68	2	65	72	67	2	64	68
IA													78	1	76	79	76	1	75	78
ED	7	1	5	8	8	0	7	8	8	1	7	8	8	0	7	9	9	0	9	10
PFO									24	1[a]	23	25	24	1	22	26	23	1	22	25
DB													12	1	11	13	13	1	12	14
AB													9	1	9	11	10	0	10	11
CP													32	1	30	34	34	1	32	36
CL									3	1	3	6	10	1	9	11	11	1	10	11
P1			4	8			10	13			13	14	16	1	15	17	16	0	16	16
P2											2	4[b]	6	1	5	8	9	0	9	10
D													18	0	17	19	19	0	18	19
A													15	1	13	16	17	1	16	18
C			3	6			6	12	17	2	14	21	24	2	21	27	27	0	26	27
ΣF[c]													79	4	73	86	88	1	87	90
LDR													14	1	11	16	17	1	15	17
LAR													11	1	10	13	14	1	13	16
Depths %SL:																				
at ME	11	1	10	12	12	1	11	13	13	1	12	13	15	1	14	16	16	1	15	18
BPE	11	0	10	11	13	1	10	14	14	1	14	15	17	1	16	18	18	1	17	19
APM	4	0	3	5	4	0	4	5	6	0	5	6	7	0	6	8	8	0	7	8
Widths %SL:																				
at BPE	10	2	8	13	13	1	12	14	15	1	14	16	17	1	16	19	18	1	17	18
APM	3	1	3	4	3	0	3	3	3	0	3	4	4	1	3	5	5	0	4	5
% HL:																				
ED	36	3	29	44	36	4	29	42	32	3	28	38	31	2	25	34	33	1	31	36
Depth at APM	22	3	15	27	20	1	17	23	23	1	21	25	27	1	25	29	29	1	26	32
% PFO:																				
P1											52	59[a]	64	3	59	69	69	2	64	73
P2											7	19[a]	26	4	21	33	42	2	40	47
CPLR[d]													75	4	70	80	85	3	82	94

[a]N=5. [b]N=10. [c]ΣF is sum of all fin lengths (i.e., P1+P2+D+A+C=ΣF). [d]CPLR (caudal peduncle length ratio) is OAPHP expressed as % OAPOP.

TABLE A-16. Summary of selected morphometrics by developmental phase for Gila robusta robusta collected from the Yampa River, Colorado (Figure 1, Methods). See Figures 4, 5 for definitions of abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Flexion Mesolarvae (N=5)				Postflexion Mesolarvae (N=5)				Metalarvae (N=13)				Juveniles (N=14)			
	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max
SL,mm	10	1	9	11	12	1	11	12	15	2	13	19	39	7	20	50
TL,mm	11	0	11	12	13	1	12	14	18	2	15	23	49	9	25	62
Lengths %SL:																
AS to AE	3	1	2	5	4	1	3	4	6	1	6	9	7	1	6	8
PE	11	1	10	12	11	1	10	13	14	1	13	16	14	1	12	15
OP1	22	1	19	24	23	1	23	25	28	1	27	31	27	1	25	28
OP2							45	45[a]	51	2	48	54	50	1	47	52
OPAF			30	33			33	36			39	56				
ODF			44	48			47	50								
OD									55	1	53	57	54	1	52	57
ID									66	1	64	68	66	2	64	68
PV	69	2	67	71	70	0	70	70	68	2	65	71	66	1	64	68
OA									69	1	66	71	67	1	65	69
IA									78	1	76	80	78	1	75	80
ED	8	1	7	9	7	0	7	8	7	0	7	9	7	0	6	7
PFO							23	24[a]	23	1	20	24	23	1	22	24
DB									11	1	10	12	12	1	10	13
AB									9	1	9	11	10	1	9	11
CP									31	1	29	34	33	1	31	35
CL					3	1	2	3	8	2	6	10	11	1	10	12
P1			10	13			12	14	14	1	13	16	16	1	14	18
P2							2	3[a]	6	2	4	9	14	1	10	15
D									17	1	17	18	20	1	18	21
A									15	1	13	16	18	1	16	19
C			6	13	12	2	10	16	21	2	18	24	25	1	23	27
ΣF[b]									69	5	62	78	93	2	89	96
LDR									13	1	11	15	18	1	16	19
LAR									11	2	8	14	16	1	14	17
Depths %SL:																
at ME	12	1	11	13	12	1	11	13	14	1	13	15	14	1	13	16
BPE	14	1	12	15	14	1	13	15	16	1	14	17	16	1	15	18
APM	5	1	4	6	6	0	5	6	8	1	7	9	8	0	7	9
Widths %SL:																
at BPE	13	0	13	13	14	0	14	15	16	0	15	17	15	1	14	16
APM	3	0	3	3	3	0	3	4	4	0	3	4	4	1	4	5
% HL:																
ED	35	5	30	41	32	1	31	35	26	2	23	30	25	1	23	27
Depth at APM	22	2	18	24	24	1	22	25	29	2	26	33	29	1	26	30
% PFO:																
P1							54	59[a]	63	5	57	74	72	5	63	81
P2							8	14[a]	27	6	20	40	60	6	41	66
CPLR[c]									78	5	70	86	82	3	78	89

[a]N=2. [b]ΣF is the sum of lengths of all fins (i.e., P1+P2+D+A+C = ΣF). [c]CPLR (caudal peduncle length ratio) is OAPHP expressed as % OAPOP.

TABLE A-17. Summary of selected morphometrics by developmental phase for Gila robusta robusta collected from the White River, Colorado (Figure 1, Methods). See Figures 4, 5 for definitions of abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Flexion Mesolarvae (N=5)				Postflexion Mesolarvae (N=5)				Metalarvae (N=22)				Juveniles (N=19)			
	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max	Mean±SD		Range Min	Max
SL,mm	10	0	9	11	11	0	11	12	15	2	12	20	29	6	20	39
TL,mm	11	1	10	12	13	0	12	13	19	3	14	25	36	7	26	49
Lengths %SL:																
AS to AE	4	1	3	5	5	0	4	5	6	0	6	7	6	0	6	7
PE	11	1	10	12	11	0	10	12	13	1	12	15	13	1	12	14
OP1	21	1	19	24	24	1	23	25	28	1	25	30	27	1	24	29
OP2									51	1	49	54	49	2	46	52
OPAF			28	35			34	37			40	55				
ODF			42	48			46	50								
OD									56	1	53	58	54	1	52	56
ID									66	1	64	69	65	1	63	67
PV	66	1	65	68	68	1	67	68	66	2	63	70	65	2	62	68
OA									66	1	64	70	65	1	64	68
IA									78	2	75	81	76	1	75	79
ED	7	0	6	7	7	0	6	7	7	1	7	8				
<25mm SL													7	0[a]	7	8
≥25mm SL													6	0[b]	6	7
PFO									23	1	21	26	22	1	21	25
DB									11	1	10	12	11	1	11	13
AB									11	1	10	13	11	1	10	13
CP									34	1	32	36	35	1	32	36
CL			3	4[c]	6	0	5	6	9	2	6	12	12	1	9	15
P1			10	13			13	14	14	1	12	16	17	1	15	18
P2													14	1	12	15
≤17mm SL									7	2[d]	4	9				
>17mm SL									12	1[e]	11	13				
D									19	1	18	21	21	1	19	23
A									17	1	15	18	18	1	16	19
C			5	13	13	1	13	14	23	2	20	28	26	2	21	29
ΣF[f]									80	7	63	91	94	3	86	100
LDR									15	1	14	17	18	1	17	20
LAR									13	1	11	15	16	1	15	18
Depths %SL:																
at ME	11	1	10	12	11	1	10	12	14	1	13	15	14	1	13	16
BPE	12	1	11	14	13	1	12	13	15	0	15	16	16	1	15	17
APM	4	1	4	6	6	0	5	6					8	0	7	9
≤13mm SL									7	0[e]	6	7				
>13mm SL									8	0[d]	7	8				
Widths %SL:																
at BPE	12	1	10	14	14	0	14	15	16	1	13	17	15	1	14	16
APM	3	0	3	4	3	0	3	4	3	0	3	4	4	0	4	5
% HL:																
ED	32	2	28	35	28	2	25	31	27	2	24	31	24	1	21	28
Depth at APM	19	3	15	24	23	2	21	27	27	2	22	30	30	2	25	34
% PFO:																
P1 length													76	4	69	85
≤17mm SL									57	5[d]	50	65				
>17mm SL									72	2[e]	68	74				
P2 length													62	6	53	72
≤17mm SL									29	6[d]	20	38				
>17mm SL									52	5[e]	46	60				
CPLR[g]									82	5	73	92	87	4	79	92

[a]N=5. [b]N=14. [c]N=3. [d]N=16. [e]N=6. [f]ΣF is the sum of lengths of all fins (i.e., P1+P2+D+A+C = ΣF). [g]CPLR (caudal peduncle length ratio) is OAPHP expressed as % OAPOP.

TABLE A-18. Summary of selected meristics by developmental phase for Gila robusta robusta cultured from brood stock collected from the Yampa River, Colorado (Figure 1, Methods). See Figures 4-6 for definitions of abbreviations and methods of counting. N_i is number of specimens out of the total number (N) having modal count. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Protolarvae (N=20)			Flexion Mesolarvae (N=8)			Postflexion Mesolarvae (N=12)			Metalarvae (N=20)			Juveniles (N=20)		
	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max
SL,mm			7 10			10 11			11 12			12 17			19 21
TL,mm			8 10			11 12			12 14			15 22			24 26
Myomeres or vertebrae[a]:															
to OP2							16	3[b]	15 17	16	10	15 17	17	10	17 17
OD										19	15	17 20	19	8	18 20
PV	29	20	29 29	29	7	28 29	29	6	28 30	28,29	8	27 30	27	8	26 28
Postvent	17	13	16 19	17	5	17 18	17	8	17 18	18	8	16 19	19	10	19 19
Total	46	12	45 48	46	6	46 47	47	6	46 48	46	14	45 48	46	8	45 47
Principal fin rays:															
P1										16	4[c]	14 16	16	11	14 17
P2										9	7[c]	9 9	9	18	8 9
D[d]							9	12	9 9	9	20	9 9	9	20	9 9
A[d]							9	12	9 9	9	20	9 9	9	18	9 10
C							19	10	19 20	19	19	19 20	19	17	19 20
Gill rakers[e]:															
1st gill arch															
External row													11	6	10 11
Internal row													14	7	13 15
Total													25	5	23 26
2nd gill arch															
External row													14	4	12 15
Internal row													13	5	11 16
Total													27	4	22 30
3rd gill arch															
External row													14	7	13 15
Internal row													13	7	11 14
Total													26	5	23 28
4th gill arch															
External row													13	7	10 15
Internal row													9	4	8 10
Total													22	6	19 24
Total															
External row													50	5	45 53
Internal row													48	3	47 54
Total													99	3	91 107

[a]For juveniles, vertebra counts on 10 cleared and stained specimens; counts include the four vertebrae of the Weberian complex and the urostylar vertebra. [b]N=5. [c]N=7. [d]For postflexion mesolarvae, counts were based on pterygiophores using whole specimens examined with polarized light or cleared and stained specimens. [e]Counts were made on gill arches excised from the left side of 10 cleared and stained specimens (four gill arches per specimen).

TABLE A-19. Summary of selected meristics by developmental phase for Gila robusta robusta collected from the Yampa River, Colorado (Figure 1, Methods). See Figures 4-6 for definitions of abbreviations and methods of counting. N_i is number of specimens out the total number (N) having modal count. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Flexion Mesolarvae (N=5)			Postflexion Mesolarvae (N=5)			Metalarvae (N=13)			Juveniles (N=14)		
	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max
SL,mm			8 11			11 12			13 19			20 50
TL,mm			8 12			12 14			15 23			25 62
Myomeres or vertebrae[a]:												
to OP2				17	2	17 17[b]	16	9	15 17	17	6	15 17
OD							19	7	18 19	19	8	19 20
PV	27,28	2	27 29	29	4	28 29	27	5	26 29	27	5	26 28
Postvent	18	3	17 18	18	4	18 19	18	11	17 19	19	6	18 20
Total	45	2	44 47	47	3	46 48	45	5	44 47	46	4	44 47
Principal fin rays:												
P1							16	2[c]	14 16	16	8	14 17
P2							9	4[c]	9 9	9	13	8 9
D[d]				9	5	9 9	9	13	9 9	9	14	9 9
A[d]				9	5	9 9	9	13	9 9	9	14	9 9
C				19	5	19 19	19	13	19 19	19	14	19 19
Gill rakers[e]:												
1st gill arch												
External row										11	4	8 12
Internal row										14	6	13 15
Total										25	3	22 26
2nd gill arch												
External row										14	4	10 15
Internal row										14	6	11 17
Total										28,29	2	22 31
3rd gill arch												
External row										14	7	13 15
Internal row										14	6	11 14
Total										27,28	3	25 29
4th gill arch												
External row										13	6	10 15
Internal row										10	9	10 11
Total										23	6	20 25
Total												
External row										51	3	44 54
Internal row										50	3	48 56
Total										94,101	2	94 110

[a]For juveniles, vertebra counts on 10 cleared and stained specimens; counts include the four vertebrae of the Weberian complex and the urostylar vertebra. [b]N=2. [c]N=4. [d]For postflexion mesolarvae, counts were based on pterygiophores using whole specimens examined with polarized light or cleared and stained specimens. [e]Counts were made on gill arches excised from the left side of 10 cleared and stained specimens (four gill arches per specimen).

TABLE A-20. Summary of selected meristics by developmental phase for Gila robusta robusta collected from the White River, Colorado (Figure 1, Methods). See Figures 4-6 for definitions of abbreviations and methods of counting. N_i is number of specimens out of the total number (N) having modal count. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Flexion Mesolarvae (N=5)				Postflexion Mesolarvae (N=5)				Metalarvae (N=22)				Juveniles (N=19)			
	Mode	Ni	Range Min	Max	Mode	Ni	Range Min	Max	Mode	Ni	Range Min	Max	Mode	Ni	Range Min	Max
SL,mm			9	11			11	12			12	20			20	39
TL,mm			10	12			12	13			14	25			26	49
Myomeres or vertebrae[a]:																
to OP2					15	1[b]			16	11	15	17	16	6	15	17
OD									19	10	18	20	18	6	18	20
PV	29	3	28	29	28,29	2	27	29	28	10	25	29	27	6	26	27
Postvent	18	4	17	18	17,18	2	17	19	18	14	17	19	19	7	18	20
Total	46	3	46	47	46	5	46	46	45	10	44	47	46	7	44	47
Principal fin rays:																
P1									15	8[c]	14	16	16	12	14	16
P2									9	12[c]	9	9	9	18	8	9
D[d]					9	5	9	9	9	22	9	9	9	19	9	9
A[d]					9	5	9	9	9	21	9	10	9	16	8	10
C					19	5	19	19	19	20	18	19	19	19	19	19
Gill rakers[e]:																
1st gill arch																
External row													11	10	10	11
Internal row													14	8	12	15
Total													25	8	22	26
2nd gill arch																
External row													13	6	12	15
Internal row													13	5	11	15
Total													26	4	23	29
3rd gill arch																
External row													15	5	12	15
Internal row													12	6	10	13
Total													26	6	23	28
4th gill arch																
External row													12	7	10	14
Internal row													9	5	8	10
Total													21	7	18	24
Total																
External row													50	6	45	54
Internal row													49	5	44	51
Total													99	3	91	103

[a]For juveniles, vertebra counts on 11 cleared and stained specimens; counts include the four vertebrae of the Weberian complex the urostylar vertebra. [b]N=1. [c]N=12. [d]For postflexion mesolarvae, counts were based on pterygiophores using whole specimens examined with polarized light or cleared and stained specimens. [e]Counts were made on gill arches excised from the left side of 11 cleared and stained specimens (four gill arches per specimen).

FIGURE A-26. Gila robusta robusta protolarva (sensu Snyder and Muth 1988, in press, see Methods), recently hatched, 7.3 mm standard length, 7.6 total length. Cultured from brood stock collected from the Yampa River, Colorado (Figure 1, Methods).

FIGURE A-27. Gila robusta robusta mesolarva (sensu Snyder and Muth 1988, in press, see Methods), recently transformed, 9.3 mm standard length, 9.8 total length. Collected from the Yampa River, Colorado (Figure 1, Methods).

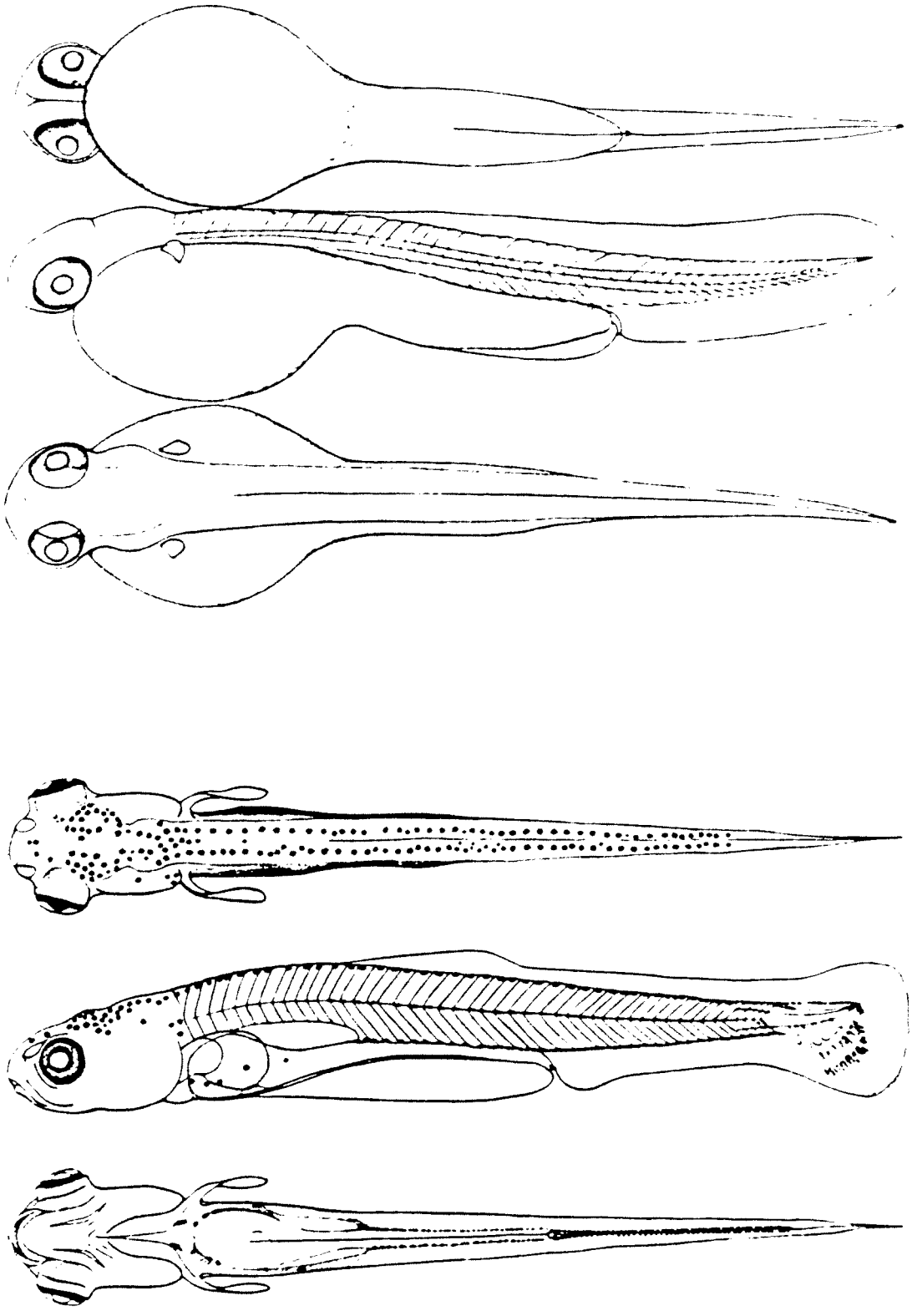
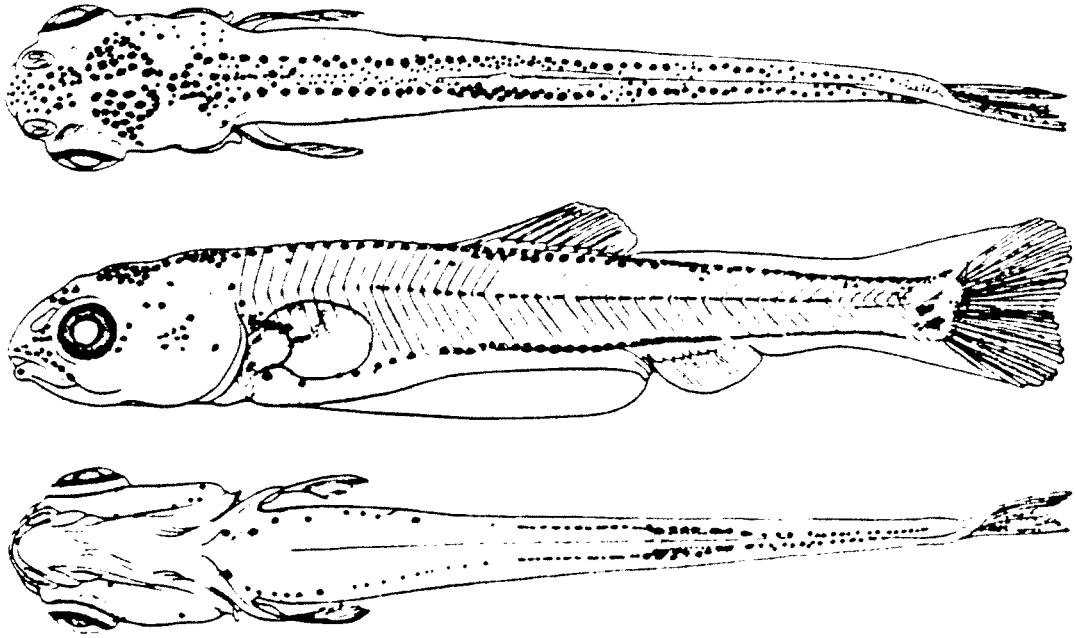


FIGURE A-28. Gila robusta robusta mesolarva (sensu Snyder and Muth 1988, in press, see Methods), 10.8 mm standard length, 12.0 total length. Collected from the Yampa River, Colorado (Figure 1, Methods).

FIGURE A-29. Gila robusta robusta metalarva (sensu Snyder and Muth 1988, in press, see Methods), recently transformed, 12.1 mm standard length, 14.0 total length. Collected from the White River, Colorado (Figure 1, Methods).



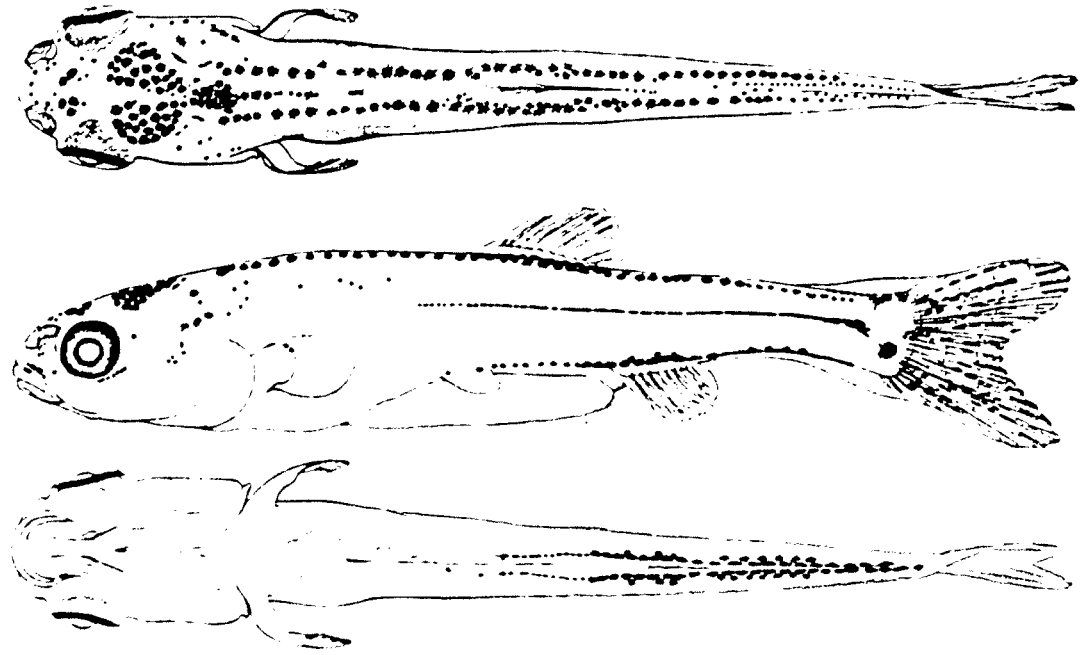
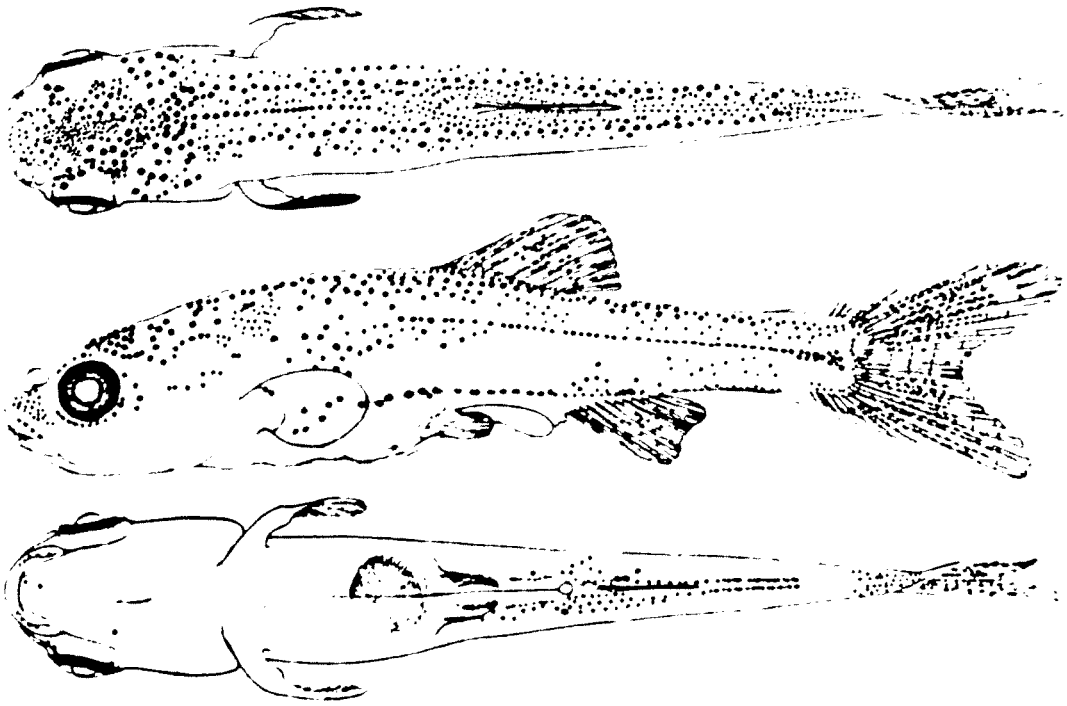


FIGURE A-30. Gila robusta robusta metalarva (sensu Snyder and Muth 1988, in press, see Methods), 14.7 mm standard length, 18.0 total length. Collected from the White River, Colorado (Figure 1, Methods).

FIGURE A-31. Gila robusta robusta juvenile (sensu Snyder and Muth 1988, in press, see Methods), recently transformed, 20.3 mm standard length, 24.1 total length. Collected from the Yampa River, Colorado (Figure 1, Methods).



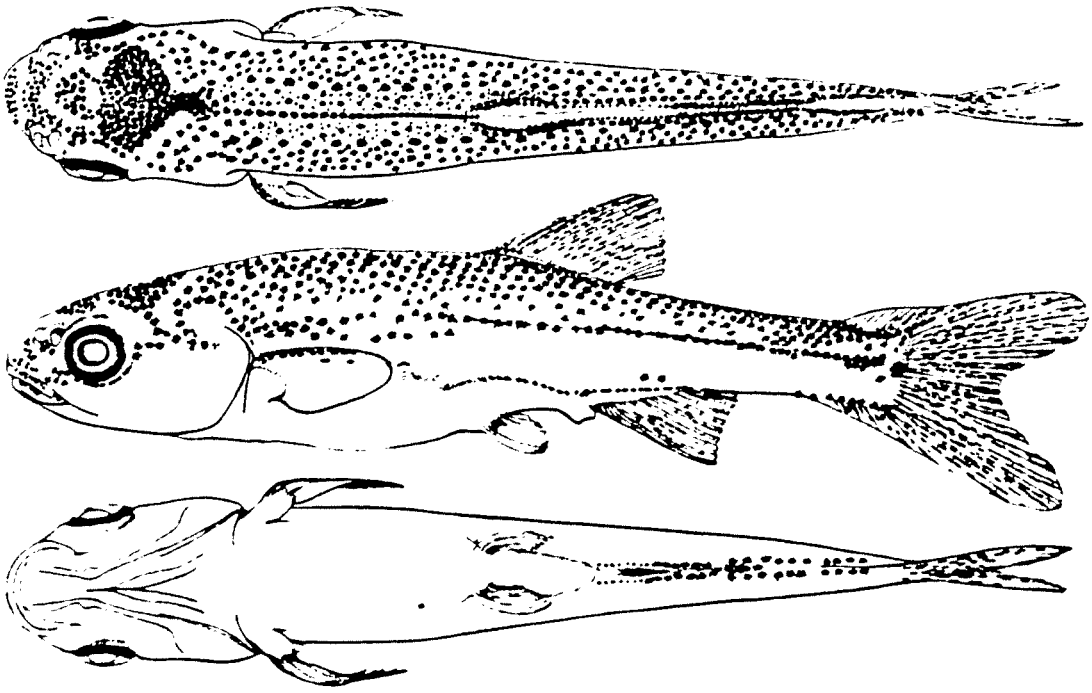
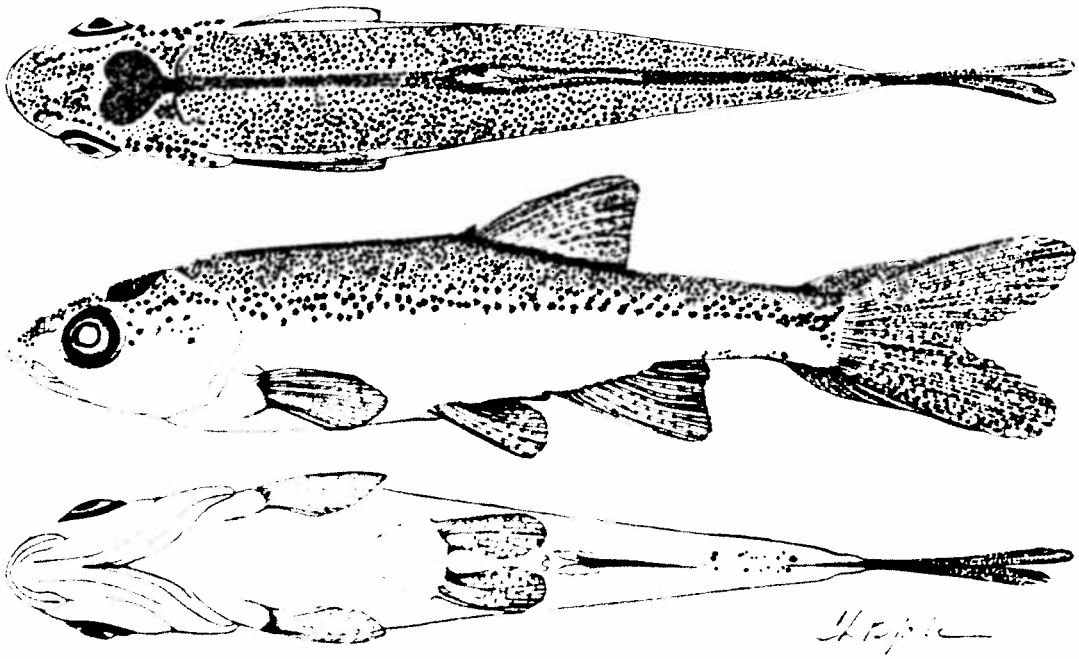


FIGURE A-32. Gila robusta robusta juvenile (sensu Snyder and Muth 1988, in press, see Methods), 29.6 mm standard length, 37.0 total length. Collected from the White River, Colorado (Figure 1, Methods).



APPENDIX B

LOG-LOG PLOTS OF SELECTED MEASUREMENTS FOR LARVAE AND YOUNG-OF-THE-YEAR JUVENILES OF SIX *GILA* GROUPS

FIGURE B-1. Log-log plots of selected measurements (**PV**, **OP1**, and **AE** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

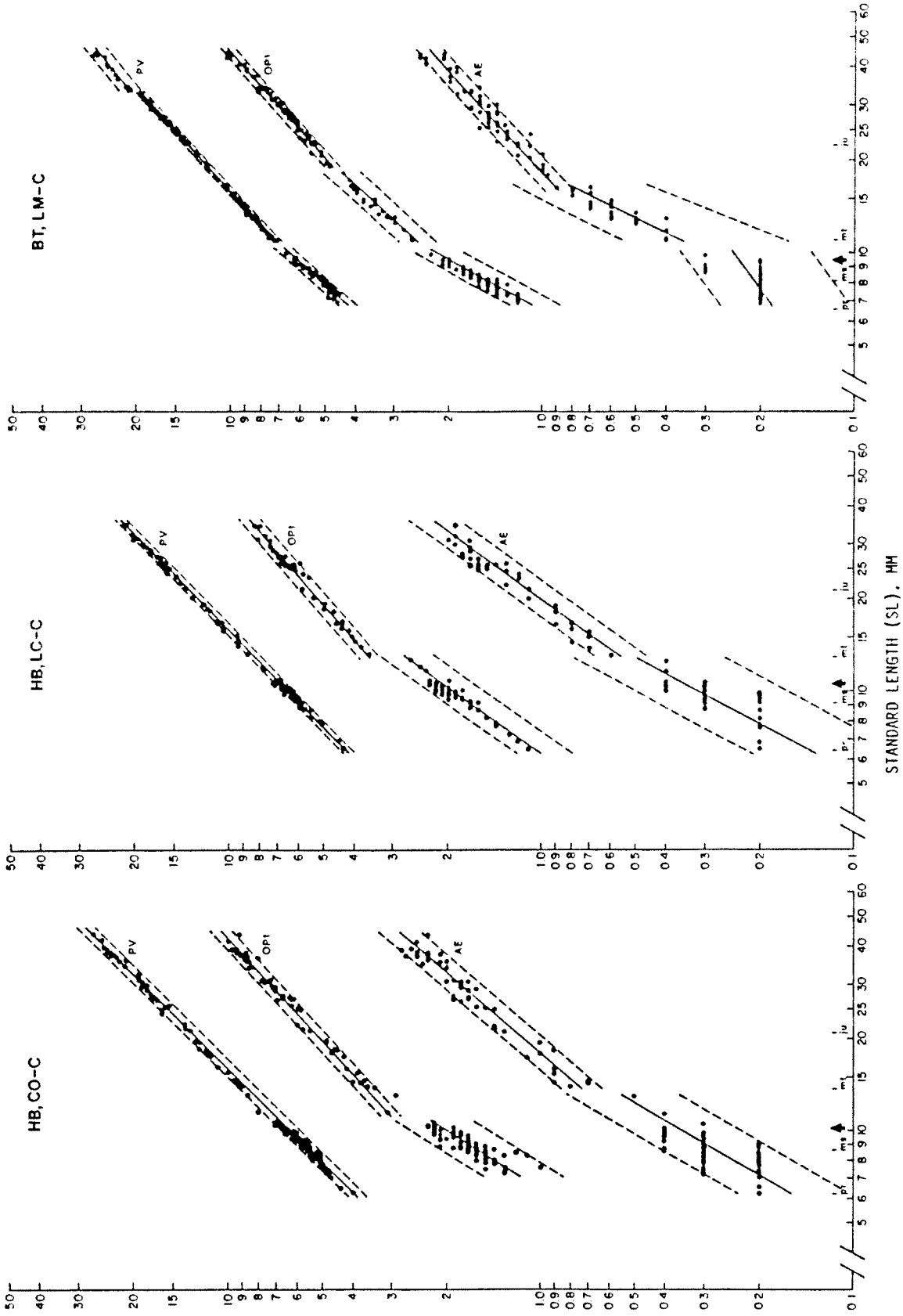

BT, LM-C
HB, LC-C
HB, CO-C
PV
OP1
AE
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-2. Log-log plots of selected measurements (**PV**, **OP1**, and **AE** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

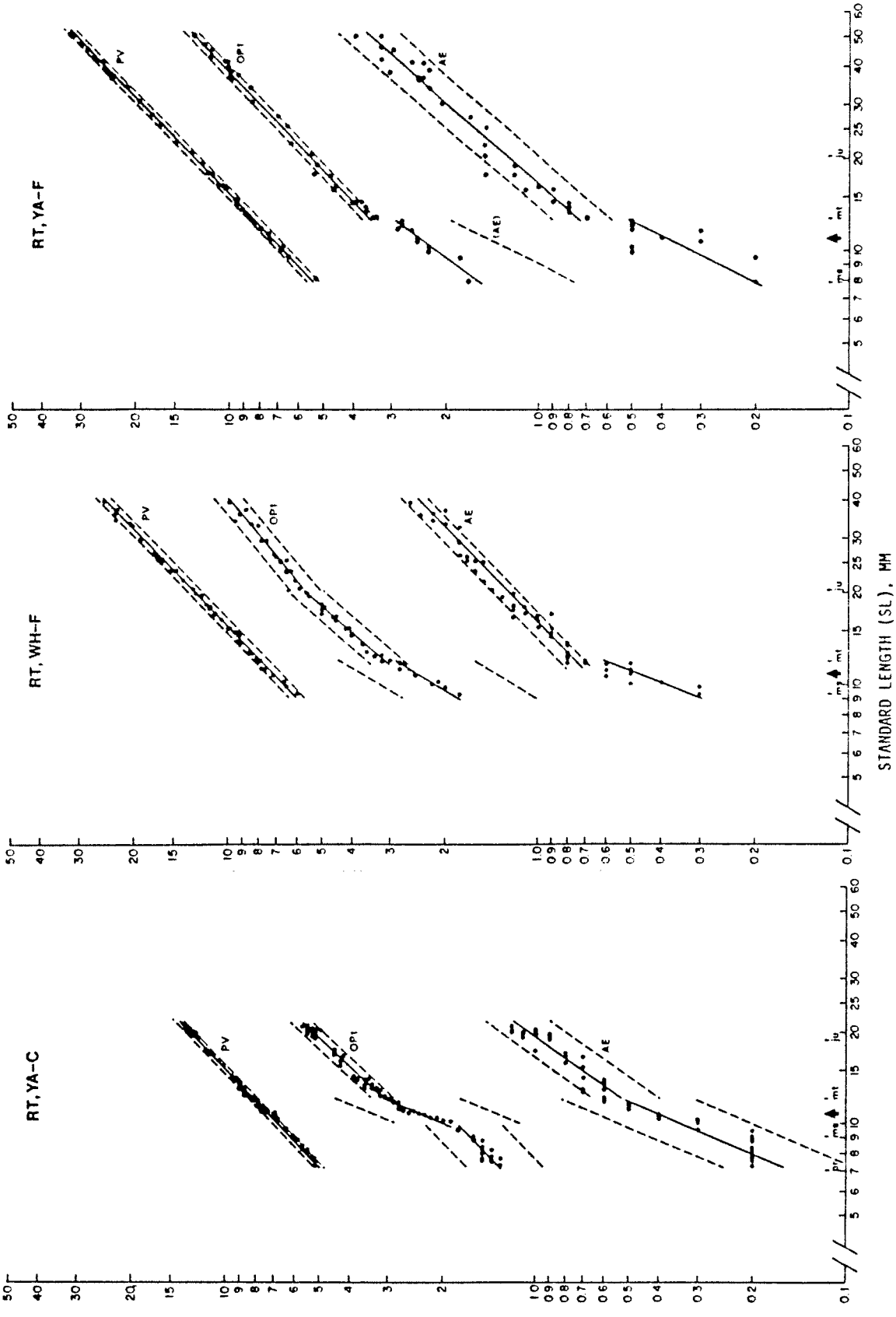

RT, YA-C
RT, WH-F
RT, YA-F
PV
OP1
AE
(AE)
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-3. Log-log plots of selected measurements (**CP**, **PE**, and **W:APM** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

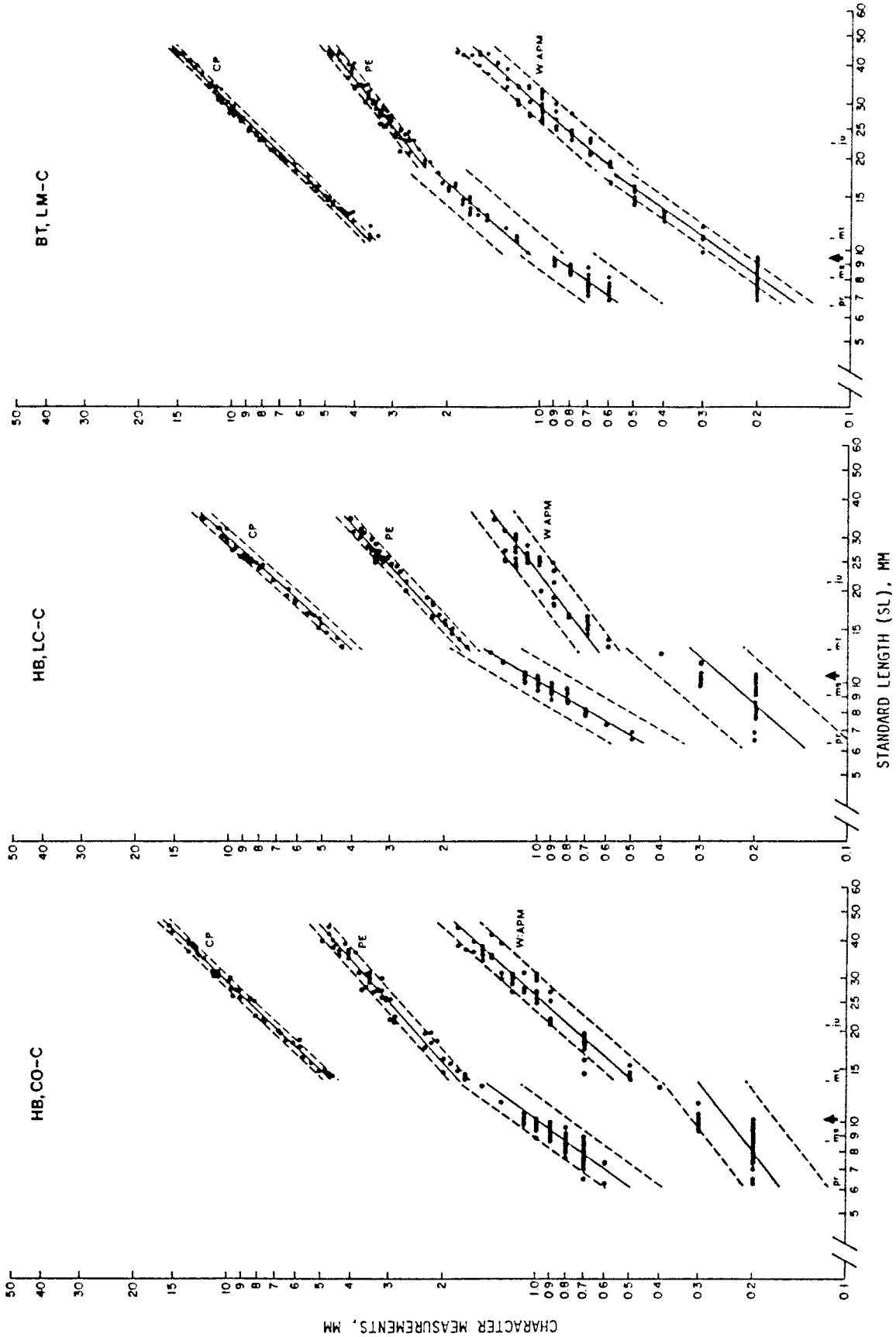

HB, CO-C
HB, LC-C
BT, LM-C
CP
PE
W:APM
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-4. Log-log plots of selected measurements (**CP**, **PE**, and **W:APM** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

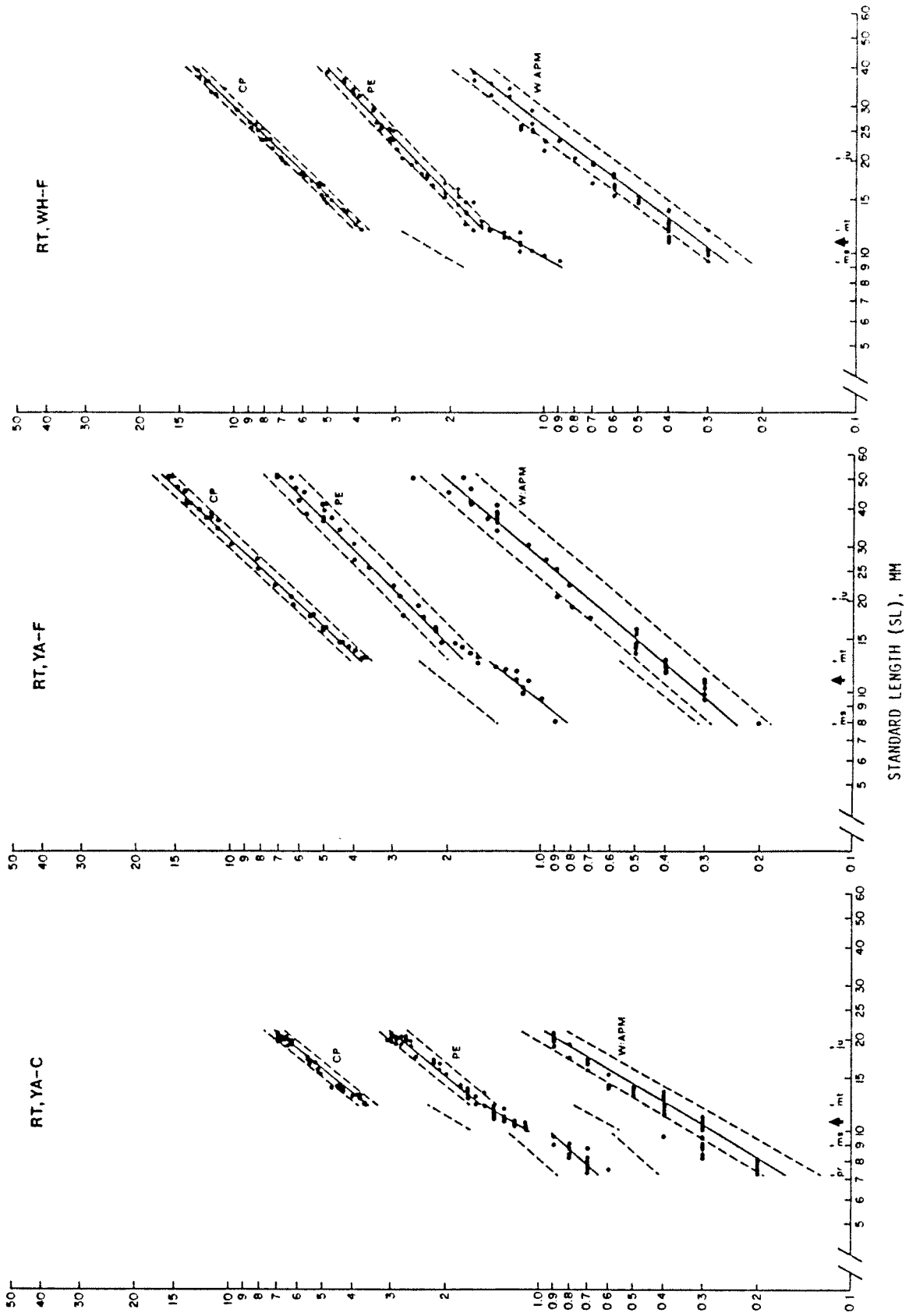

RT, YA-C
RT, YA-F
RT, WH-F
CP
PE
W.APM
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-5. Log-log plots of selected measurements (**OP2** and **A** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and **95%** confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

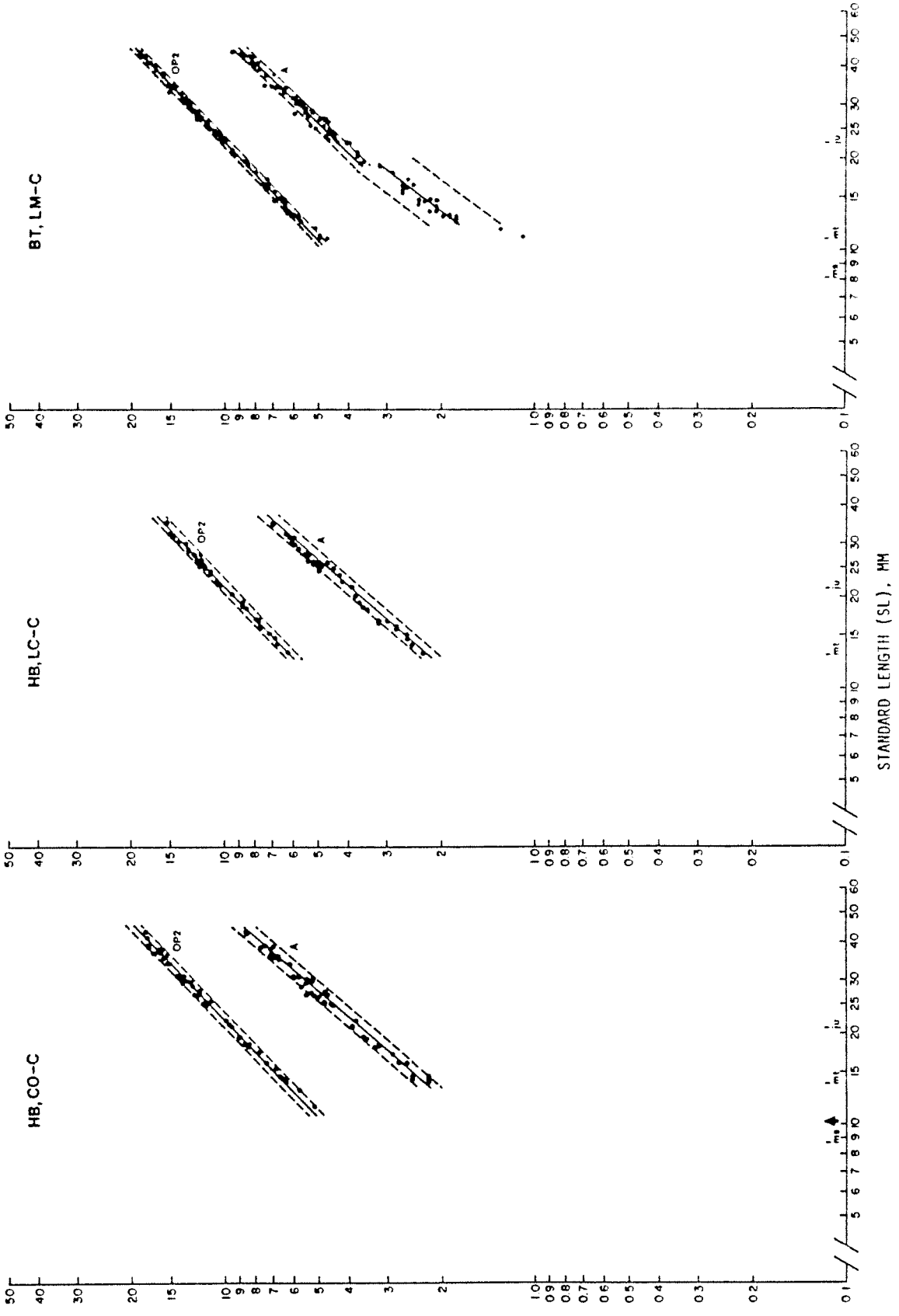

BT, LM-C
HB, LC-C
HB, CO-C
OP2
A
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-6. Log-log plots of selected measurements (**OP2** and **A** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

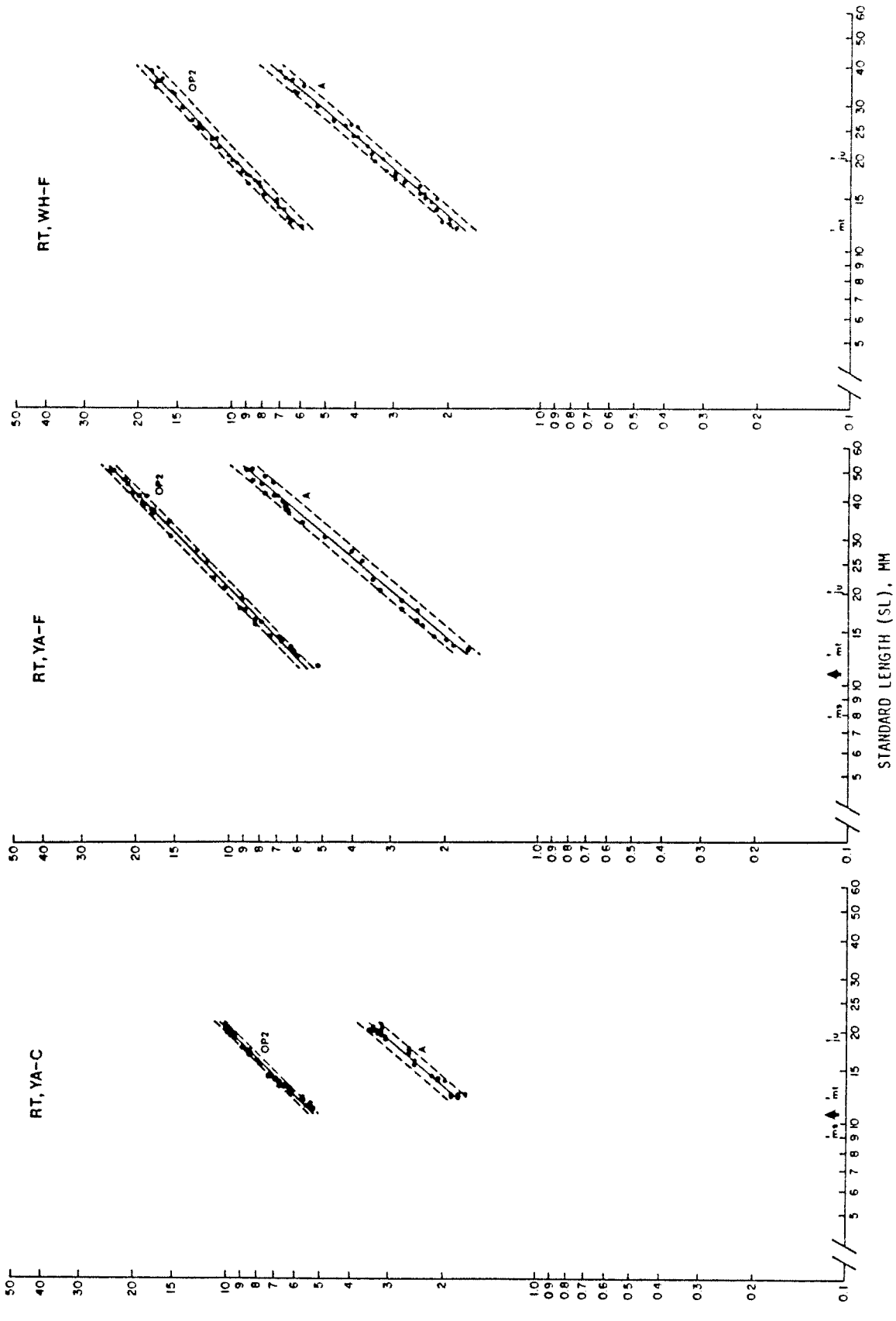

RT, WH-F
RT, YA-F
RT, YA-C
OP2
A
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-7. Log-log plots of selected measurements (**OD** and **D:ME** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

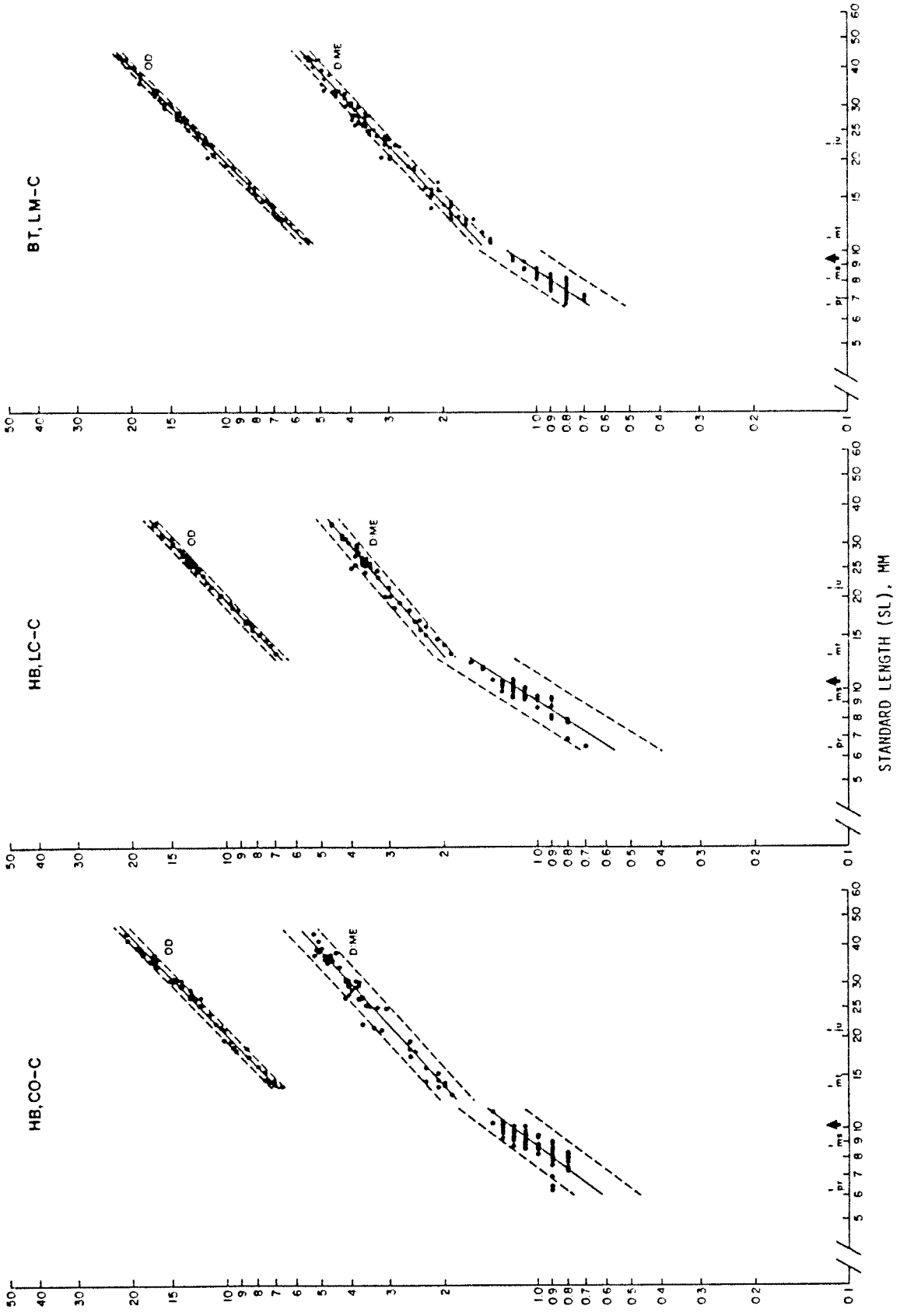

BT, LM-C
HB, LC-C
HB, CO-C
OD
DME
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-8. Log-log plots of selected measurements (**OD** and **D:ME** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

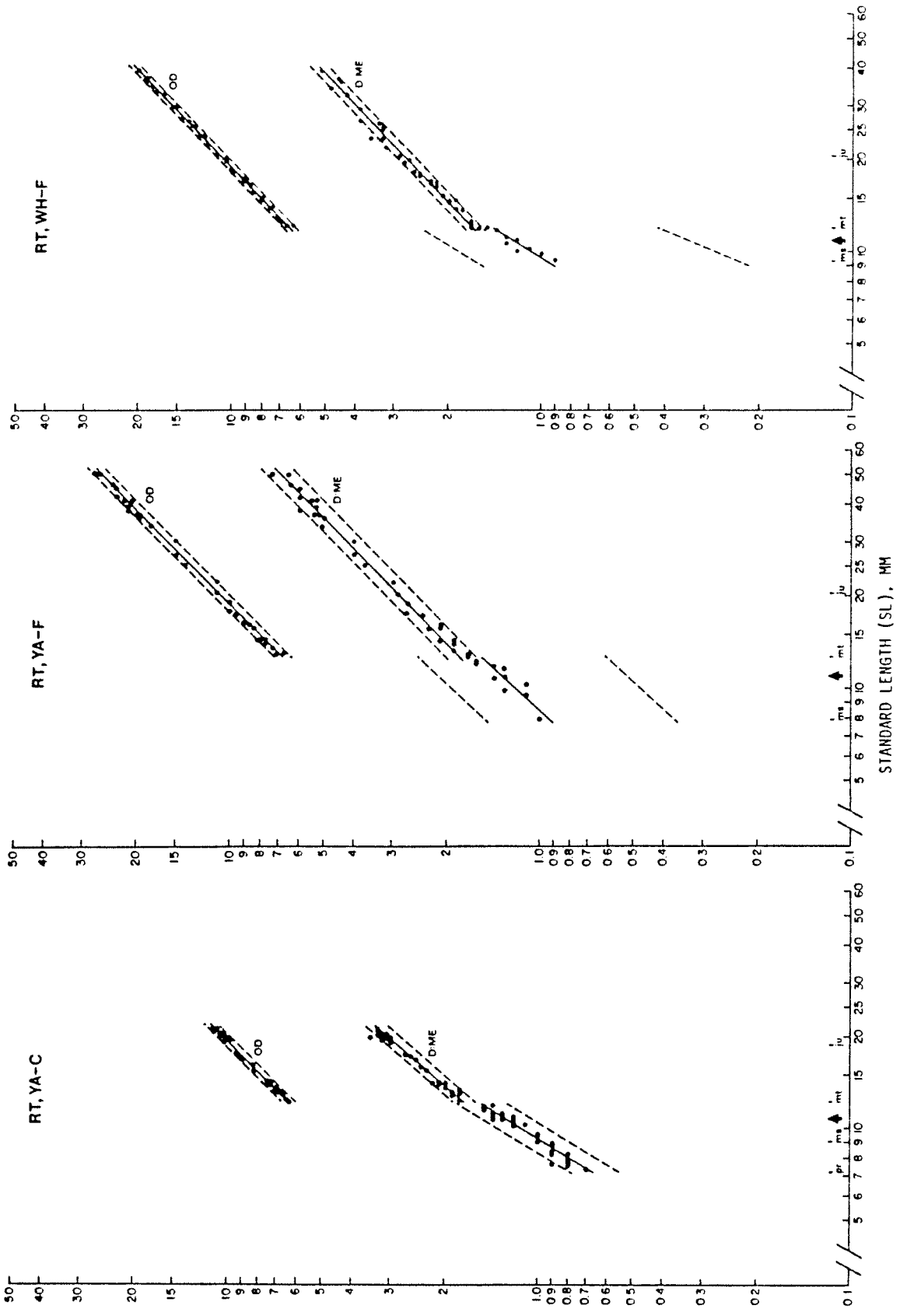

RT, YA-C
RT, YA-F
RT, WH-F
OD
D ME
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-9. Log-log plots of selected measurements (**ID** and **CL** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

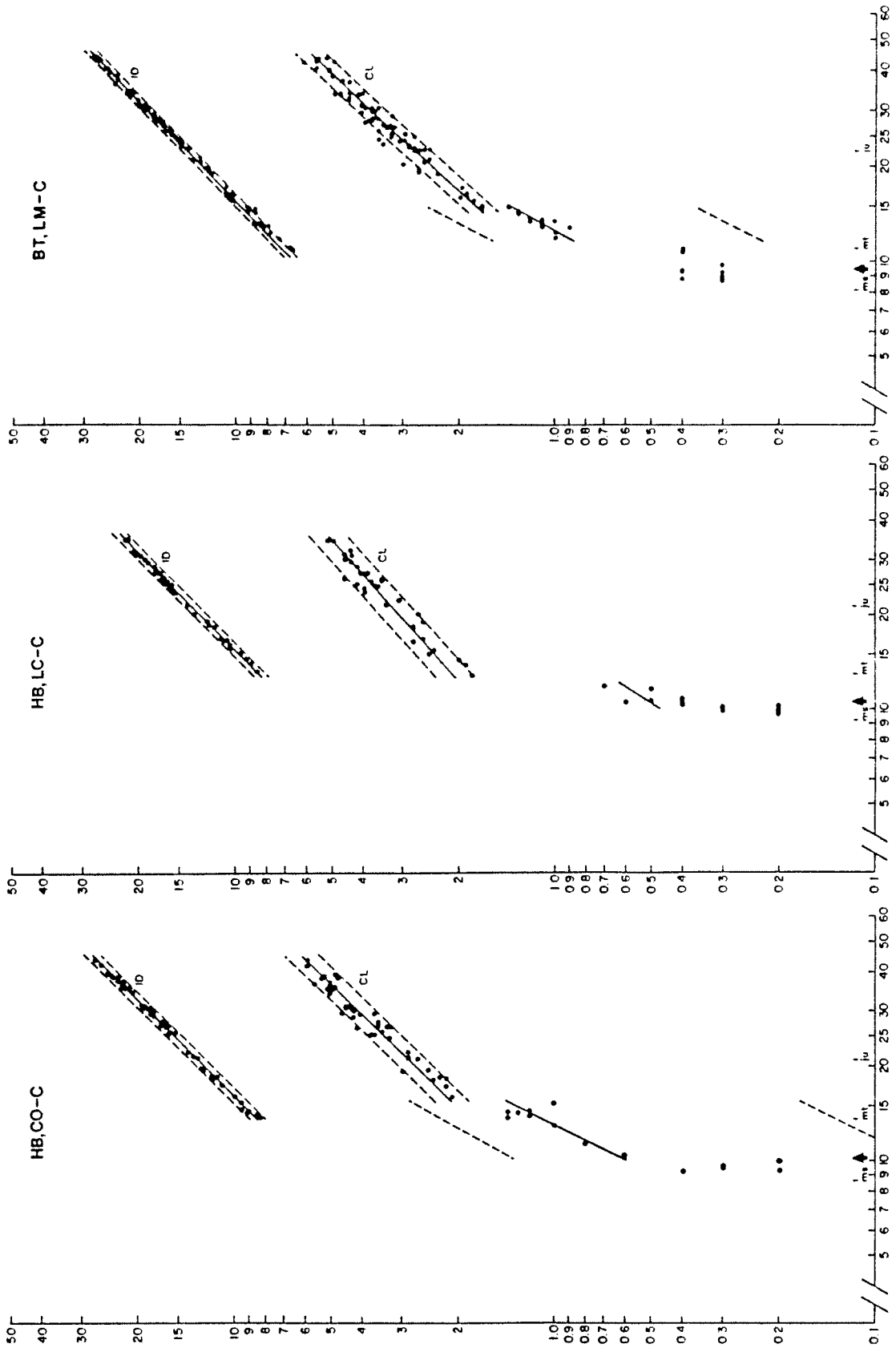

BT,LM-C
HB,LC-C
HB,CO-C
ID
CL
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-10. Log-log plots of selected measurements (**ID** and **CL** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

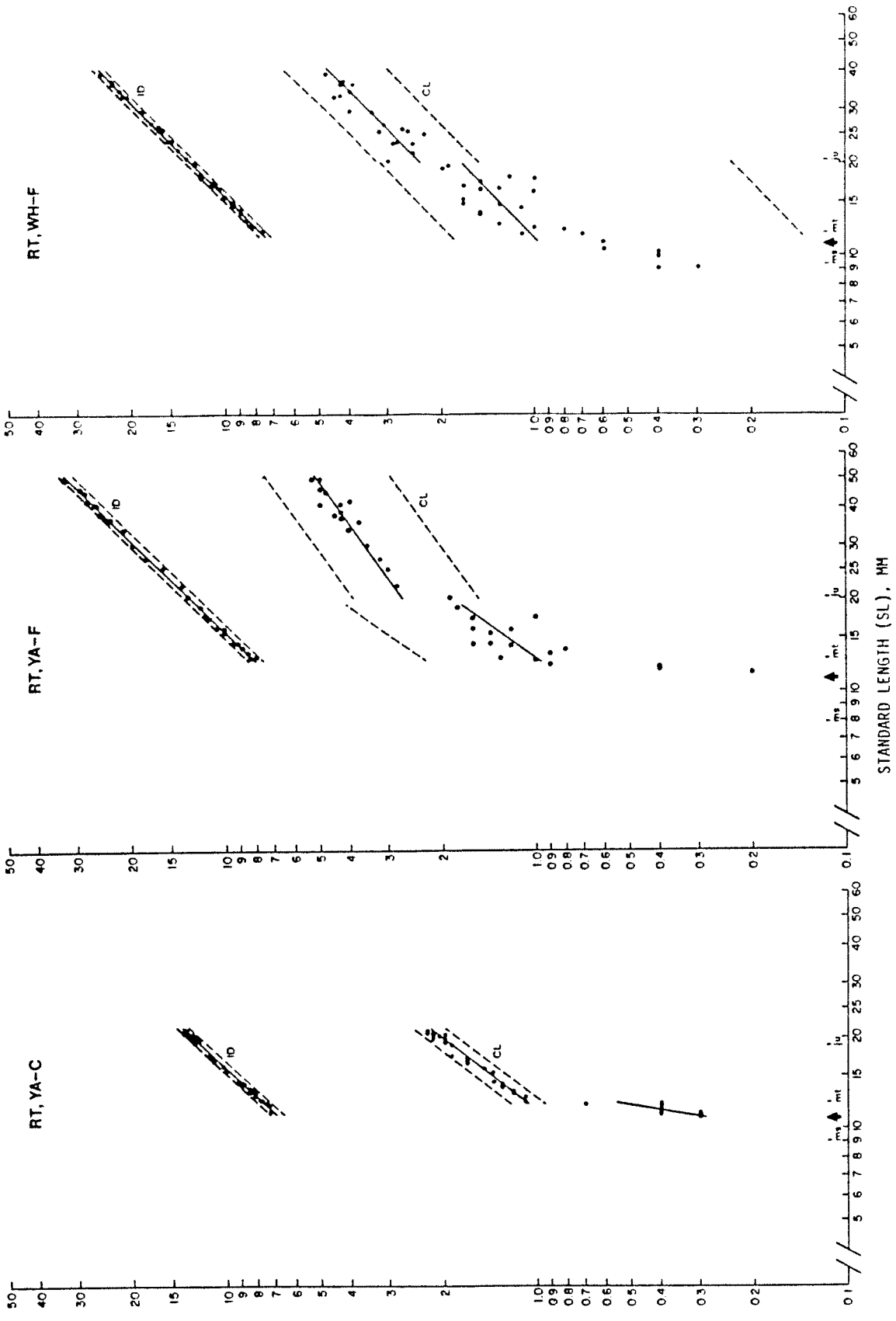

RT, YA-C
RT, YA-F
RT, WH-F
ID
CL
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-11. Log-log plots of selected measurements (**OA** and **P2** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

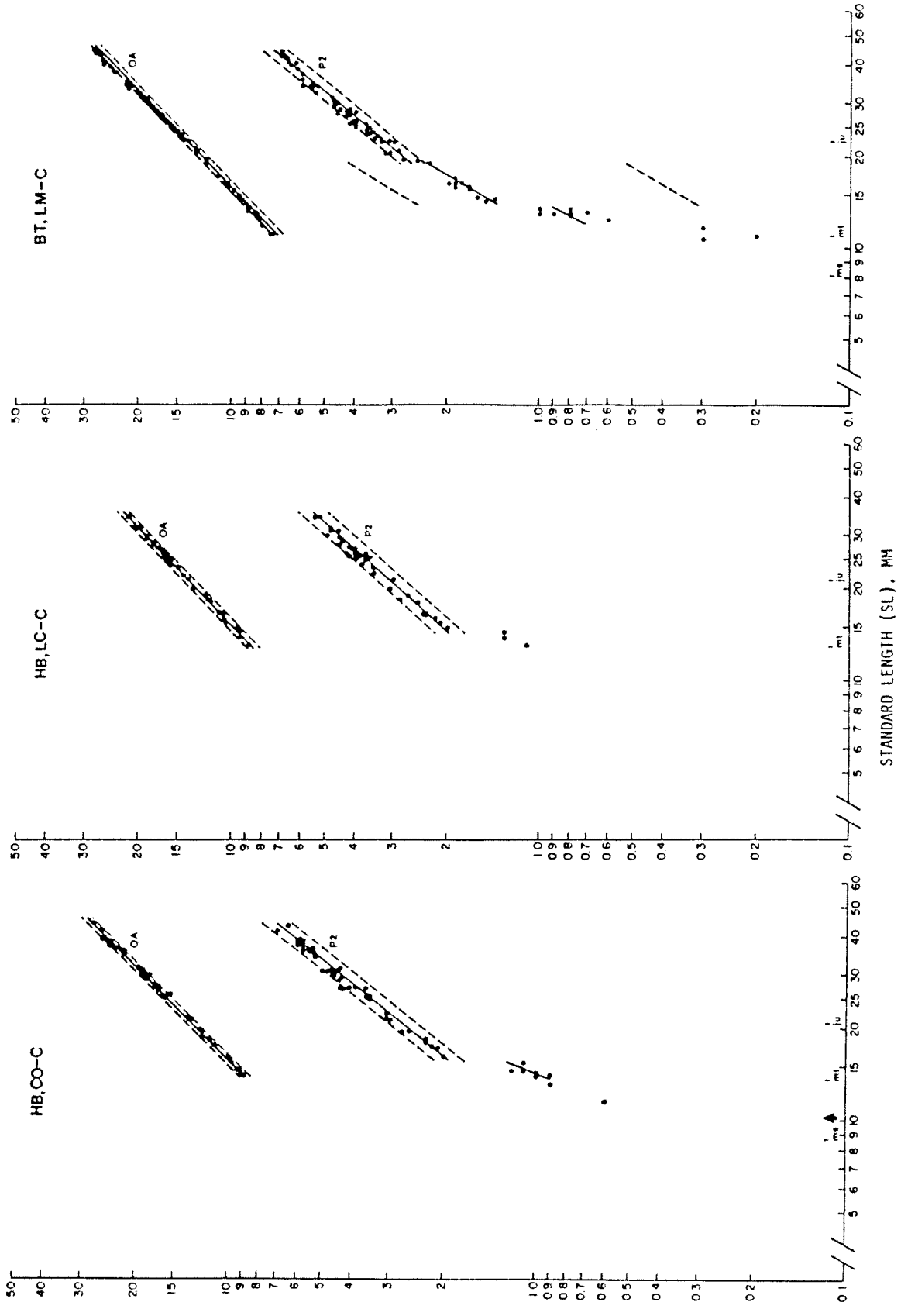

BT, LM-C
HB, LC-C
HB, CO-C
OA
P2
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-12. Log-log plots of selected measurements (**OA** and **P2** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

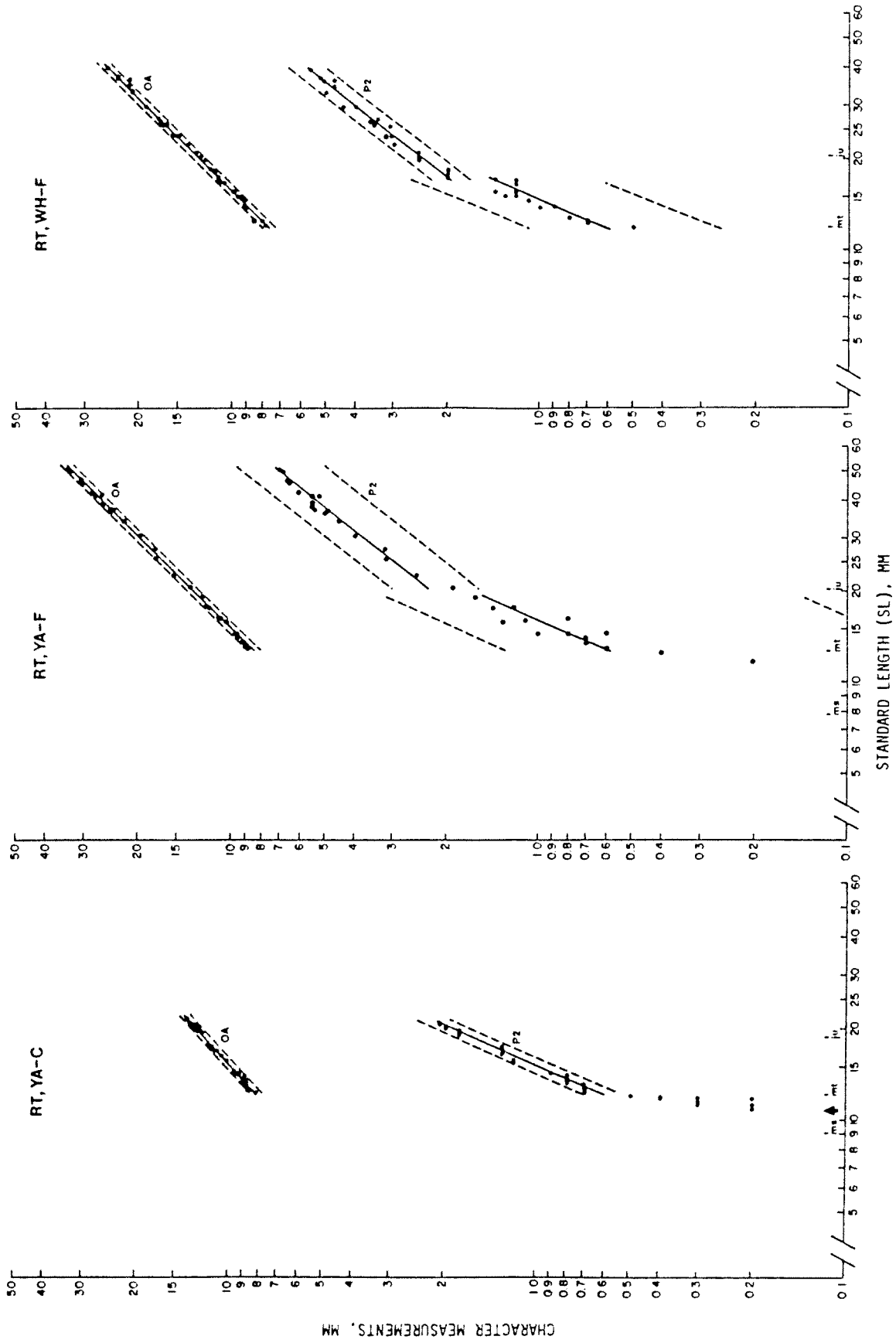

RT, WH-F
RT, YA-F
RT, YA-C
OA
P2
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-13. Log-log plots of selected measurements (**IA**, **PFO**, and **ED** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

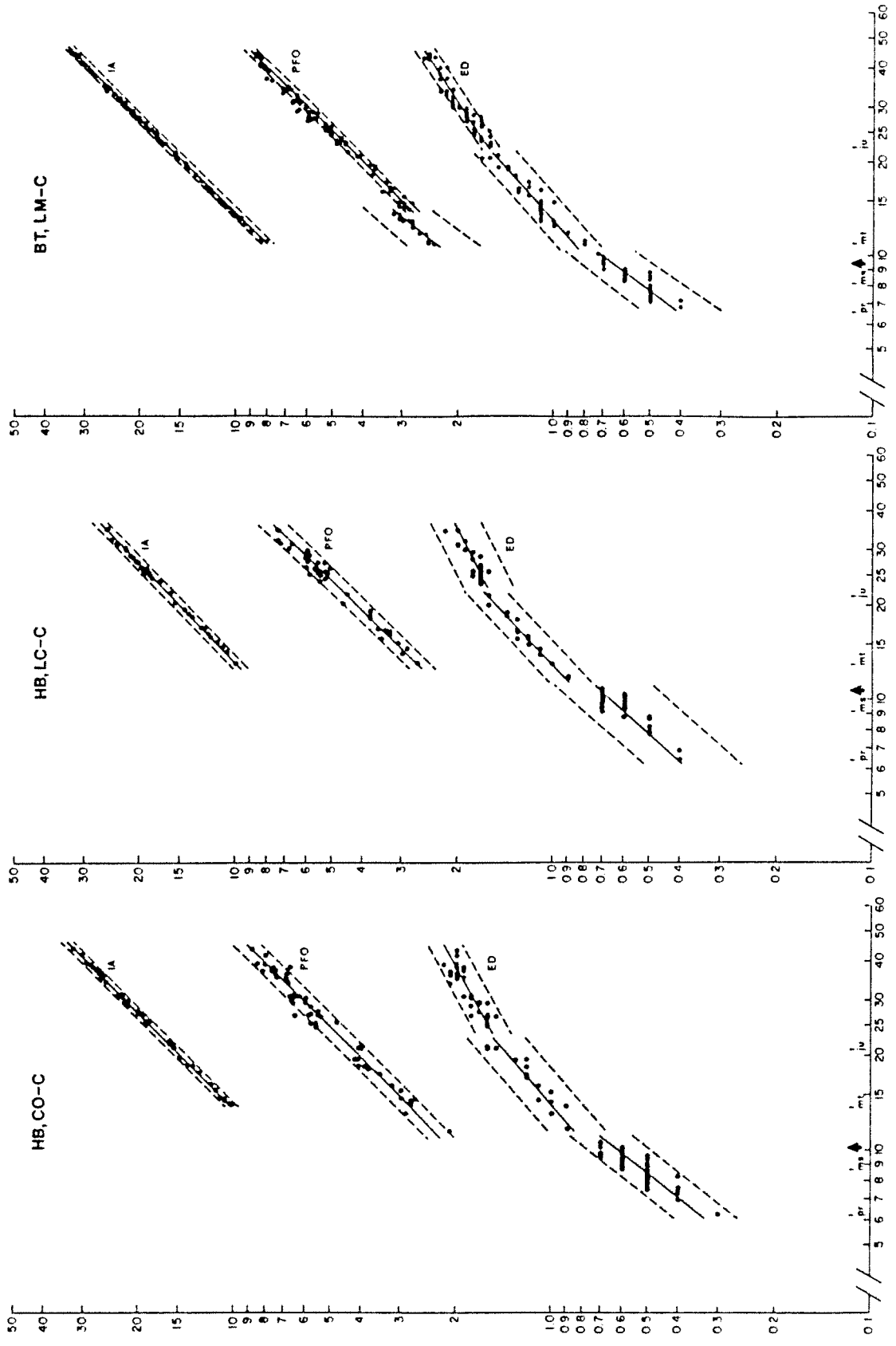

BT, LM-C
HB, LC-C
HB, CO-C
IA
PFO
ED
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-14. Log-log plots of selected measurements (**IA**, **PFO**, and **ED** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

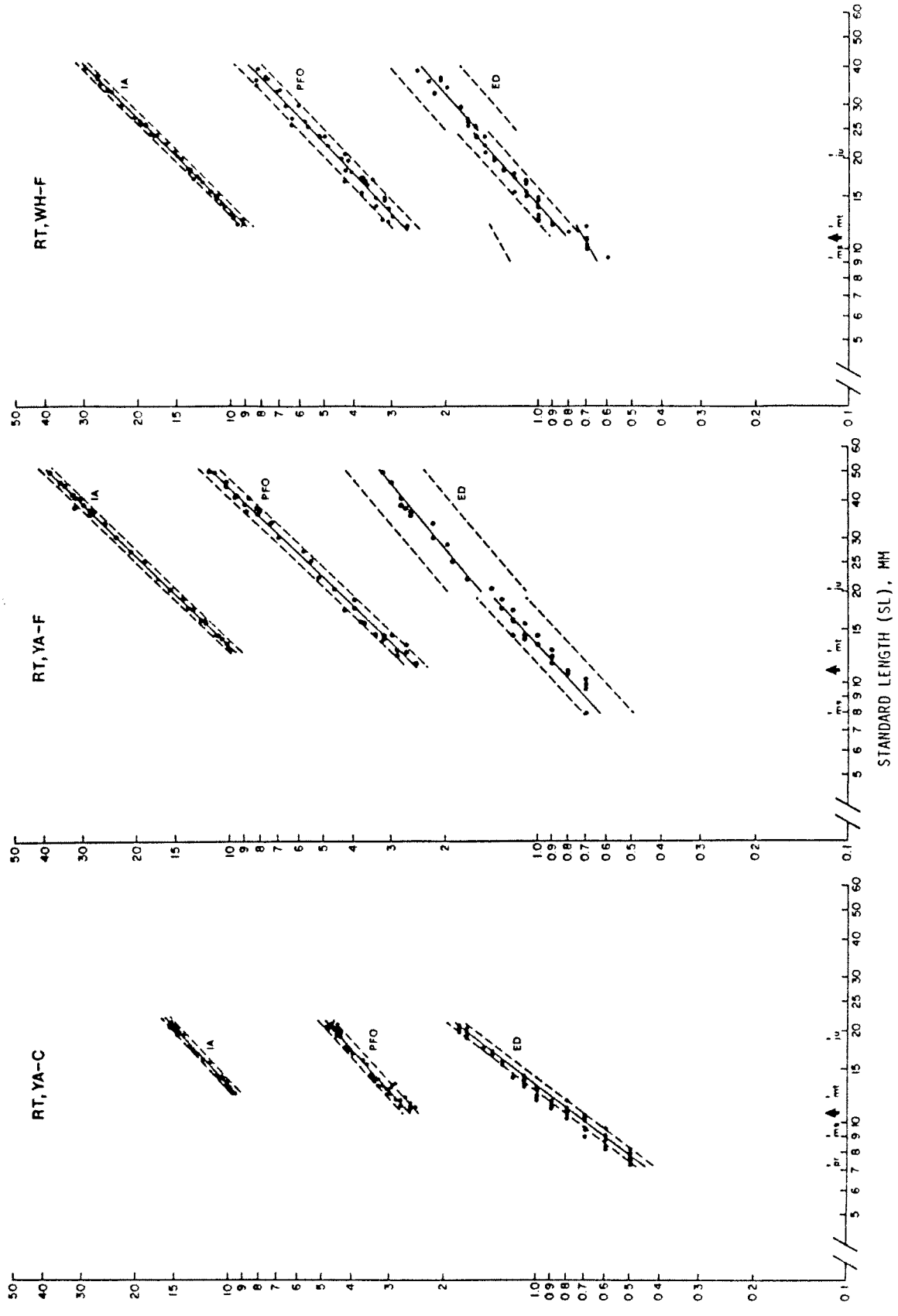

RT, YA-C
RT, YA-F
RT, WH-F
IA
PFO
ED
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-15. Log-log plots of selected measurements (**DB** against **SL**) for *Gila cypha* and *G. elegans* metalarvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

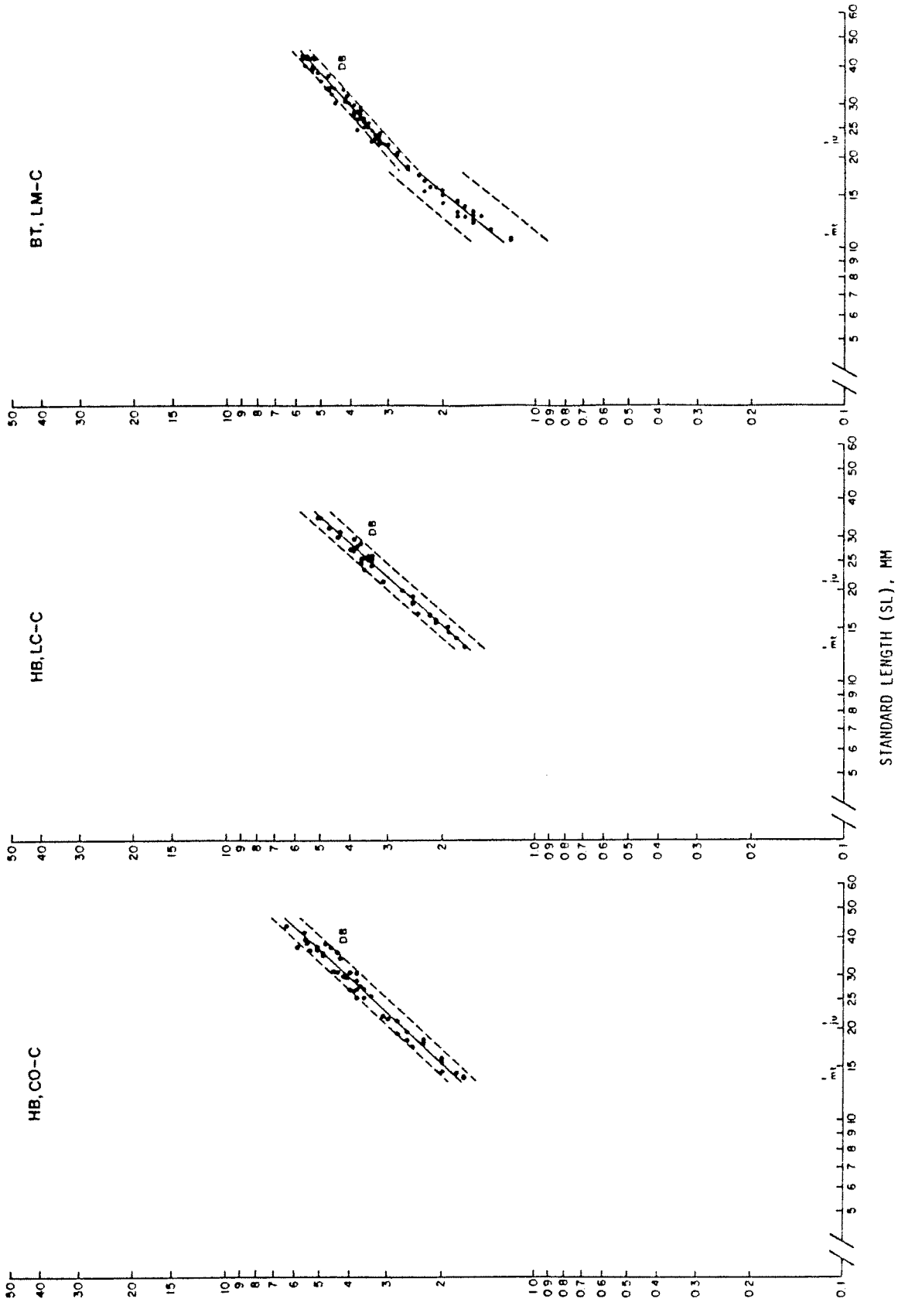

BT, LM-C
HB, LC-C
HB, CO-C
DB
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-16. Log-log plots of selected measurements (**DB** against **SL**) for *Gila robusta robusta* metalarvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

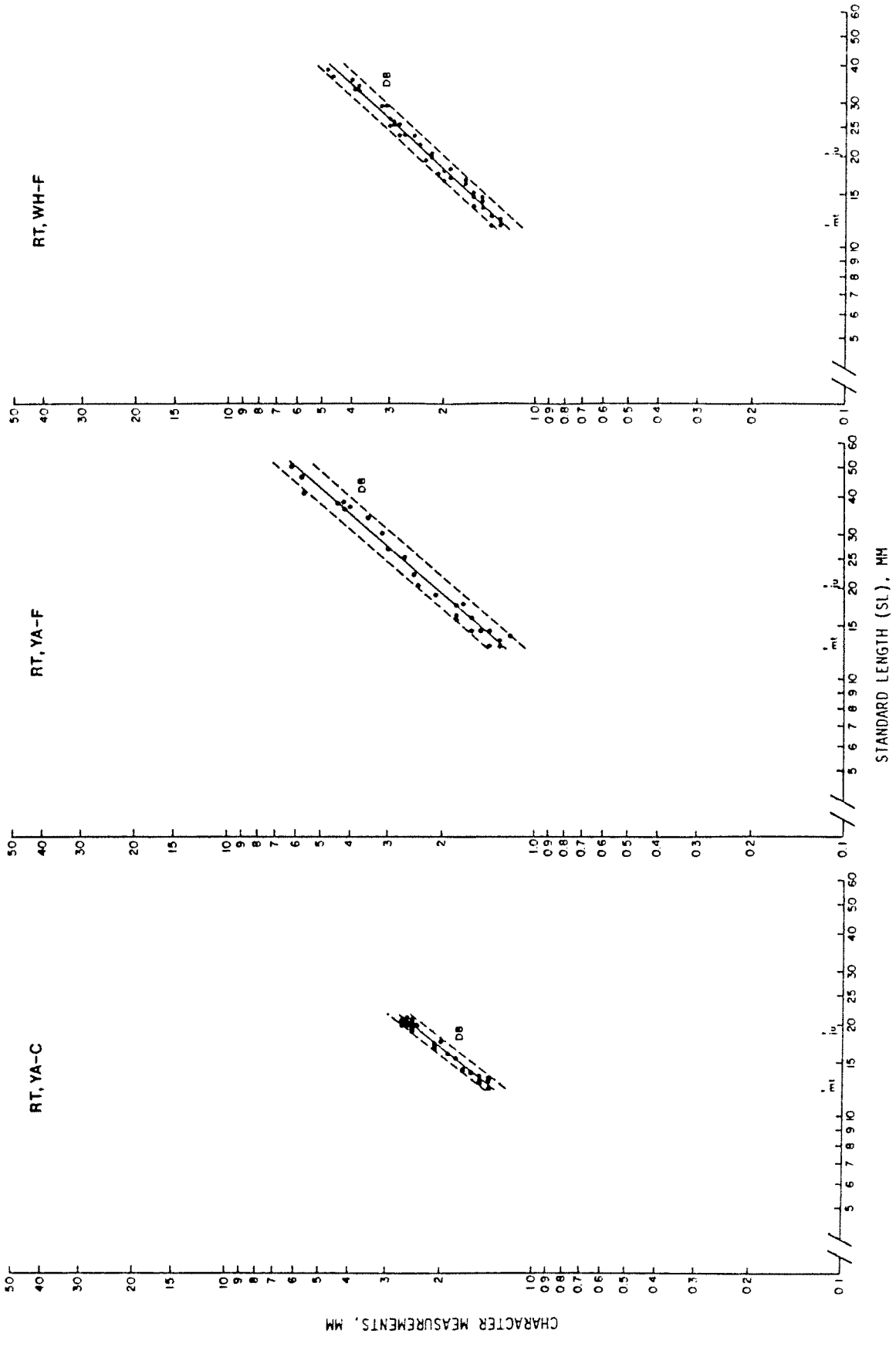

RT, YA-C
RT, YA-F
RT, WH-F
DB
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-17. Log-log plots of selected measurements (**AB** against **SL**) for *Gila cypha* and *G. elegans* metalarvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

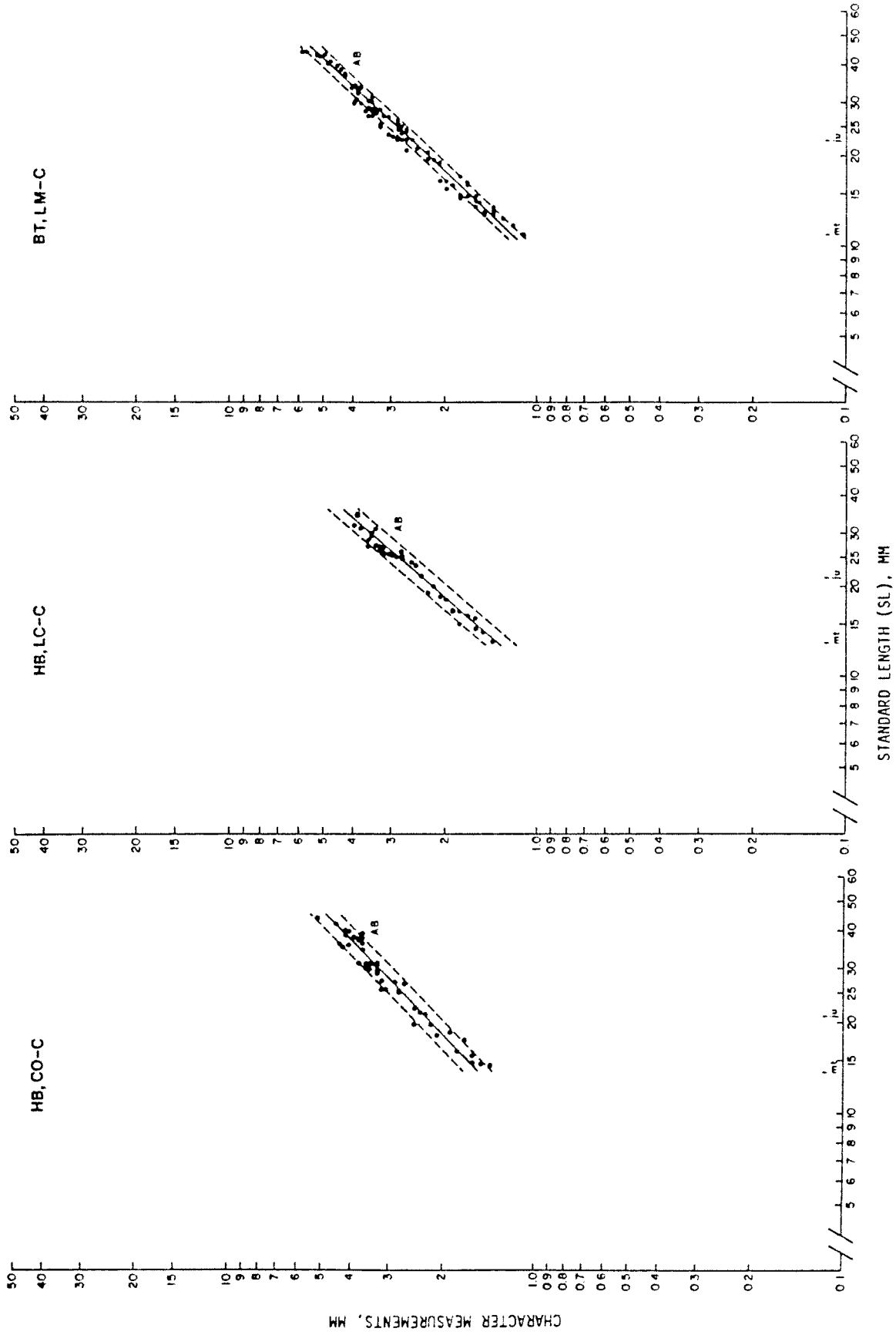

BT, LM-C
HB, LC-C
HB, CO-C
AB
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-18. Log-log plots of selected measurements (**AB** against **SL**) for *Gila robusta robusta* metalarvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

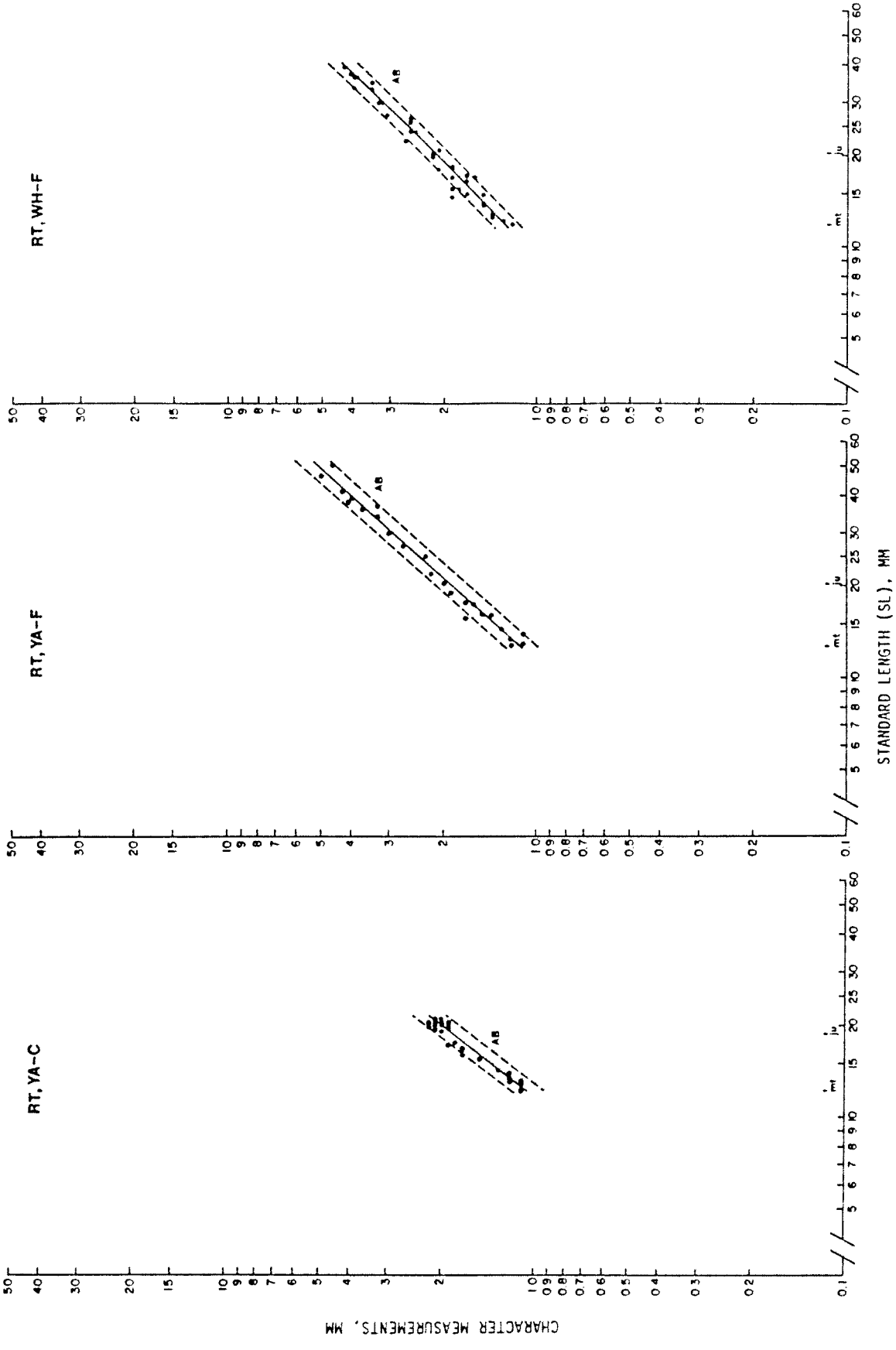

RT, WH-F
RT, YA-F
RT, YA-C
AB
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-19. Log-log plots of selected measurements (**P1** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

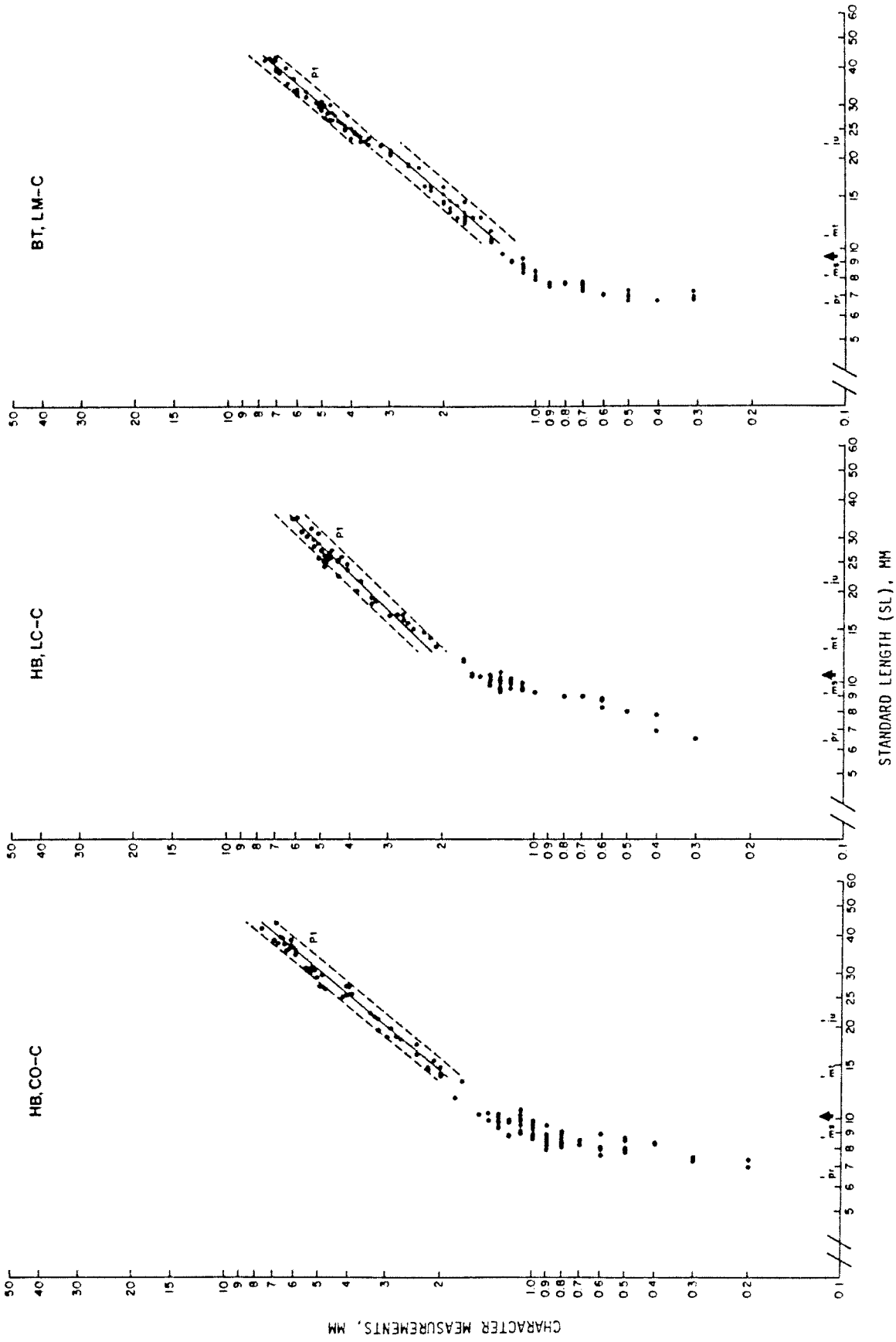

BT, LM-C
HB, LC-C
HB, CO-C
P1
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-20. Log-log plots of selected measurements (**P1** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

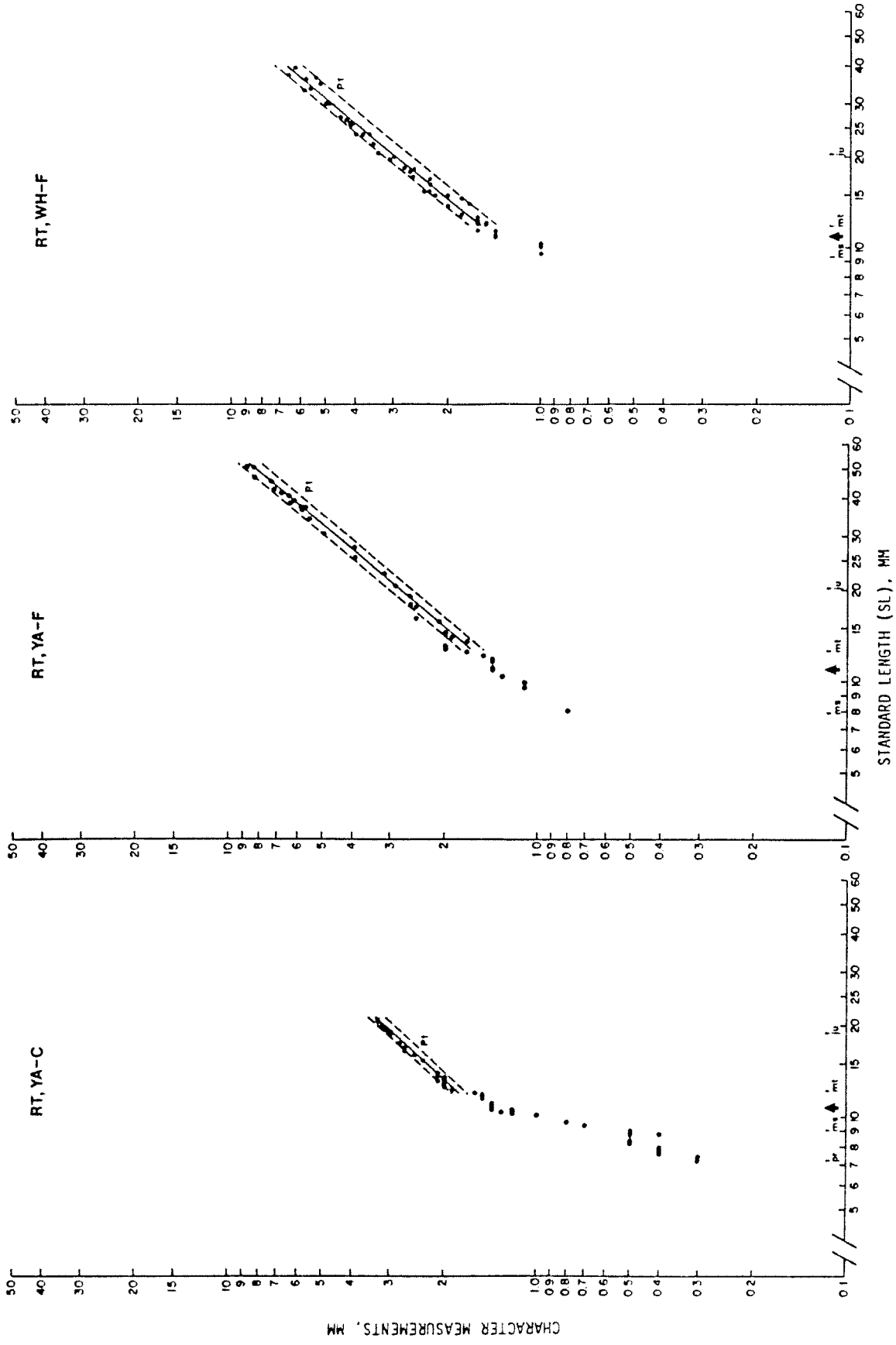

RT, WH-F
RT, YA-F
RT, YA-C
P1
STANDARD LENGTH (SL), MM
CHARACTER MEASUREMENTS, MM

FIGURE B-21. Log-log plots of selected measurements (**ΣFL**, **D**, and **D:APM** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

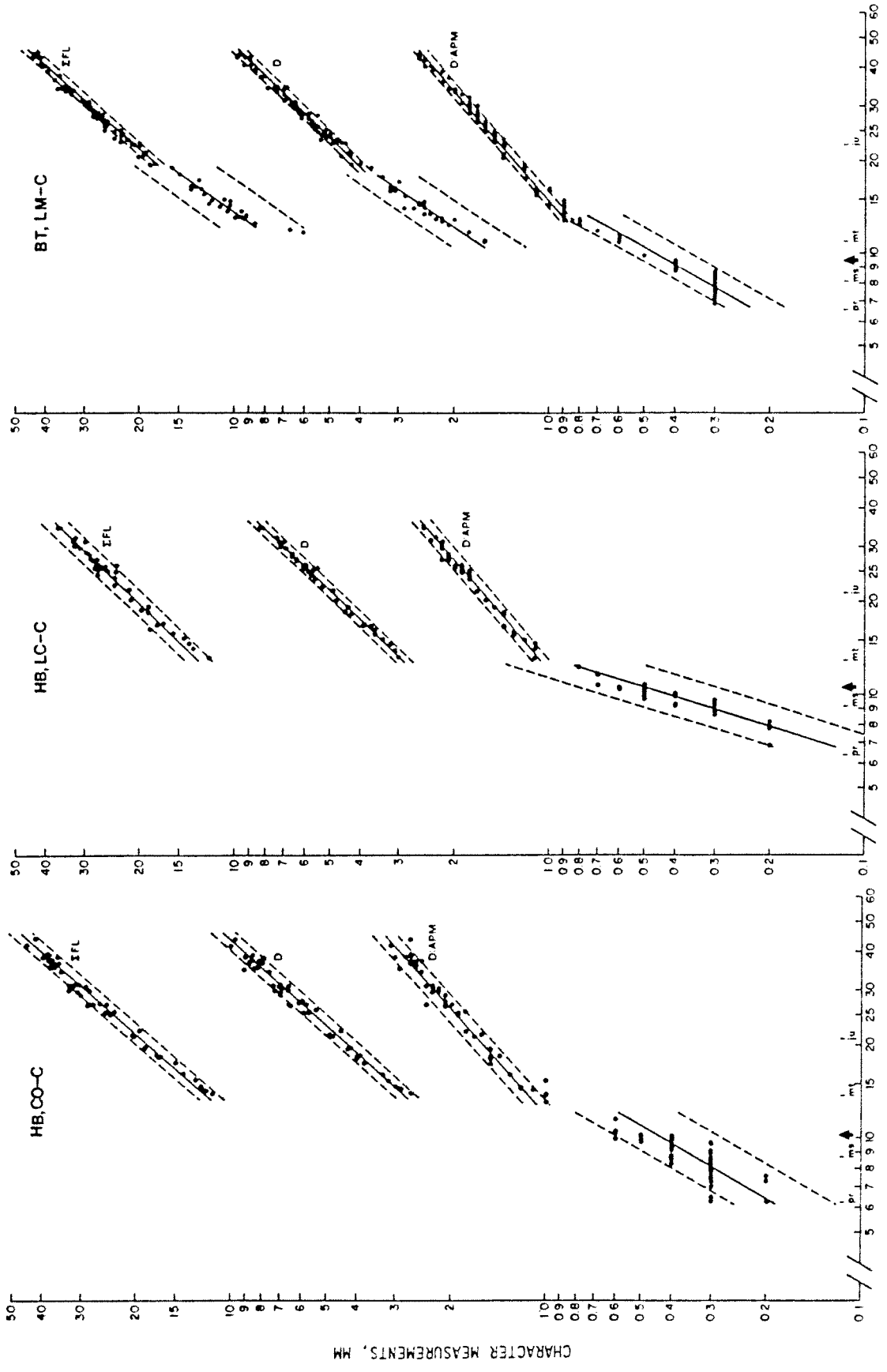

BT, LM-C
HB, LC-C
HB, CO-C
ΣFL
D
D APM
STANDARD LENGTH (SL), MM
CHARACTER MEASUREMENTS, MM

FIGURE B-22. Log-log plots of selected measurements (**ΣFL**, **D**, and **D:APM** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

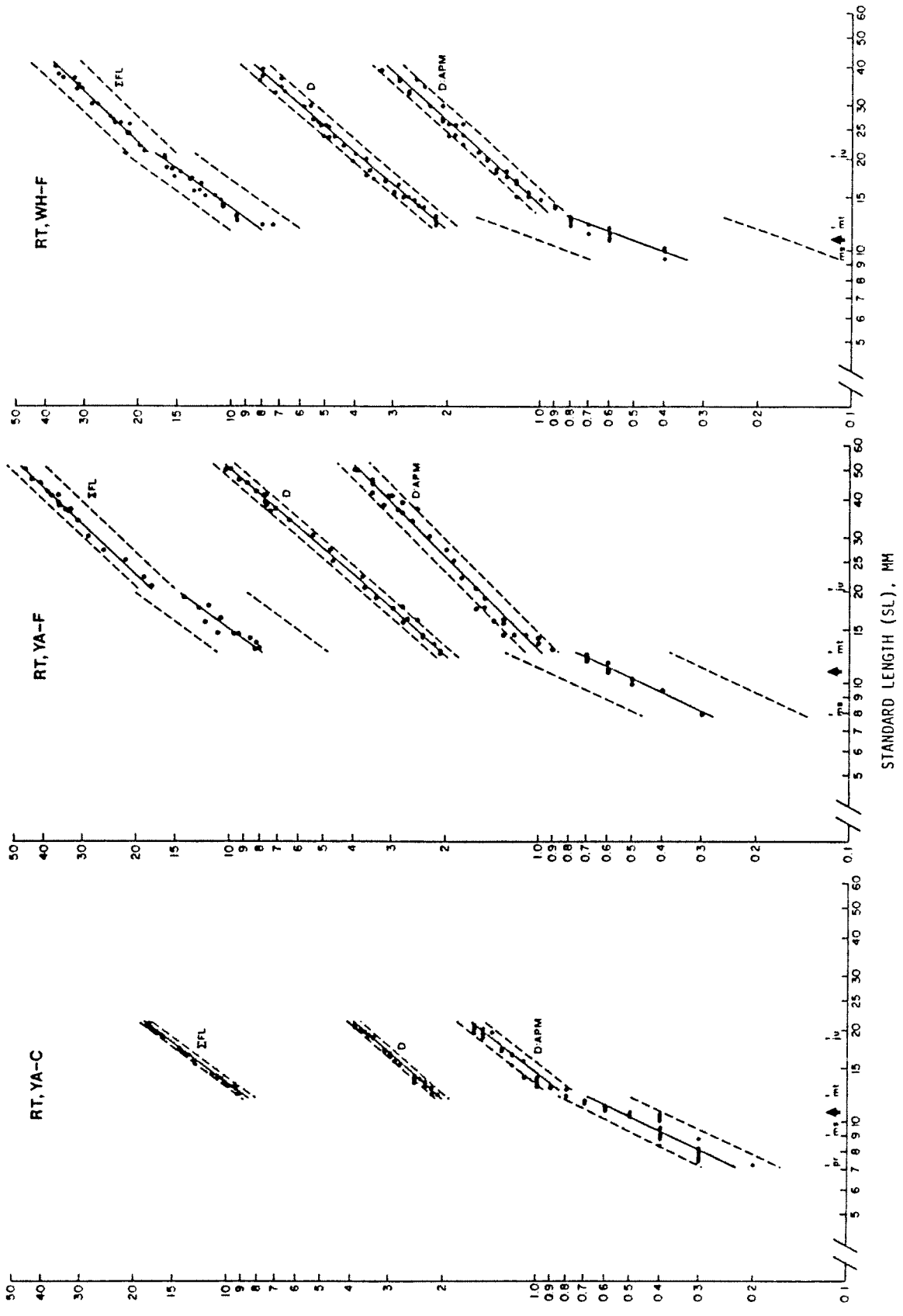

RT, YA-C
RT, YA-F
RT, WH-F
ΣFL
D
D·APM
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-23. Log-log plots of selected measurements (**C** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

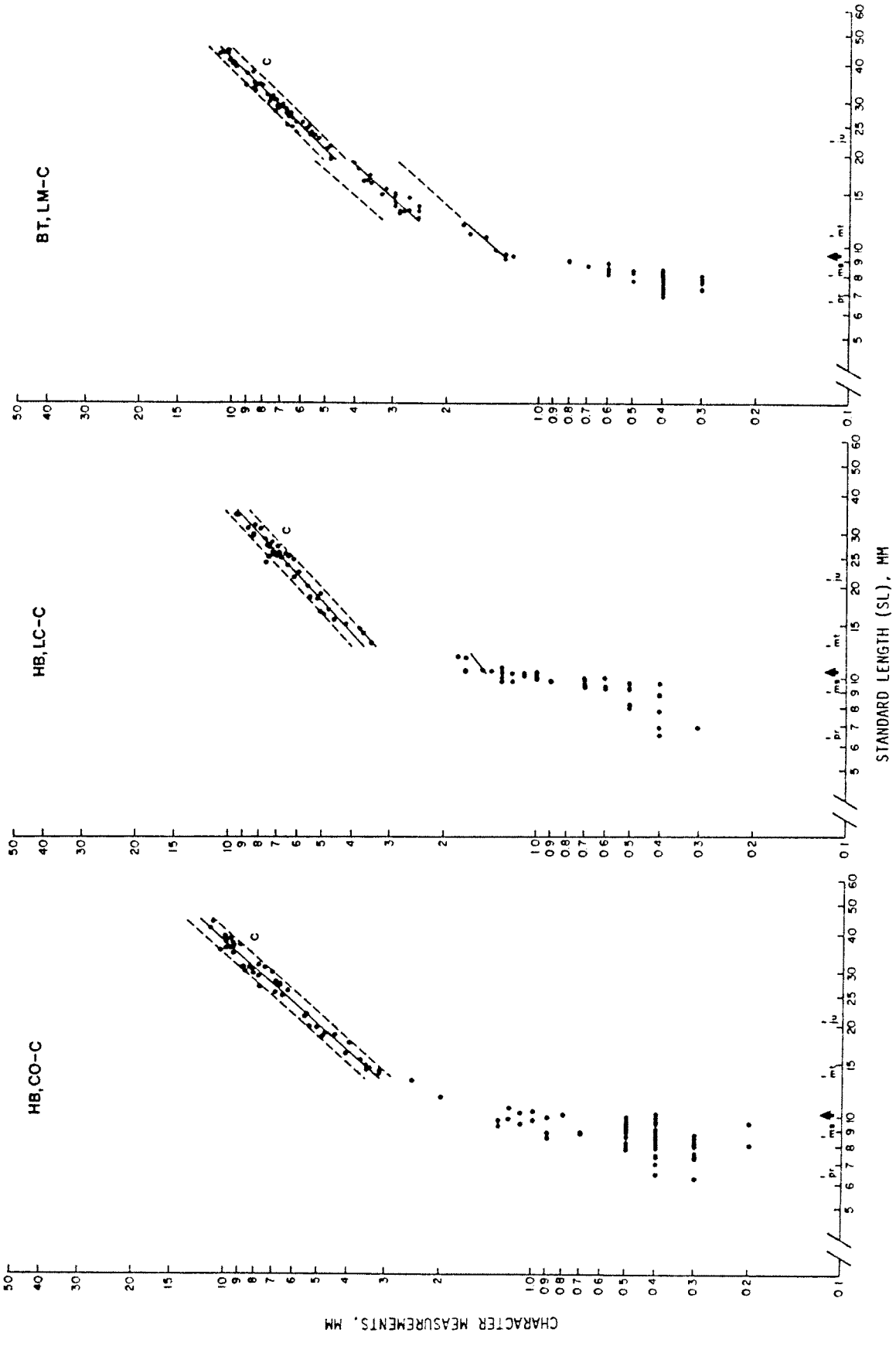

BT, LM-C
HB, LC-C
HB, CO-C
C
STANDARD LENGTH (SL), MM
CHARACTER MEASUREMENTS, MM

FIGURE B-24. Log-log plots of selected measurements (**C** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

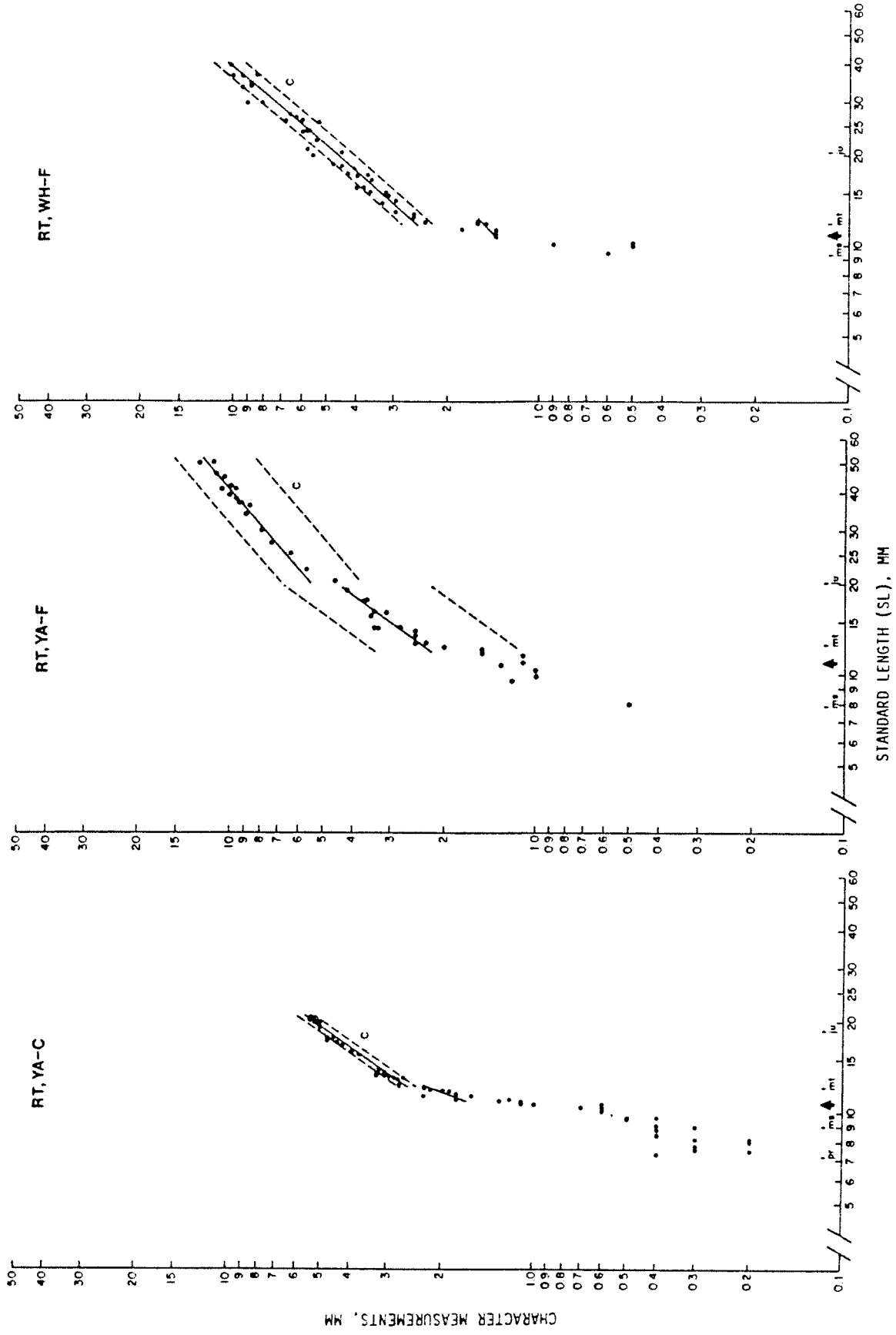

RT, YA-C
RT, YA-F
RT, WH-F
c
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-25. Log-log plots of selected measurements (**LDR** against **SL**) for *Gila cypha* and *G. elegans* metalarvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

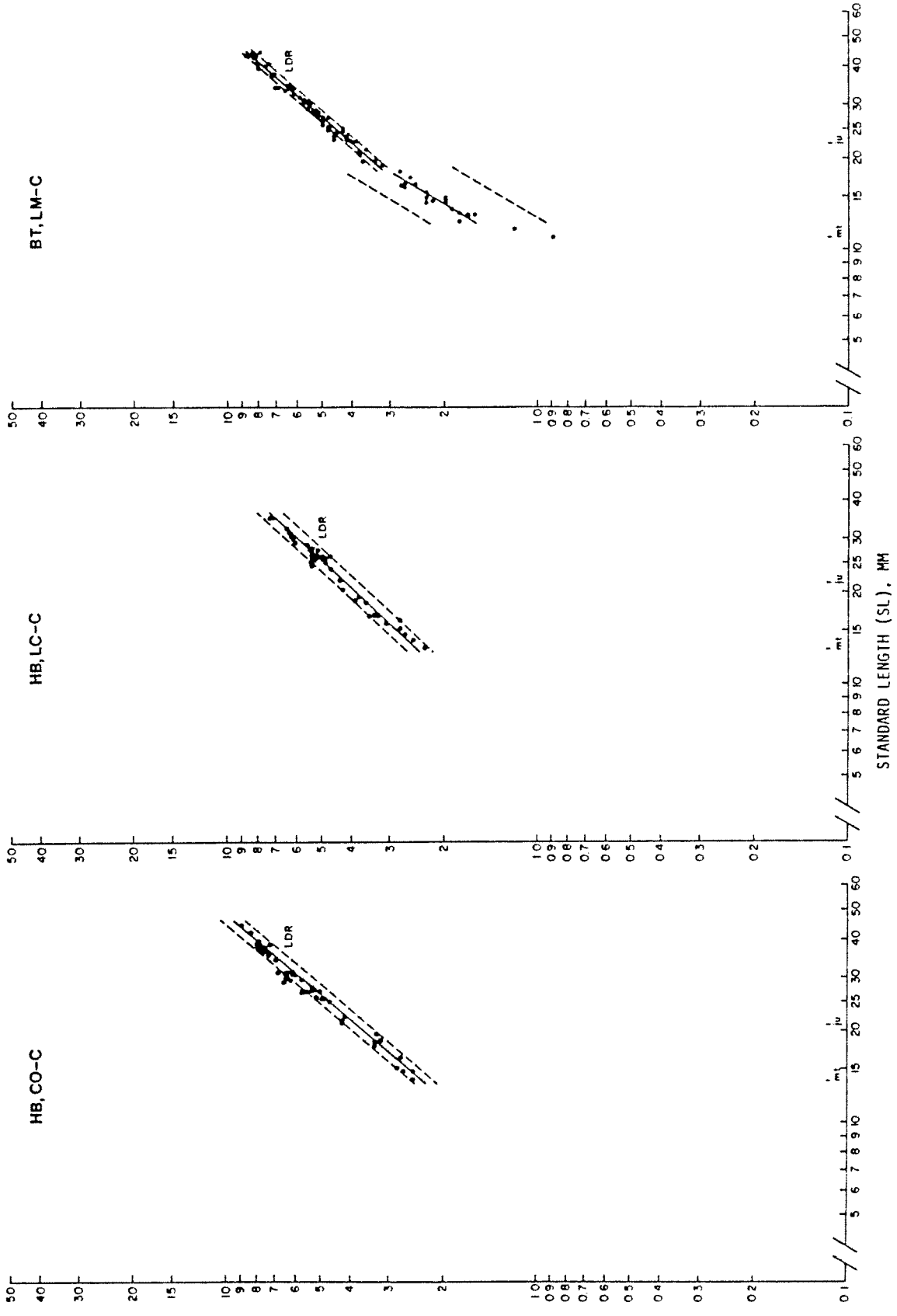

BT, LM-C
HB, LC-C
HB, CO-C
LDR
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-26. Log-log plots of selected measurements (**LDR** against **SL**) for *Gila robusta robusta* metalarvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

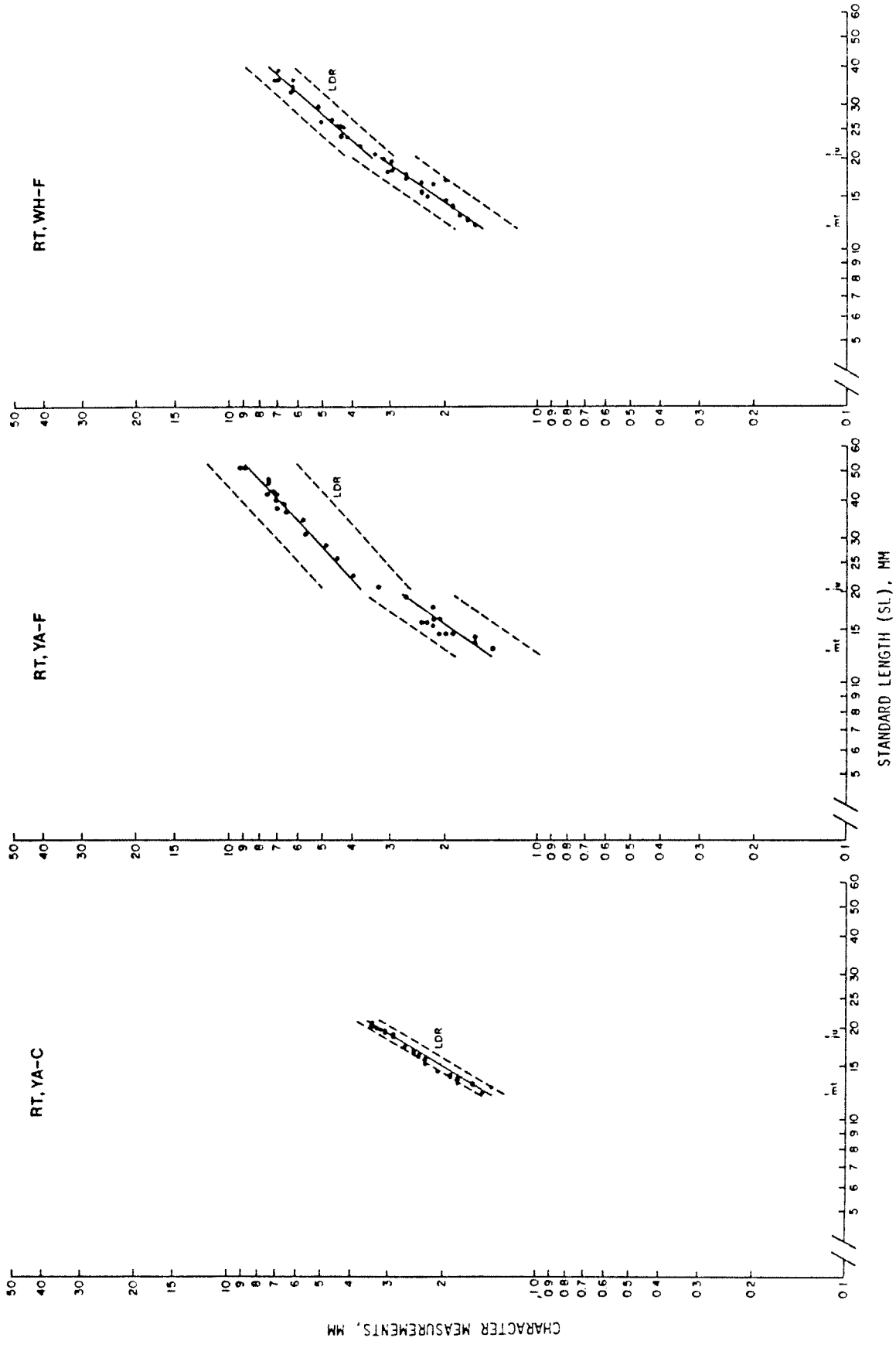

RT, YA-C
RT, YA-F
RT, WH-F
LDR
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-27. Log-log plots of selected measurements (**LAR** against **SL**) for *Gila cypha* and *G. elegans* metalarvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

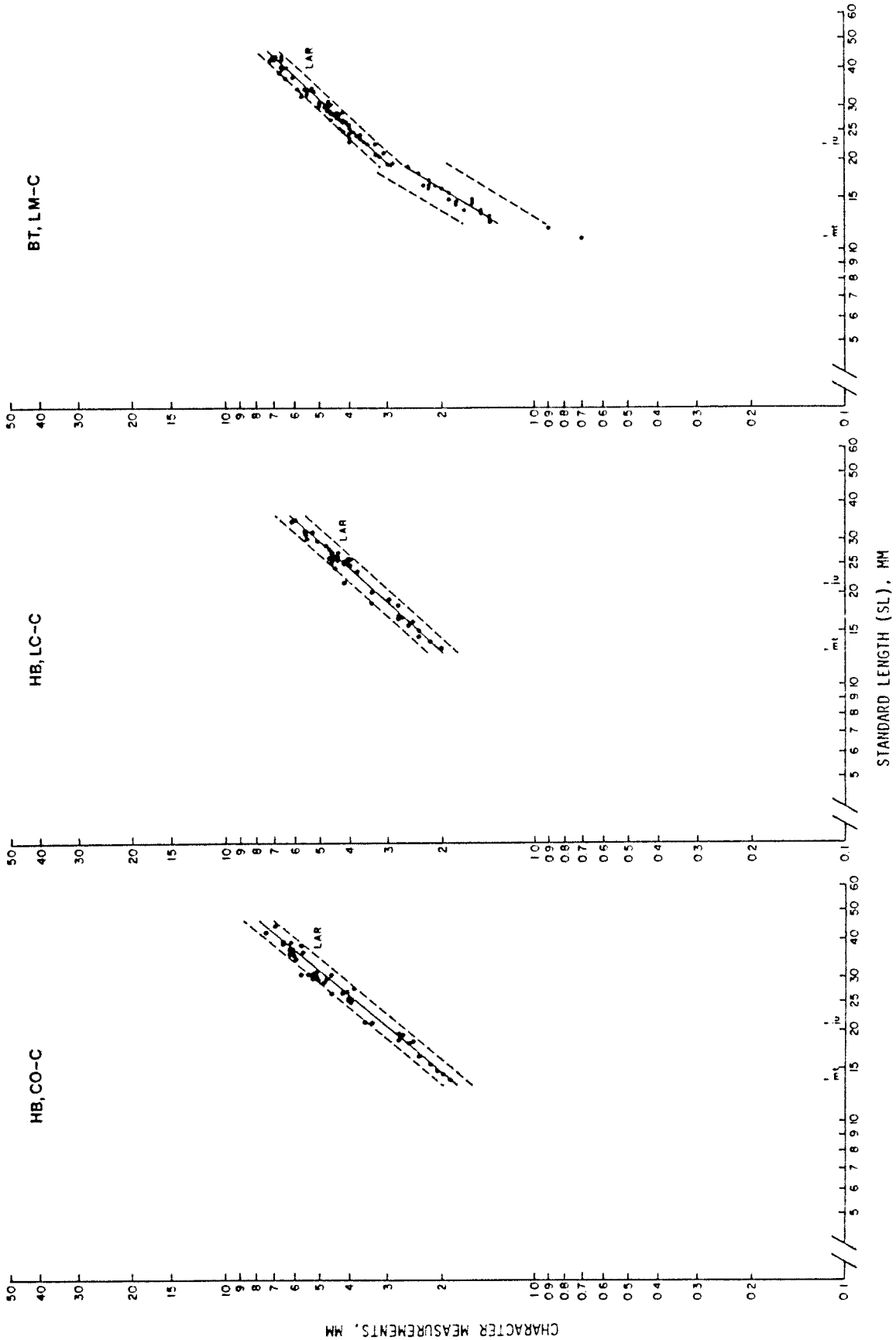

BT, LM-C
HB, LC-C
HB, CO-C
LAR
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-28. Log-log plots of selected measurements (**LAR** against **SL**) for *Gila robusta robusta* metalarvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

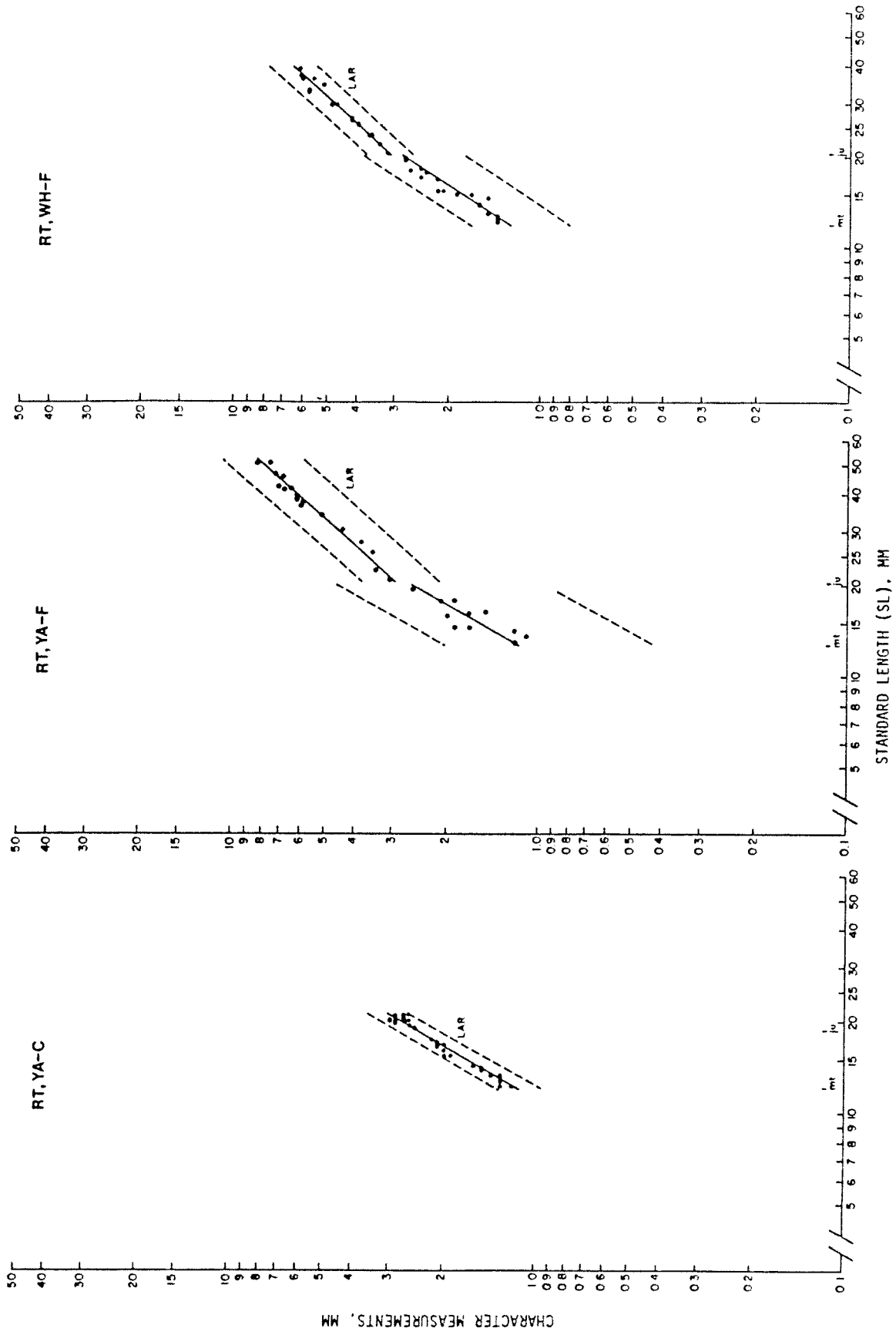

RT, WH-F
RT, YA-F
RT, YA-C
LAR
STANDARD LENGTH (SL), MM
CHARACTER MEASUREMENTS, MM

FIGURE B-29. Log-log plots of selected measurements (**D:BPE** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

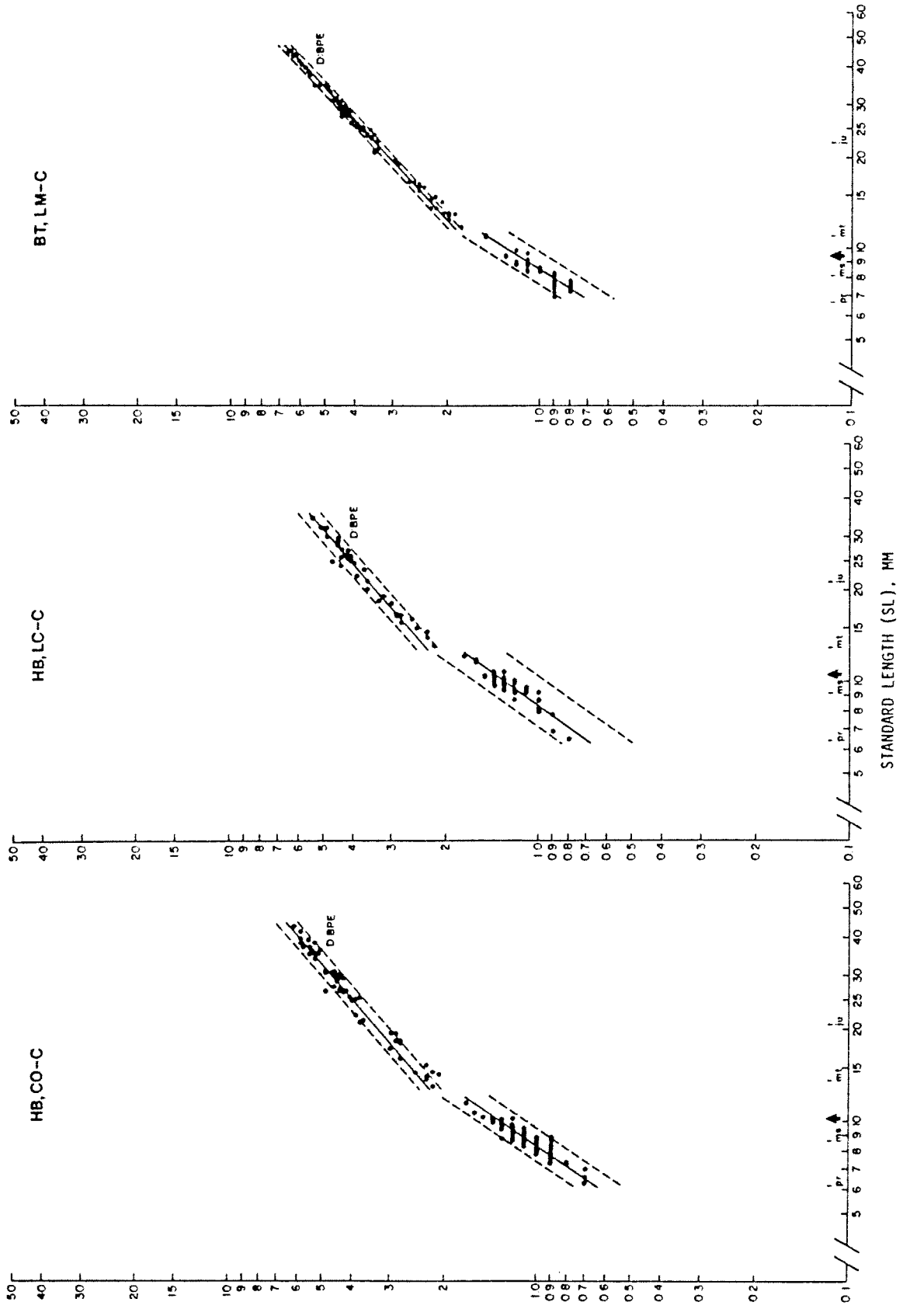

BT, LM-C
HB, LC-C
HB, CO-C
DBPE
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-30. Log-log plots of selected measurements (**D:BPE** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

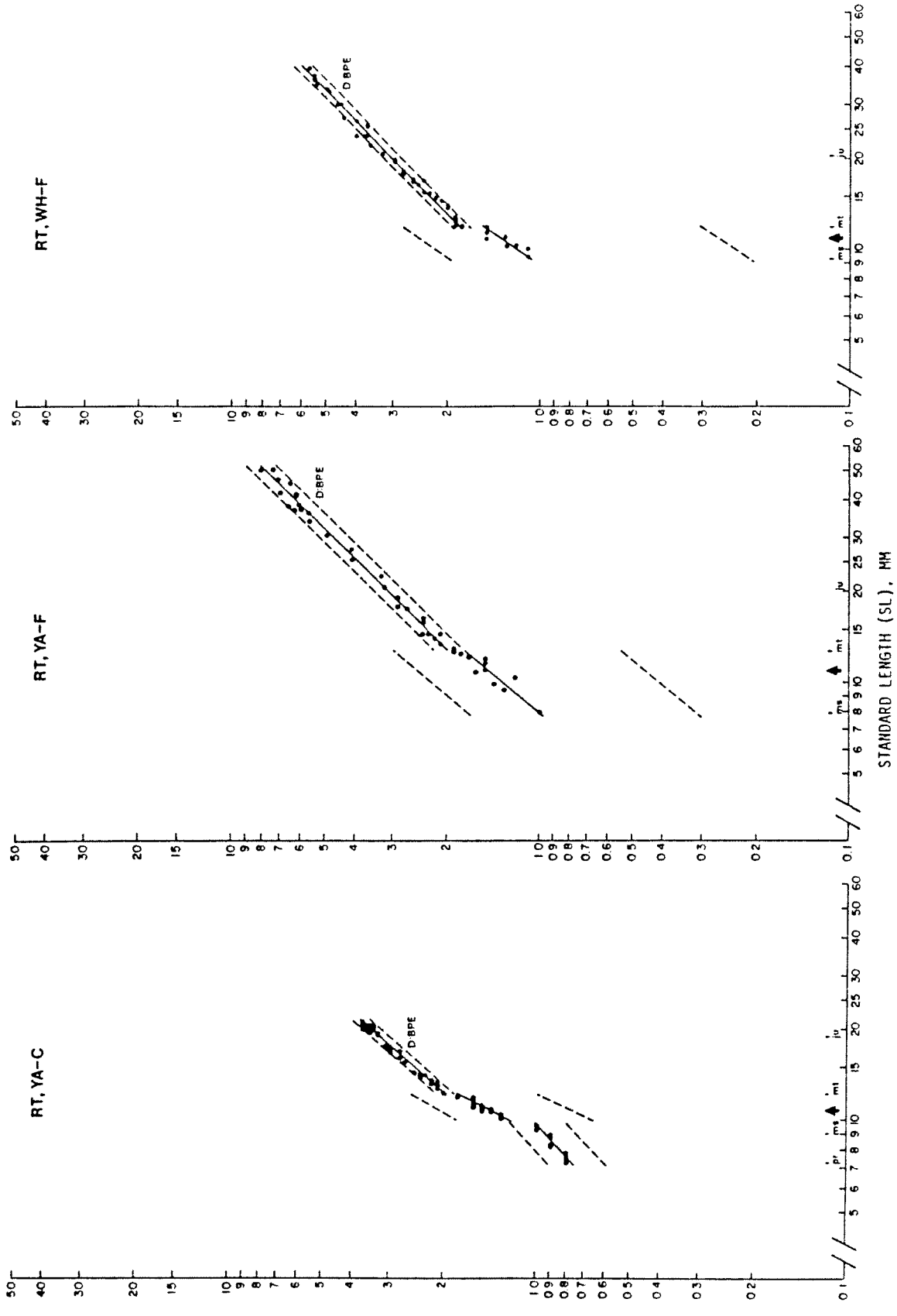

RT, YA-C
RT, YA-F
RT, WH-F
DBPE
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-31. Log-log plots of selected measurements (**W:BPE** against **SL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

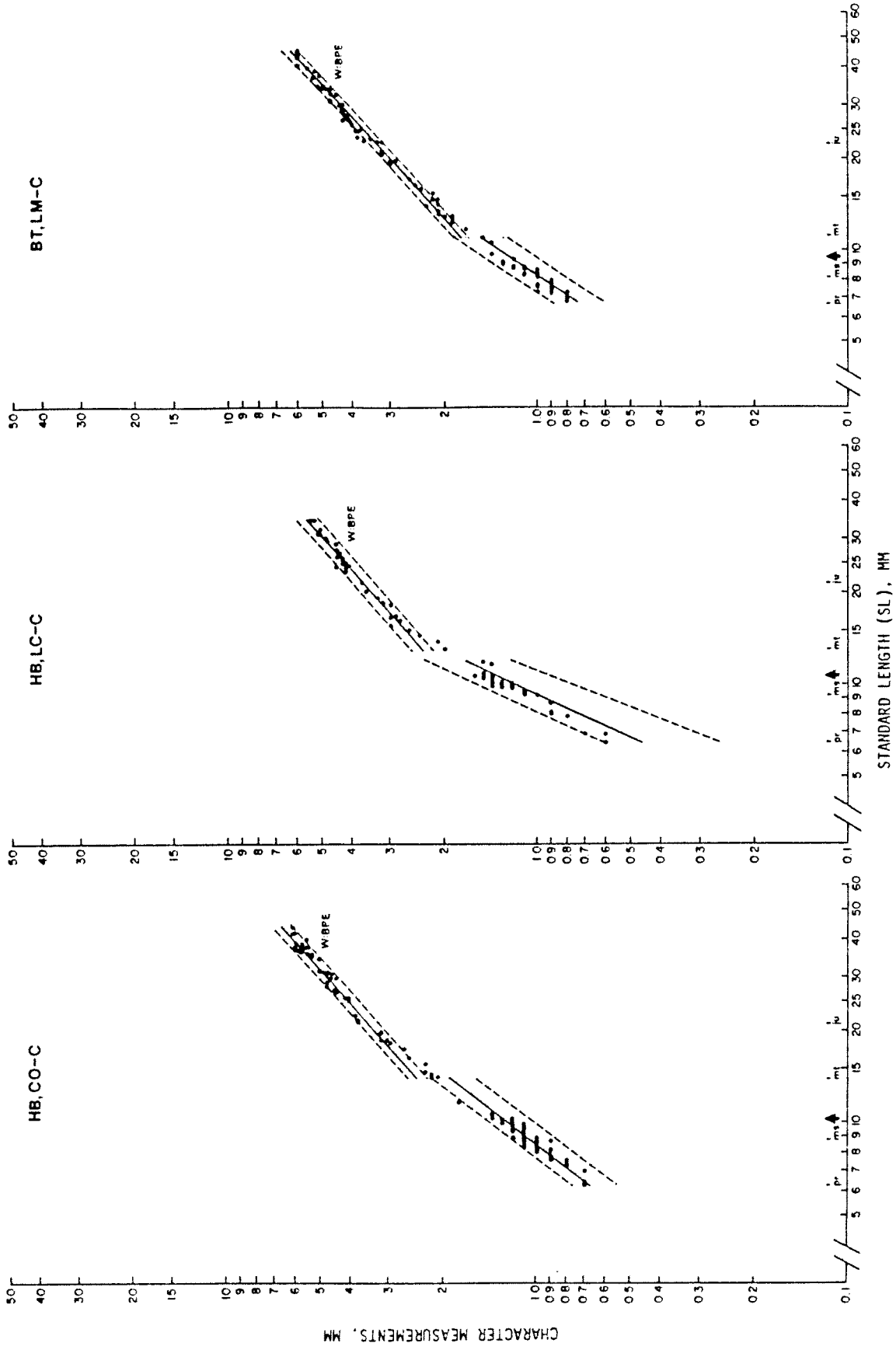

HB,CO-C
HB,LC-C
BT,LM-C
W·BPE
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-32. Log-log plots of selected measurements (**W:BPE** against **SL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Arrow indicates completion of notochord flexion (point at which criteria for measuring standard length change). Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

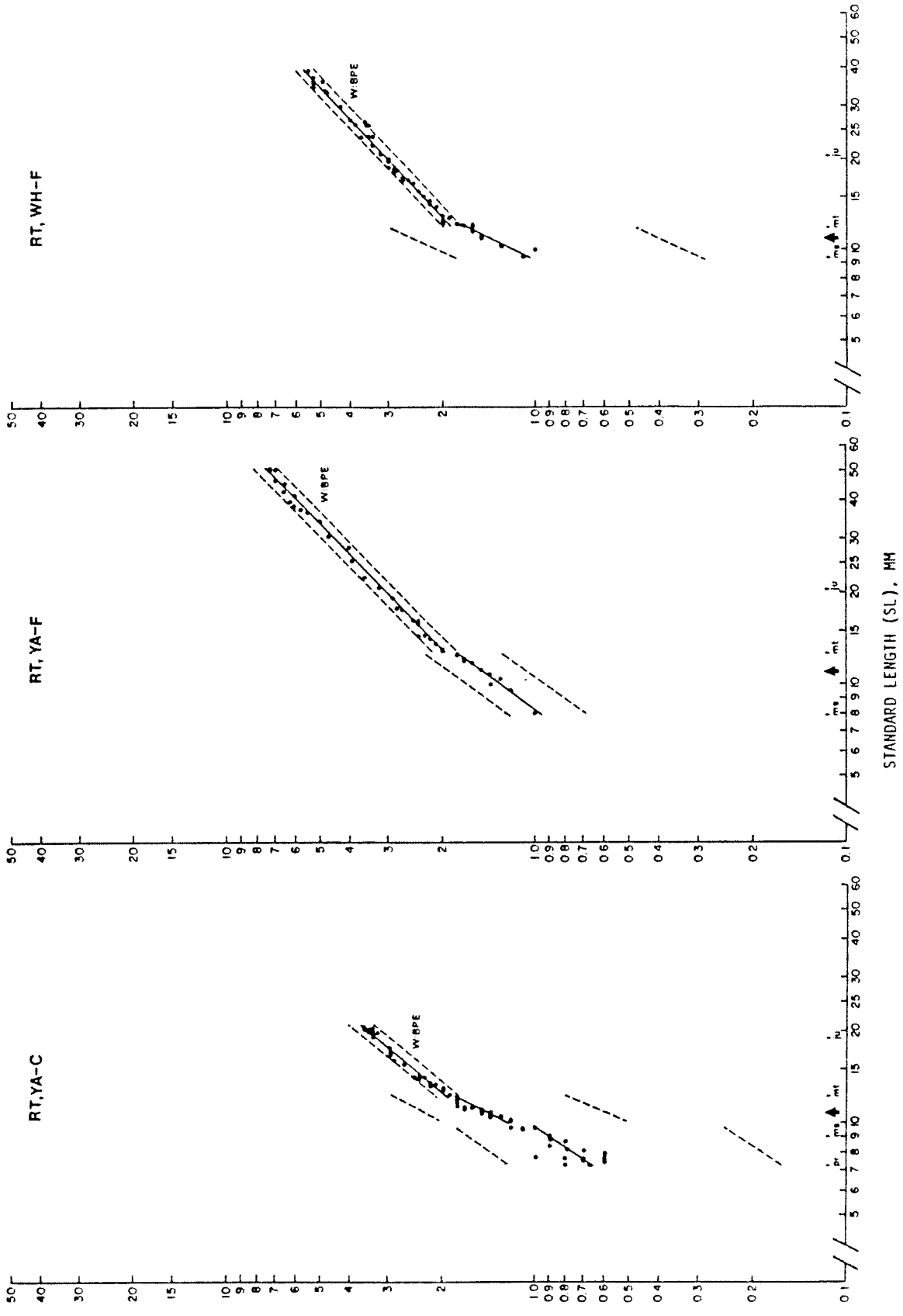

RT, WH-F
RT, YA-F
RT, YA-C
W:BPE
CHARACTER MEASUREMENTS, MM
STANDARD LENGTH (SL), MM

FIGURE B-33. Log-log plots of selected measurements (**ED** against **HL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

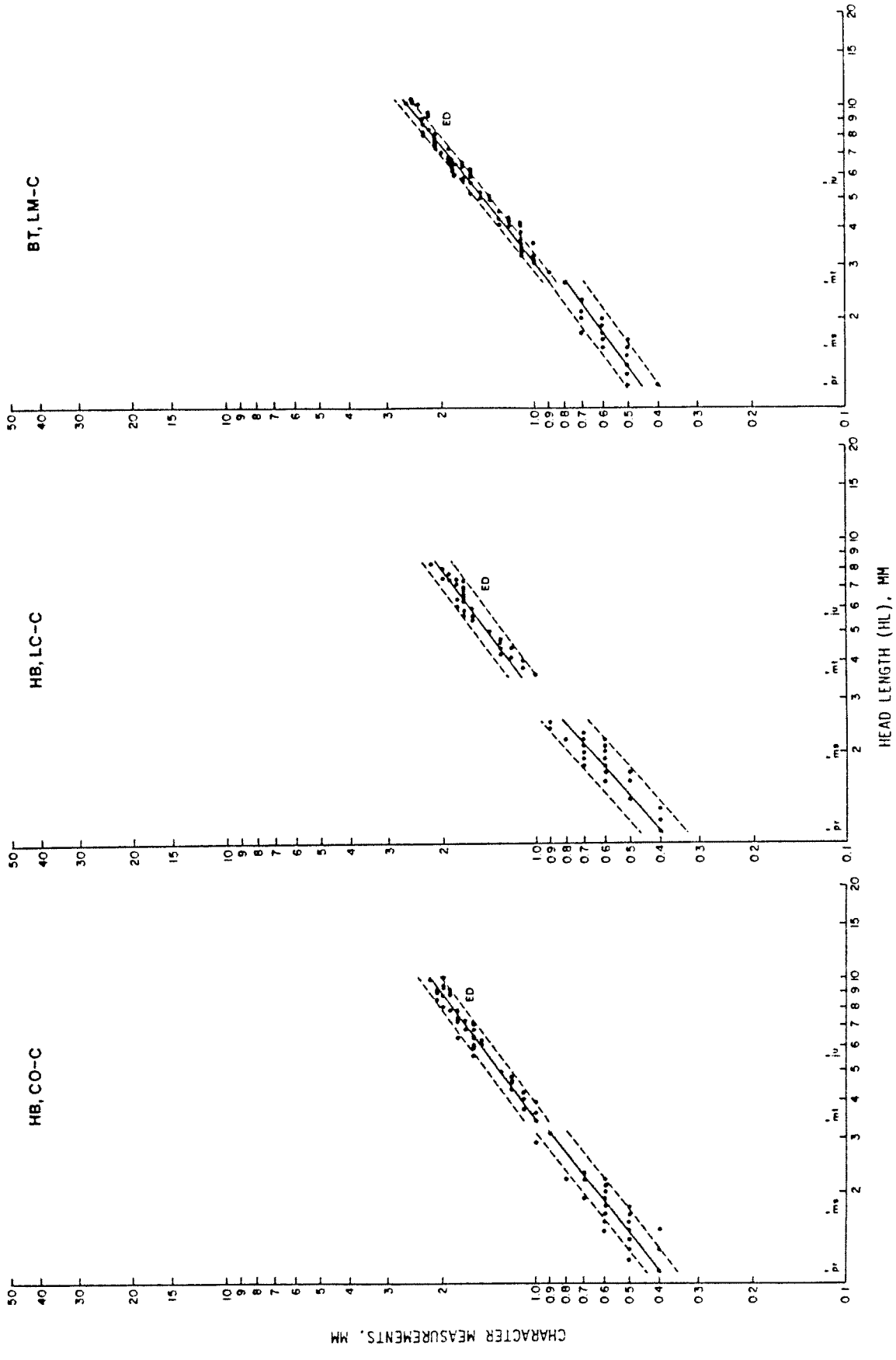

BT, LM-C
HB, LC-C
HB, CO-C
ED
HEAD LENGTH (HL), MM
CHARACTER MEASUREMENTS, MM

FIGURE B-34. Log-log plots of selected measurements (**ED** against **HL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

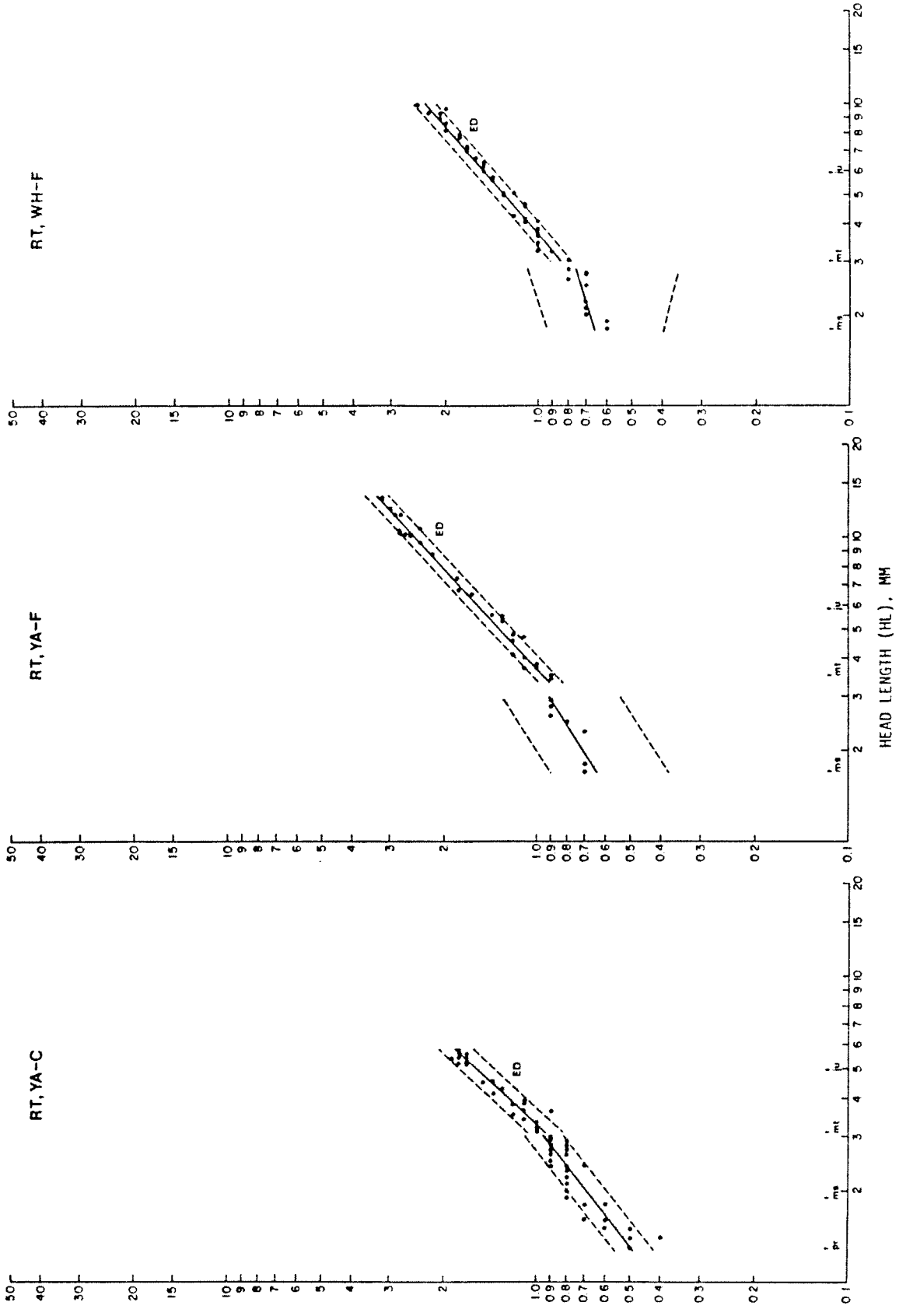

RT, WH-F
RT, YA-F
RT, YA-C
ED
HEAD LENGTH (HL), MM
CHARACTER MEASUREMENTS, MM

FIGURE B-35. Log-log plots of selected measurements (**D:APM** against **HL**) for *Gila cypha* and *G. elegans* larvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

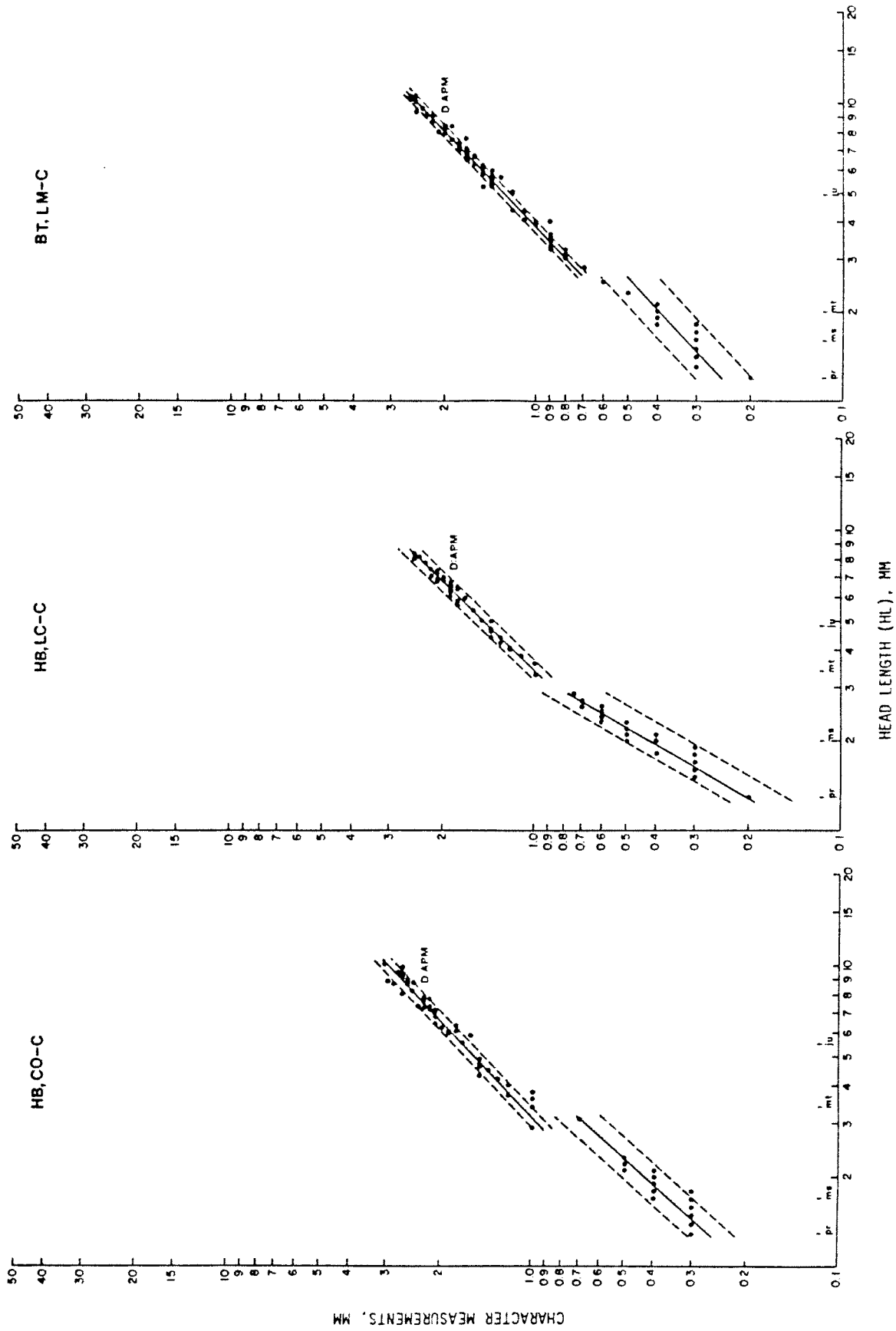

BT, LM-C
HB, LC-C
HB, CO-C
D APM
CHARACTER MEASUREMENTS, MM
HEAD LENGTH (HL), MM

FIGURE B-36. Log-log plots of selected measurements (**D:APM** against **HL**) for *Gila robusta robusta* larvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Onset of various developmental intervals (sensu Snyder and Muth 1988, in press, see Methods) is indicated by **pr**, protolarva phase; **ms**, mesolarva phase; **mt**, metalarva phase; and **ju**, juvenile period. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

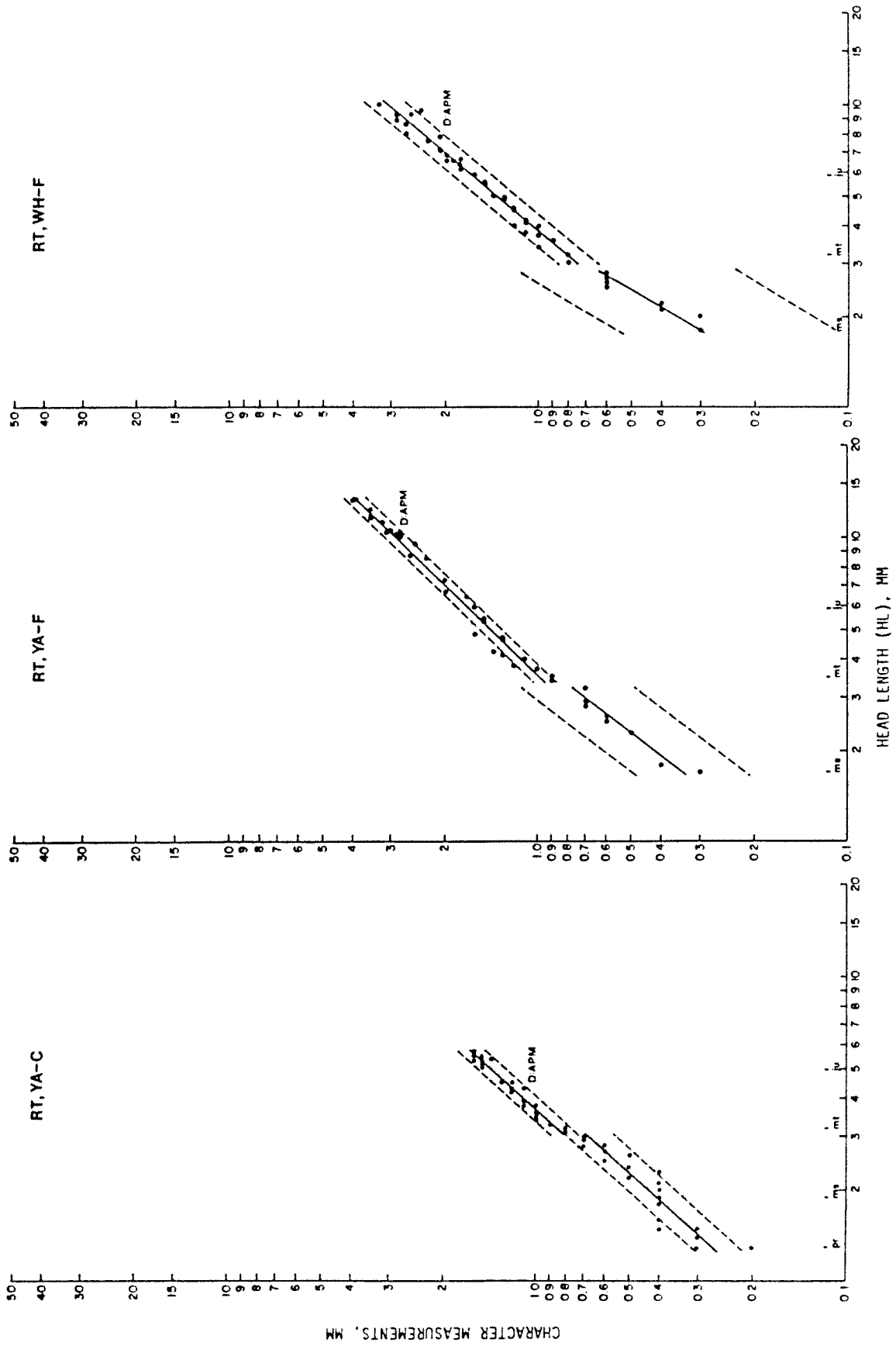

RT, WH-F
RT, YA-F
RT, YA-C
DAPM
HEAD LENGTH (HL), MM
CHARACTER MEASUREMENTS, MM

FIGURE B-37. Log-log plots of selected measurements (**P1** against **PFO**) for *Gila cypha* and *G. elegans* metalarvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

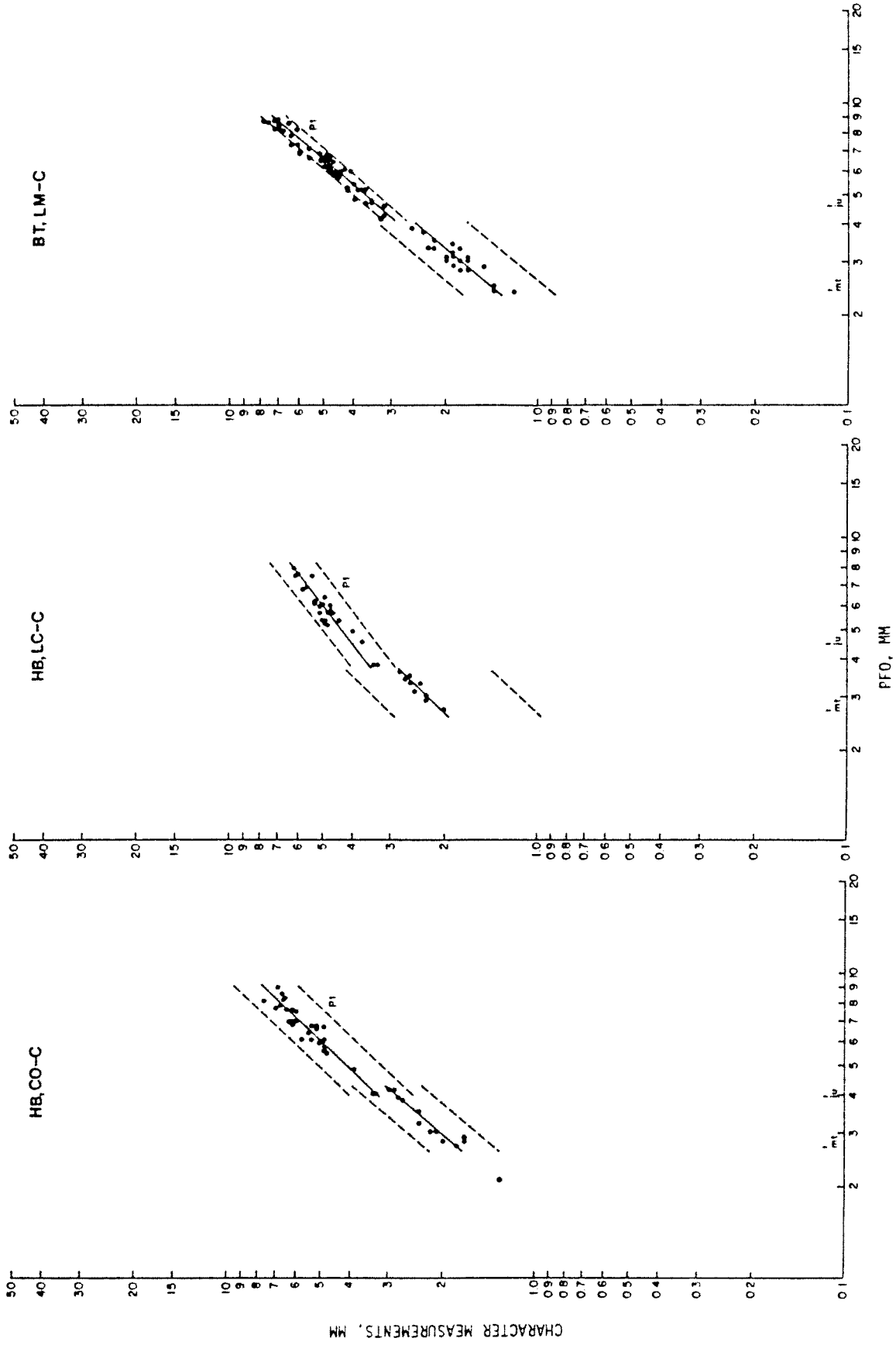

HB, CO-C
HB, LC-C
BT, LM-C
P1
CHARACTER MEASUREMENTS, MM
PFO, MM

FIGURE B-38. Log-log plots of selected measurements (**P1** against **PFO**) for *Gila robusta robusta* metalarvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

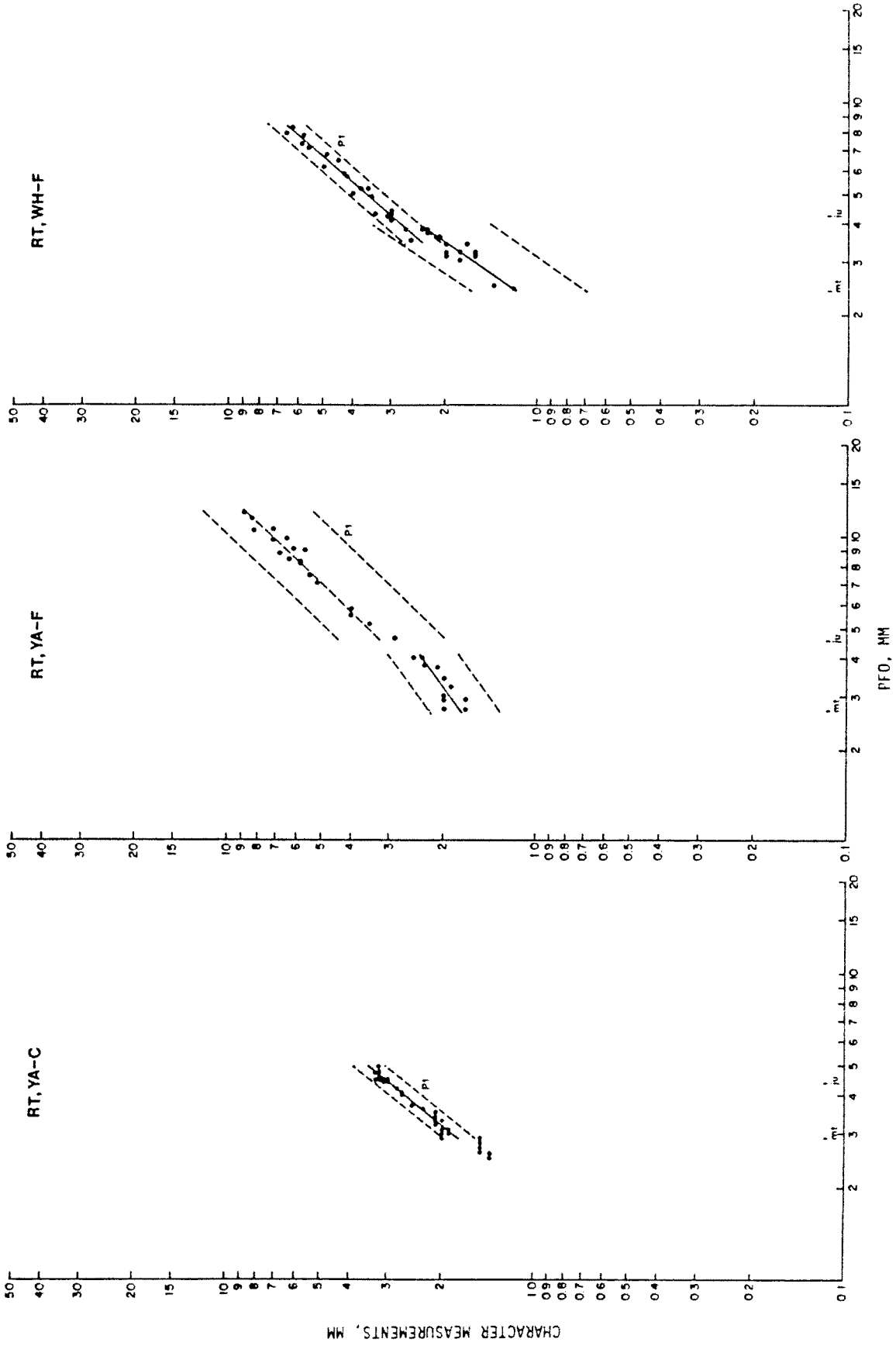

RT, WH-F
RT, YA-F
RT, YA-C
P1
PFO, MM
CHARACTER MEASUREMENTS, MM

FIGURE B-39. Log-log plots of selected measurements (**P2** against **PFO**) for *Gila cypha* and *G. elegans* metalarvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

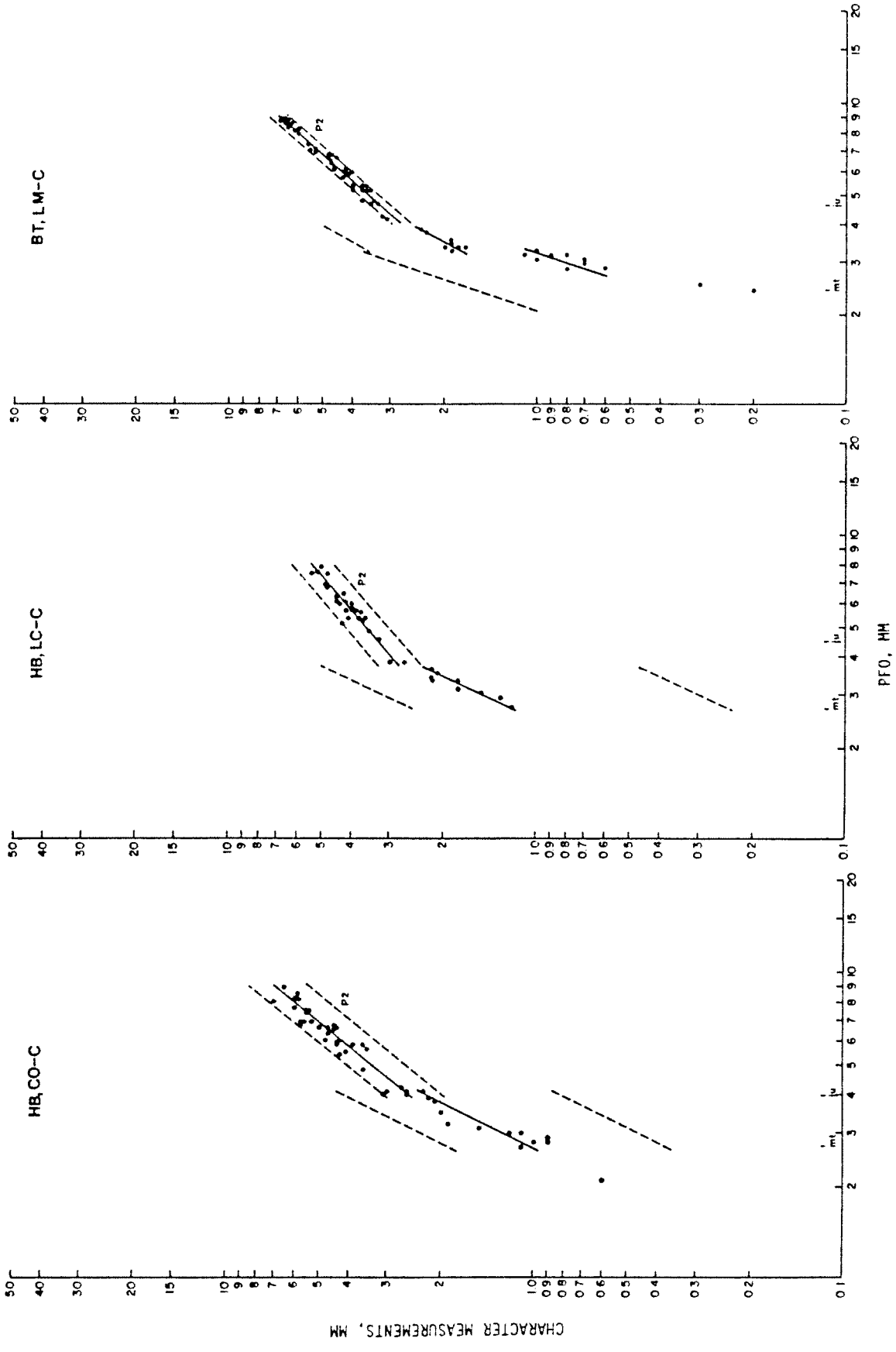

BT, LM-C
HB, LC-C
HB, CO-C
P2
CHARACTER MEASUREMENTS, MM
PFO, MM

FIGURE B-40. Log-log plots of selected measurements (**P2** against **PFO**) for *Gila robusta robusta* metalarvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 4 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

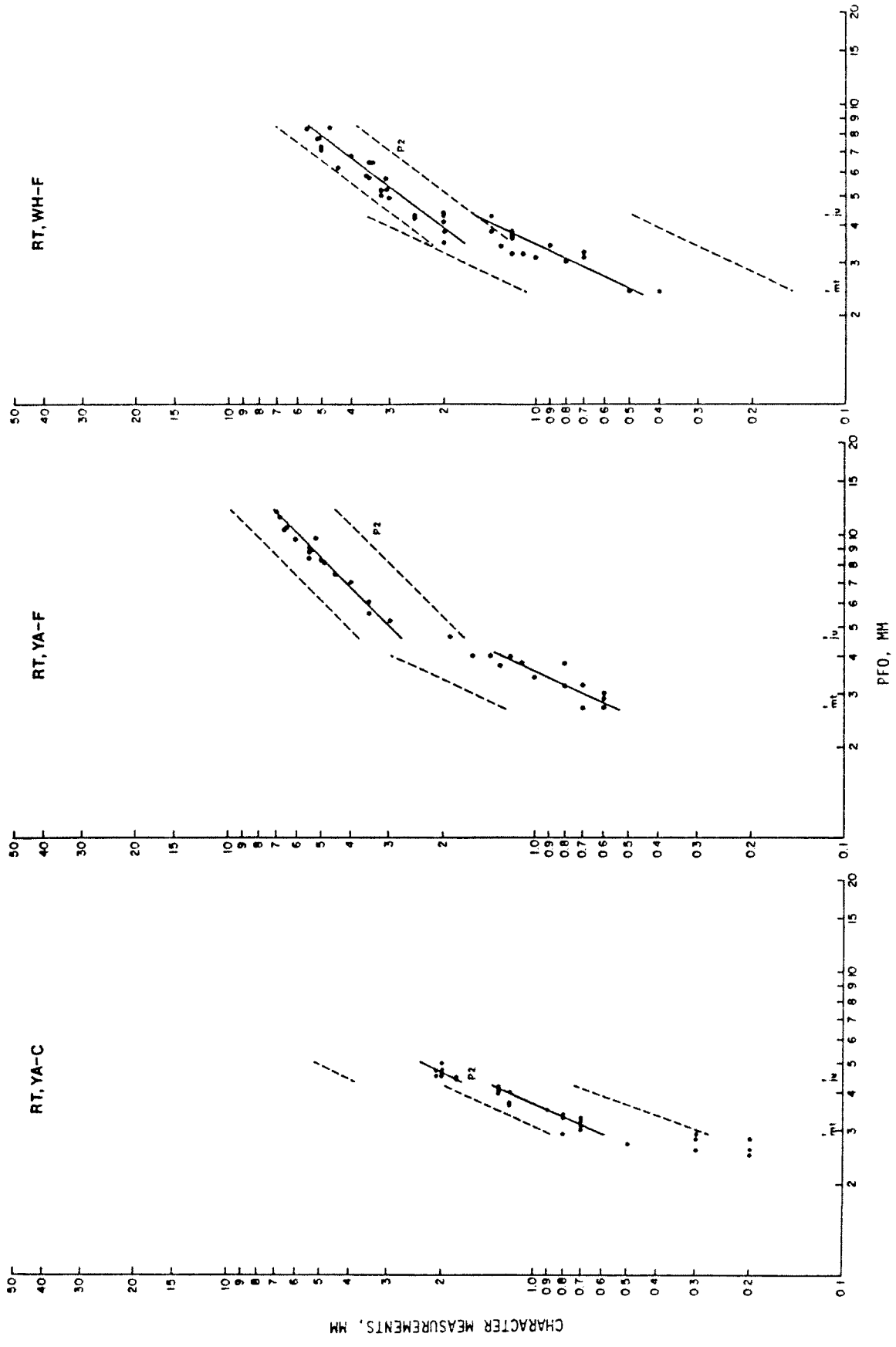

RT, WH-F
RT, YA-F
RT, YA-C
P2
CHARACTER MEASUREMENTS, MM
PFO, MM

FIGURE B-41. Log-log plots of selected measurements (**OAPHP** against **OAPOP**) for *Gila cypha* and *G. elegans* metalarvae and young-of-the-year juveniles. **HB, CO-C** = *G. cypha* specimens cultured from brood stock collected from the Colorado River, Colorado; **HB, LC-C** = *G. cypha* specimens cultured from brood stock collected from the Little Colorado River, Arizona; **BT, LM-C** = *G. elegans* specimens cultured from brood stock collected from Lake Mohave, Nevada side. See Methods for clarification of capture locations. See Figure 5 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Inflection points, indicating a change in growth stanza, were chosen by inspection. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".

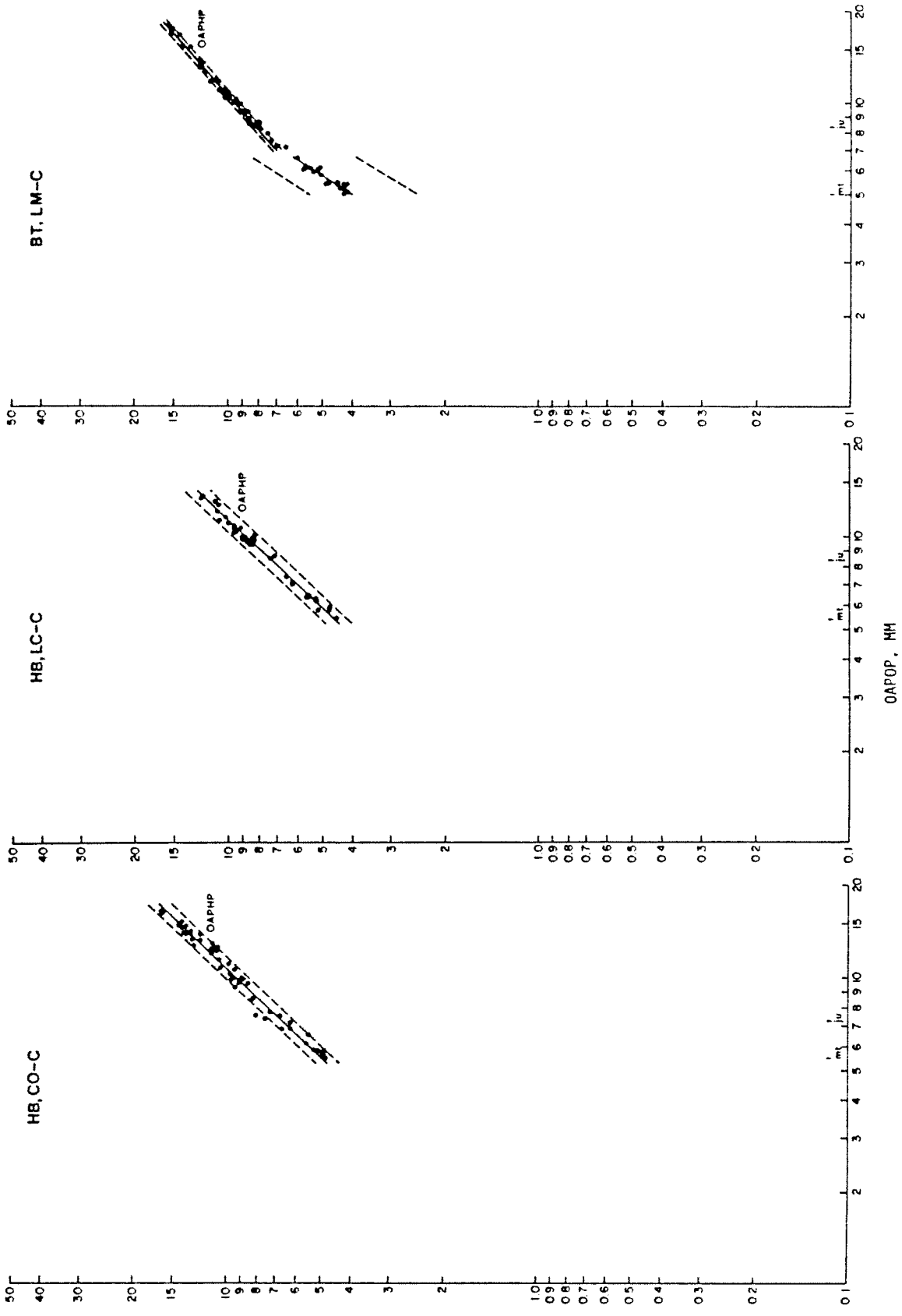
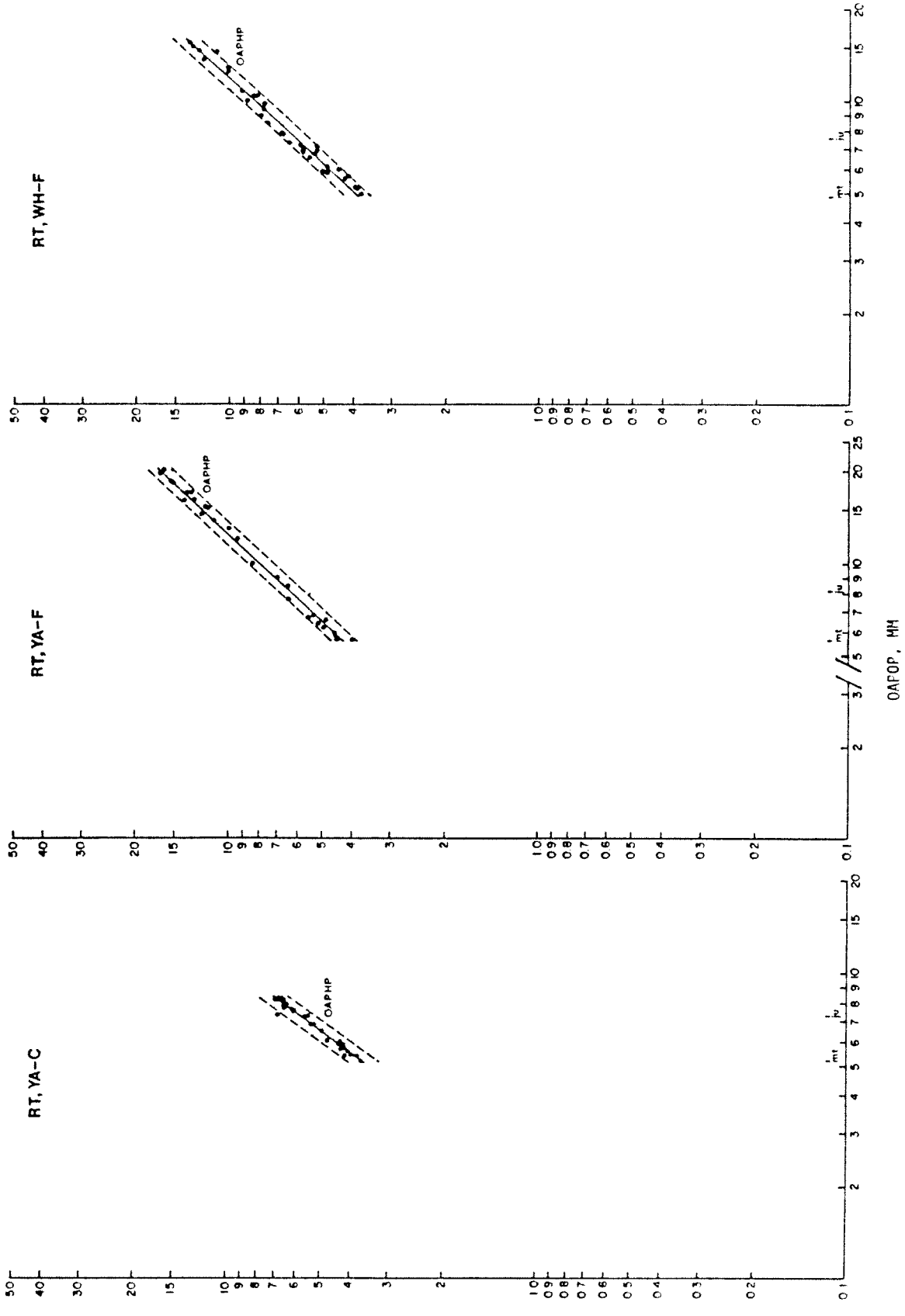

BT, LM-C
HB, LC-C
HB, CO-C
OAPHP
OAPOP, MM
CHARACTER MEASUREMENTS, MM

FIGURE B-42. Log-log plots of selected measurements (**OAPHP** against **OAPOP**) for *Gila robusta robusta* metalarvae and young-of-the-year juveniles. **RT, YA-C** = specimens cultured from brood stock collected from the Yampa River, Colorado; **RT, WH-F** = specimens collected from the White River, Colorado; **RT, YA-F** = specimens collected from the Yampa River, Colorado. See Methods for clarification of capture locations. See Figure 5 for definitions of character abbreviations and methods of measurement. Developmental-interval terminology for fish early-life stages is as defined by Snyder and Muth (1988, in press, see Methods). Onset of metalarva phase is indicated by **mt**, and onset of juvenile period is indicated by **ju**. Constants for regression lines (solid lines) and 95% confidence intervals (dashed lines) for each growth stanza were calculated using Bartlett's (1949) method of "best fit".


RT, YA-C
RT, YA-F
RT, WH-F
OAPHP
CHARACTER MEASUREMENTS, MM
OAPOP, MM

APPENDIX C

REGRESSION CONSTANTS FOR LOG-LOG PLOTS OF SELECTED MEASUREMENTS FOR LARVAE AND YOUNG-OF-THE-YEAR JUVENILES OF SIX *GILA* GROUPS PRESENTED IN APPENDIX B

TABLE C-1. Regression constants for log-log plots (log Y = log b + k log X) of selected measurements for larvae and young-of-the-year juveniles of six Gila groups presented in Appendix B. Growth stanzas proceed from left to right on plots. CI is the 95% confidence interval. Regression constants and confidence intervals for each growth stanza were calculated using Bartlett's (1949) method of "best fit". See Figures B-1, B-2 for definitions of Gila group abbreviations, and Figures 4, 5 for definitions of body measurements.

Body Measurements			Stanza 1			Stanza 2			Stanza 3		
Y	X	Gila group	X (mm) range	b CI	k CI	X (mm) range	b CI	k CI	X (mm) range	b CI	k CI
AE	SL	HB, CO-C	6.2-12.9	-0.2±0.01	0.06±0.01	13.6-43.0	-0.18±0.04	0.07±0.01			
		HB, LC-C	6.4-11.7	-0.27±0.01	0.06±0.02	12.9-34.1	-0.38±0.04	0.07±0.01			
		BT, LM-C	6.8-9.7	0.06±0.0	0.02±0.01	10.9-16.1	-0.52±0.02	0.08±0.02	16.1-43.7	0.1±0.03	0.05±0.005
		RT, YA-C	7.2-11.9	-0.41±0.02	0.08±0.02	12.1-20.7	-0.32±0.03	0.07±0.01			
		RT, YA-F	7.9-12.3	-0.33±0.08	0.07±0.08	12.6-49.8	-0.19±0.09	0.08±0.01			
		RT, WH-F	9.3-11.7	-0.69±0.05	0.11±0.08	11.8-38.8	0.02±0.03	0.06±0.004			
OP1	SL	HB, CO-C	7.2-10.5	-1.12±0.04	0.32±0.05	11.4-43.0	0.54±0.08	0.23±0.01			
		HB, LC-C	6.4-11.7	-0.77±0.03	0.28±0.04	12.9-34.1	0.79±0.07	0.22±0.01			
		BT, LM-C	6.8-9.7	-1.34±0.02	0.36±0.03	10.9-17.6	-0.61±0.05	0.3±0.03	18.6-43.7	0.74±0.06	0.22±0.01
		RT, YA-C	7.2-9.5	0.12±0.03	0.17±0.05	10.0-11.9	-3.54±0.05	0.56±0.1	12.1-20.7	-0.17±0.05	0.28±0.02
		RT, YA-F	7.9-12.3	-0.84±0.11	0.31±0.11	12.6-49.8	0.37±0.11	0.25±0.01			
		RT, WH-F	9.3-11.7	-1.66±0.07	0.38±0.12	11.8-19.7	-0.48±0.06	0.31±0.03	20.4-38.8	1.24±0.12	0.22±0.03
PV	SL	HB, CO-C	6.2-43.0	0.26±0.09	0.63±0.01						
		HB, LC-C	6.4-34.1	0.31±0.04	0.63±0.01						
		BT, LM-C	6.8-9.7	-0.72±0.03	0.75±0.05	10.7-32.0	1.0±0.04	0.59±0.01	32.7-43.7	2.64±0.18	0.56±0.05
		RT, YA-C	7.2-20.7	0.42±0.03	0.65±0.01						
		RT, YA-F	7.9-49.8	0.49±0.1	0.65±0.01						
		RT, WH-F	9.3-38.8	0.55±0.08	0.62±0.01						
W:APM	SL	HB, CO-C	6.2-12.9	0.05±0.01	0.02±0.01	13.6-43.0	-0.09±0.03	0.04±0.004			
		HB, LC-C	6.4-11.7	-0.03±0.01	0.03±0.01	12.9-34.1	0.22±0.03	0.03±0.01			
		BT, LM-C	6.8-17.6	-0.1±0.01	0.04±0.002	18.6-43.7	-0.16±0.03	0.04±0.004			
		RT, YA-C	7.2-20.7	-0.25±0.14	0.06±0.003						
		RT, YA-F	7.9-49.8	-0.1±0.04	0.04±0.004						
		RT, WH-F	9.3-38.8	-0.19±0.02	0.05±0.003						

TABLE C-1. Continued.

Body Measurements Y	X	Gila group	Stanza 1 X (mm) range	Stanza 1 b CI	Stanza 1 k CI	Stanza 2 X (mm) range	Stanza 2 b CI	Stanza 2 k CI	Stanza 3 X (mm) range	Stanza 3 b CI	Stanza 3 k CI
PE	SL	HB, CO-C	6.2-12.9	-0.33±0.02	0.14±0.02	13.6-43.0	0.29±0.05	0.11±0.01			
		HB, LC-C	6.4-11.7	-0.5±0.02	0.15±0.02	12.9-34.1	0.19±0.04	0.12±0.01			
		BT, LM-C	6.8-9.3	-0.24±0.01	0.12±0.02	9.7-17.6	-0.26±0.04	0.14±0.02	18.6-43.7	0.65±0.04	0.1±0.01
		RT, YA-C	7.2-9.5	-0.12±0.02	0.11±0.03	10.0-11.9	-0.81±0.03	0.19±0.06	12.1-20.7	-0.55±0.03	0.17±0.01
		RT, YA-F	7.9-12.3	-0.24±0.07	0.14±0.06	12.6-49.8	0.001±0.11	0.14±0.01			
		RT, WH-F	9.3-11.8	-0.84±0.09	0.19±0.11	11.9-38.8	0.12±0.04	0.12±0.01			
CP	SL	HB, CO-C	10.2-43.0	-0.27±0.08	0.37±0.01						
		HB, LC-C	12.9-34.1	-0.68±0.07	0.38±0.01						
		BT, LM-C	12.3-43.7	-0.09±0.05	0.36±0.01						
		RT, YA-C	12.1-20.7	-1.12±0.05	0.4±0.18						
		RT, YA-F	12.6-49.8	0.35±0.15	0.34±0.01						
		RT, WH-F	11.8-38.8	-0.16±0.09	0.35±0.01						
A	SL	HB, CO-C	13.6-43.0	-0.56±0.07	0.21±0.01						
		HB, LC-C	12.9-34.1	-0.6±0.05	0.22±0.01						
		BT, LM-C	12.3-18.6	-0.79±0.05	0.21±0.04	19.0-43.7	-0.72±0.07	0.22±0.01			
		RT, YA-C	12.1-20.7	-0.88±0.03	0.21±0.01						
		RT, YA-F	12.6-49.8	-0.65±0.08	0.2±0.01						
		RT, WH-F	11.8-38.8	-0.54±0.05	0.2±0.01						
OP2	SL	HB, CO-C	11.4-43.0	0.58±0.1	0.43±0.01						
		HB, LC-C	12.9-34.1	0.48±0.08	0.46±0.02						
		BT, LM-C	10.7-43.7	0.53±0.05	0.43±0.01						
		RT, YA-C	10.8-20.7	-0.05±0.04	0.51±0.01						
		RT, YA-F	11.5-49.8	0.1±0.16	0.5±0.01						
		RT, WH-F	11.8-38.8	0.62±0.12	0.47±0.02						

TABLE C-1. Continued.

Body Measurements Y	X	Gila group	Stanza 1 X (mm) range	b CI	k CI	Stanza 2 X (mm) range	b CI	k CI	Stanza 3 X (mm) range	b CI	k CI
D:ME	SL	HB, CO-C	6.2-11.4	-0.29±0.02	0.15±0.02	12.9-43.0	0.3±0.09	0.13±0.01			
		HB, LC-C	6.4-11.7	-0.5±0.02	0.17±0.03	12.9-34.1	0.49±0.04	0.12±0.01			
		BT, LM-C	6.8-9.7	-0.38±0.01	0.16±0.02	10.7-43.7	0.19±0.04	0.13±0.004			
		RT, YA-C	7.2-11.9	-0.54±0.02	0.17±0.02	12.1-20.7	-0.46±0.03	0.18±0.01			
		RT, YA-F	7.9-12.3	-0.14±0.07	0.14±0.07	12.6-49.8	0.06±0.1	0.14±0.01			
		RT, WH-F	9.3-11.7	-0.72±0.05	0.18±0.08	11.8-38.8	0.15±0.04	0.13±0.01			
OD	SL	HB, CO-C	10.2-43.0	0.44±0.1	0.48±0.01						
		HB, LC-C	12.9-34.1	0.76±0.07	0.48±0.01						
		BT, LM-C	10.9-43.7	0.27±0.07	0.5±0.01						
		RT, YA-C	12.1-20.7	0.09±0.06	0.53±0.02						
		RT, YA-F	12.6-49.8	0.25±0.17	0.54±0.01						
		RT, WH-F	11.8-38.8	0.69±0.07	0.51±0.01						
CL	SL	HB, CO-C	10.3-15.2	-0.89±0.12	0.15±0.07	15.8-43.0	0.53±0.09	0.23±0.01			
		HB, LC-C	10.4-11.7	-0.37±0.13	0.08±0.29	12.9-30.7	0.26±0.1	0.14±0.02			
		BT, LM-C	9.4-11.0	0.01±0.11	0.04±0.22	11.6-14.3	-0.52±0.05	0.13±0.08	14.5-43.7	-0.32±0.06	0.14±0.01
		RT, YA-C	10.8-11.9	-2.0±0.06	0.21±0.16	12.1-20.7	-0.46±0.03	0.13±0.01			
		RT, YA-F	11.2-16.0	-0.5±0.16	0.12±0.1	20.1-49.8	1.07±0.22	0.08±0.05			
		RT, WH-F	11.8-19.7	0.09±0.14	0.08±0.07	20.4-38.8	-0.09±0.18	0.12±0.04			
ID	SL	HB, CO-C	10.2-43.0	0.25±0.1	0.62±0.01						
		HB, LC-C	12.9-34.1	0.46±0.07	0.64±0.14						
		BT, LM-C	10.9-43.7	0.18±0.06	0.64±0.01						
		RT, YA-C	12.1-20.7	-0.53±0.07	0.7±0.02						
		RT, YA-F	12.6-49.8	-0.09±0.19	0.66±0.02						
		RT, WH-F	11.8-38.8	0.49±0.08	0.63±0.01						

TABLE C-1. Continued.

Body Measurements Y	X	Gila group	Stanza 1 X (mm) range	Stanza 1 b CI	Stanza 1 k CI	Stanza 2 X (mm) range	Stanza 2 b CI	Stanza 2 k CI	Stanza 3 X (mm) range	Stanza 3 b CI	Stanza 3 k CI
P2	SL	HB, CO-C	13.6-15.2	-1.54±0.15	0.18±70.79	15.8-43.0	-0.8±0.07	0.18±0.01			
		HB, LC-C	14.8-34.1	-0.47±0.06	0.17±0.01						
		BT, LM-C	12.3-13.4	-0.93±0.1	0.14±0.4	13.8-18.6	-1.26±0.07	0.19±0.09	19.0-43.7	-0.77±0.05	0.18±0.01
		RT, YA-C	12.1-20.7	-1.66±0.02	0.18±0.01						
		RT, YA-F	12.6-18.8	-1.15±0.1	0.14±0.07	20.1-49.8	-1.0±0.17	0.16±0.03			
		RT, WH-F	11.8-16.6	-1.4±0.07	0.17±0.05	16.9-38.8	-0.84±0.08	0.17±0.01			
OA	SL	HB, CO-C	10.2-43.0	0.26±0.08	0.63±0.01						
		HB, LC-C	12.9-34.1	0.76±0.07	0.62±0.01						
		BT, LM-C	10.9-43.7	0.19±0.05	0.64±0.01						
		RT, YA-C	12.1-20.7	1.14±0.06	0.6±0.02						
		RT, YA-F	12.6-49.8	0.26±0.14	0.67±0.01						
		RT, WH-F	11.8-38.8	0.24±0.08	0.65±0.01						
ED	SL	HB, CO-C	6.2-10.5	-0.13±0.01	0.08±0.01	11.4-21.8	0.16±0.03	0.06±0.01	24.5-43.0	0.84±0.03	0.03±0.01
		HB, LC-C	6.4-10.7	-0.06±0.01	0.07±0.02	11.5-21.2	0.09±0.02	0.07±0.01	23.1-34.1	0.85±0.03	0.03±0.01
		BT, LM-C	6.8-9.7	-0.18±0.01	0.09±0.02	10.7-20.8	0.14±0.03	0.07±0.01	22.4-43.7	0.65±0.03	0.04±0.004
		RT, YA-C	7.2-20.7	-0.3±0.01	0.1±0.003						
		RT, YA-F	7.9-18.8	0.03±0.03	0.07±0.01	20.1-49.8	0.41±0.09	0.06±0.02			
		RT, WH-F	9.3-11.7	0.32±0.04	0.04±0.06	11.8-23.4	0.13±0.2	0.06±0.01	25.0-38.8	0.36±0.06	0.05±0.02
PFO	SL	HB, CO-C	11.4-43.0	0.03±0.09	0.21±0.01						
		HB, LC-C	12.9-34.1	-0.19±0.08	0.23±0.02						
		BT, LM-C	10.7-13.4	-0.69±0.04	0.29±0.05	13.8-43.7	0.02±0.05	0.21±0.01			
		RT, YA-C	10.8-20.7	0.34±0.04	0.22±0.01						
		RT, YA-F	11.5-49.8	-0.11±0.1	0.23±0.01						
		RT, WH-F	11.8-38.8	0.25±0.09	0.22±0.01						

TABLE C-1. Continued.

Body Measurements Y	X	Gila group	Stanza 1 X (mm) range	b CI	k CI	Stanza 2 X (mm) range	b CI	k CI	Stanza 3 X (mm) range	b CI	k CI
IA	SL	HB, CO-C	10.2-43.0	0.2±0.09	0.74±0.01						
		HB, LC-C	12.9-34.1	0.37±0.08	0.75±0.01						
		BT, LM-C	10.9-43.7	0.09±0.05	0.76±0.01						
		RT, YA-C	12.1-20.7	0.68±0.05	0.73±0.02						
		RT, YA-F	12.6-49.8	-0.04±0.15	0.78±0.01						
		RT, WH-F	11.8-38.8	0.25±0.09	0.76±0.01						
DB	SL	HB, CO-C	10.2-43.0	-0.19±0.07	0.15±0.01						
		HB, LC-C	12.9-34.1	-0.3±0.05	0.15±0.01						
		BT, LM-C	10.9-17.6	-0.25±0.04	0.15±0.03	18.6-43.7	0.41±0.04	0.12±0.01			
		RT, YA-C	12.1-20.7	-0.55±0.03	0.16±0.01						
		RT, YA-F	12.6-49.8	-0.36±0.1	0.13±0.01						
		RT, WH-F	11.8-38.8	-0.14±0.04	0.12±0.01						
AB	SL	HB, CO-C	13.6-43.0	0.1±0.07	0.11±0.01						
		HB, LC-C	12.9-34.1	-0.33±0.05	0.13±0.01						
		BT, LM-C	10.9-43.7	-0.13±0.04	0.13±0.005						
		RT, YA-C	12.1-20.7	-0.44±0.03	0.13±0.01						
		RT, YA-F	12.6-49.8	-0.25±0.08	0.11±0.01						
		RT, WH-F	11.8-38.8	-0.01±0.05	0.11±0.01						
P1	SL	HB, CO-C	13.6-43.0	-0.72±0.08	0.2±0.01						
		HB, LC-C	12.9-34.1	-0.16±0.08	0.19±0.01						
		BT, LM-C	10.9-22.4	-0.29±0.04	0.15±0.01	22.4-43.7	-0.6±0.07	0.19±0.01			
		RT, YA-C	12.1-20.7	-0.21±0.15	0.17±0.01						
		RT, YA-F	12.6-49.8	-0.62±0.09	0.18±0.01						
		RT, WH-F	11.8-38.8	-0.63±0.07	0.19±0.01						

TABLE C-1. Continued.

Body Measurements Y	X	Gila group	Stanza 1 X (mm) range	Stanza 1 b CI	Stanza 1 k CI	Stanza 2 X (mm) range	Stanza 2 b CI	Stanza 2 k CI	Stanza 3 X (mm) range	Stanza 3 b CI	Stanza 3 k CI
D:APM	SL	HB, CO-C	6.2-11.4	-0.23±0.01	0.07±0.01	12.9-43.0	0.22±0.04	0.07±0.005			
		HB, LC-C	6.4-11.7	-0.86±0.02	0.13±0.02	12.9-34.1	0.22±0.02	0.07±0.004			
		BT, LM-C	6.8-12.8	-0.28±0.01	0.08±0.01	12.7-43.7	0.2±0.01	0.05±0.002			
		RT, YA-C	7.2-11.9	-0.44±0.01	0.09±0.01	12.1-20.7	-0.22±0.02	0.09±0.005			
		RT, YA-F	7.9-12.3	-0.53±0.03	0.1±0.03	12.6-49.8	0.03±0.06	0.08±0.005			
		RT, WH-F	9.3-12.6	-1.09±0.04	0.15±0.04	13.5-38.8	-0.14±0.04	0.08±0.01			
D	SL	HB, CO-C	13.6-43.0	-0.49±0.09	0.25±0.01						
		HB, LC-C	12.9-34.1	-0.12±0.05	0.24±0.01						
		BT, LM-C	10.9-17.6	-1.24±0.06	0.27±0.04	18.6-43.7	-0.23±0.06	0.23±0.01			
		RT, YA-C	12.1-20.7	-0.39±0.02	0.21±0.01						
		RT, YA-F	12.6-49.8	-0.64±0.07	0.22±0.01						
		RT, WH-F	11.8-38.8	-0.53±0.08	0.23±0.01						
ΣFL	SL	HB, CO-C	13.6-43.0	-3.06±0.36	1.11±0.05						
		HB, LC-C	12.9-34.1	-0.38±0.37	1.06±0.07						
		BT, LM-C	12.3-18.6	-5.07±0.29	1.14±0.2	19.0-43.7	-2.69±0.25	1.08±0.04			
		RT, YA-C	12.1-20.7	-4.57±0.06	1.11±0.02						
		RT, YA-F	12.6-18.8	-3.63±0.39	0.94±0.24	20.1-49.8	-1.71±0.51	0.98±0.1			
		RT, WH-F	11.8-19.7	-4.45±0.39	1.1±0.18	20.4-37.2	-2.85±0.67	1.05±0.14			
C	SL	HB, CO-C	13.6-43.0	-0.6±0.15	0.29±0.02						
		HB, LC-C	10.4-11.7	******	*******	12.9-34.1	0.53±0.11	0.26±0.02			
		BT, LM-C	9.4-11.6	-0.28±0.14	0.17±0.26	12.3-18.6	-0.52±0.09	0.25±0.06	19.0-43.7	-0.16±0.08	0.26±0.01
		RT, YA-C	10.8-11.9	-3.04±0.16	0.44±0.54						
		RT, YA-F	11.2-18.8	-1.33±0.15	0.3±0.09	20.1-49.8	1.33±0.33	0.22±0.07			
		RT, WH-F	10.8-11.7	-0.2±0.15	0.15±0.3	11.8-38.8	-0.78±0.14	0.29±0.02			

TABLE C-1. Continued.

Body Measurements Y	X	Gila group	Stanza 1 X (mm) range	Stanza 1 b CI	Stanza 1 k CI	Stanza 2 X (mm) range	Stanza 2 b CI	Stanza 2 k CI	Stanza 3 X (mm) range	Stanza 3 b CI	Stanza 3 k CI
LDR	SL	HB, CO-C	13.6-43.0	-0.76±0.07	0.23±0.01						
		HB, LC-C	12.9-34.1	-0.34±0.07	0.22±0.01						
		BT, LM-C	12.3-17.6	-1.42±0.07	0.25±0.06	18.6-43.7	-0.59±0.06	0.21±0.01			
		RT, YA-C	12.1-20.7	-1.49±0.03	0.24±0.01						
		RT, YA-F	12.6-18.8	-0.83±0.06	0.19±0.04	20.1-49.8	0.6±0.24	0.16±0.05			
		RT, WH-F	11.8-19.7	-0.89±0.06	0.21±0.03	20.4-38.8	-0.55±0.13	0.2±0.03			
LAR	SL	HB, CO-C	13.6-43.0	-0.67±0.08	0.19±0.01						
		HB, LC-C	12.9-34.1	-0.31±0.07	0.19±0.01						
		BT, LM-C	12.3-18.6	-1.23±0.05	0.21±0.03	19.0-43.7	-0.36±0.06	0.17±0.01			
		RT, YA-C	12.1-20.7	-1.44±0.04	0.22±0.02						
		RT, YA-F	12.6-18.8	-1.3±0.12	0.2±0.08	20.1-49.8	-0.4±0.19	0.17±0.04			
		RT, WH-F	11.8-19.7	-0.94±0.08	0.19±0.04	20.4-38.8	-0.33±0.11	0.18±0.02			
D:BPE	SL	HB, CO-C	6.2-11.4	-0.49±0.02	0.18±0.02	12.9-43.0	0.53±0.06	0.14±0.01			
		HB, LC-C	6.4-11.7	-0.43±0.02	0.18±0.03	12.9-34.1	0.47±0.05	0.15±0.01			
		BT, LM-C	6.8-11.0	-0.57±0.02	0.19±0.02	11.6-43.7	0.21±0.03	0.15±0.004			
		RT, YA-C	7.2-9.5	0.07±0.013	0.1±0.02	10.0-11.9	-1.21±0.03	0.25±0.06	12.1-20.7	-0.44±0.03	0.20±0.01
		RT, YA-F	7.9-12.3	-0.12±0.09	0.15±0.09	12.6-49.8	0.01±0.11	0.16±0.01			
		RT, WH-F	9.3-11.7	-0.59±0.07	0.18±0.1	11.8-38.8	0.04±0.04	0.15±0.01			
W:BPE	SL	HB, CO-C	6.2-13.8	-0.32±0.02	0.16±0.02	13.6-43.0	0.53±0.06	0.14±0.01			
		HB, LC-C	6.4-11.7	-1.06±0.02	0.24±0.03	12.9-34.1	0.47±0.05	0.15±0.01			
		BT, LM-C	6.8-11.0	-0.51±0.01	0.19±0.02	10.9-43.7	0.29±0.03	0.14±0.004			
		RT, YA-C	7.2-9.5	-0.5±0.05	0.16±0.08	10.0-11.9	-1.7±0.04	0.3±0.08	12.1-20.7	-0.37±0.03	0.2±0.01
		RT, YA-F	7.9-12.3	-0.47±0.03	0.18±0.03	12.6-49.8	0.17±0.08	0.15±0.01			
		RT, WH-F	9.3-11.7	-1.48±0.06	0.27±0.1	11.8-38.8	0.28±0.05	0.14±0.01			

TABLE C-1. Continued.

Body Measurements Y	X	Gila group	Stanza 1 X (mm) range	Stanza 1 b CI	Stanza 1 k CI	Stanza 2 X (mm) range	Stanza 2 b CI	Stanza 2 k CI	Stanza 3 X (mm) range	Stanza 3 b CI	Stanza 3 k CI
ED	HL	HB, CO-C	1.0-3.1	0.13±0.01	0.25±0.04	3.4-10.0	0.41±0.03	0.18±0.02			
		HB, LC-C	1.1-2.5	0.07±0.01	0.3±0.05	3.6-8.3	0.42±0.03	0.2±0.02			
		BT, LM-C	1.2-2.6	0.18±0.01	0.23±0.04	2.6-10.5	0.3±0.02	0.23±0.01			
		RT, YA-C	1.3-3.0	0.15±0.02	0.27±0.04	3.1-5.7	-0.14±0.03	0.35±0.03			
		RT, YA-F	1.7-2.9	0.26±0.04	0.22±0.13	3.4-13.3	0.13±0.04	0.24±0.02			
		RT, WH-F	1.8-2.8	0.51±0.04	0.08±0.13	3.0-9.9	0.2±0.03	0.22±0.02			
D:APM	HL	HB, CO-C	1.3-3.1	-0.06±0.01	0.25±0.03	2.9-10.0	0.09±0.03	0.29±0.02			
		HB, LC-C	1.0-2.7	-0.31±0.01	0.37±0.05	3.6-8.3	-0.03±0.02	0.3±0.02			
		BT, LM-C	1.2-2.5	0.05±0.01	0.17±0.04	2.8-10.5	0.06±0.01	0.25±0.01			
		RT, YA-C	1.3-3.0	-0.04±0.02	0.24±0.03	3.1-5.7	-0.12±0.02	0.31±0.02			
		RT, YA-F	1.7-3.2	-0.15±0.03	0.29±0.08	3.4-13.3	-0.04±0.05	0.29±0.02			
		RT, WH-F	1.8-2.8	-0.29±0.04	0.33±0.13	3.0-9.9	-0.24±0.04	0.33±0.03			
P1	PFO	HB, CO-C	2.7-4.2	-0.26±0.07	0.78±0.15	4.0-8.9	-0.19±0.16	0.87±0.16			
		HB, LC-C	2.7-3.6	-0.06±0.08	0.79±0.35	3.8-7.8	1.09±0.01	0.65±0.12			
		BT, LM-C	2.4-3.8	-0.48±0.06	0.77±0.18	4.1-8.8	-0.83±0.08	0.93±0.06			
		RT, YA-C	2.9-5.0	-0.65±0.04	0.83±0.06						
		RT, YA-F	2.7-4.0	0.47±0.06	0.48±0.14	4.6-11.8	-0.22±0.28	0.75±0.22			
		RT, WH-F	2.4-4.3	-0.6±0.09	0.76±0.2	3.5-8.3	-0.54±0.1	0.85±0.08			
P2	PFO	HB, CO-C	2.7-4.1	-1.69±0.14	1.0±0.34	4.0-8.9	-0.99±0.14	0.89±0.13			
		HB, LC-C	2.7-3.6	-2.4±0.12	1.32±0.53	3.8-7.8	0.57±0.08	0.61±0.1			
		BT, LM-C	2.6-3.2	-1.95±0.09	0.94±0.7	3.2-3.8	-1.94±0.11	1.14±0.63	4.1-8.8	-0.57±0.05	0.84±0.04
		RT, YA-C	2.9-4.2	-1.16±0.04	0.6±0.11	4.4-5.0	-2.12±0.05	0.89±0.53			
		RT, YA-F	2.7-4.0	-0.94±0.12	0.56±0.28	4.6-11.8	-0.04±0.23	0.61±0.19			
		RT, WH-F	2.4-4.3	-0.91±0.09	0.58±0.23	3.5-8.3	-0.97±0.16	0.77±0.12			

TABLE C-1. Continued.

Body Measurements Y	X	Gila group	Stanza 1 X (mm) range	b	CI	k	CI	Stanza 2 X (mm) range	b	CI	k	CI	Stanza 3 X (mm) range	b	CI	k	CI
OAPHP	OAPOP	HB, CO-C	5.5-16.5	-0.34	±0.15	0.97	±0.05										
		HB, LC-C	5.4-13.3	-0.59	±0.1	0.97	±0.05										
		BT, LM-C	5.0-6.6	-2.33	±0.1	1.28	±0.31	7.1-12.6	1.41	±0.07	0.81	±0.03					
		RT, YA-C	5.2-8.3	-1.97	±0.07	1.09	±0.08										
		RT, YA-F	5.6-20.0	-0.49	±0.17	0.86	±0.04										
		RT, WH-F	4.9-15.3	-0.57	±0.13	0.92	±0.05										

APPENDIX D

SELECTED MERISTICS FOR LARVAE AND YOUNG-OF-THE-YEAR JUVENILES FROM *GILA ELEGANS* X *G. ROBUSTA ROBUSTA* AND *G. ELEGANS* X *G. CYPHA* CROSSES

TABLE D-1. Summary of selected meristics by developmental phase for Gila elegans X G. robusta robusta cross cultured from brood stock collected from Lake Mohave, Nevada side, or from the Colorado River, Colorado (Figure 1, Methods). See Figures 4-6 for definitions of abbreviations and methods of counting. N_i is number of specimens out of the total number (N) having modal count. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Protolarvae (N=18)				Flexion Mesolarvae (N=11)				Postflexion Mesolarvae (N=10)				Metalarvae (N=16)				Juveniles (N=22)			
			Range				Range				Range				Range				Range	
	Mode	N_i	Min	Max	Mode	N_i	Min	Max	Mode	N_i	Min	Max	Mode	N_i	Min	Max	Mode	N_i	Min	Max
SL,mm			5	8			8	9			9	12			12	20			20	54
TL,mm			6	9			8	10			10	14			14	25			26	72
Myomeres or vertebrae[a]:																				
to OP2											16	16[b]	16	9	14	17	17	5	16	19
OD													18	8	17	19	19	9	18	20
PV	29	10	27	31	29	9	29	30	30	5	29	31	29	7	26	30	28	7	27	29
Postvent	17	10	15	18	17	6	15	18	17	6	15	18	17	5	16	18	19	8	16	20
Total	47	9	45	48	47	6	44	48	47	6	45	48	47	7	44	48	47	5	44	49
Principal fin rays:																				
P1													16	5[c]	15	16	16	11	14	17
P2													9	8[c]	9	9	9	21	8	9
D[d]									9	3[e]	9	9	9	15	9	10	9	19	9	10
A[d]									10	3[e]	10	10	10	13	9	10	10	14	9	10
C									19	9	19	20	19	16	19	19	19	21	19	20
Gill rakers[f]:																				
1st gill arch																				
External row																	11	6	9	12
Internal row																	14	6	14	16
Total																	25	6	24	28
2nd gill arch																				
External row																	14	6	14	16
Internal row																	15	6	15	17
Total																	30	7	29	32
3rd gill arch																				
External row																	17	7	16	18
Internal row																	17	4	14	17
Total																	34	4	30	34
4th gill arch																				
External row																	12	4	12	16
Internal row																	12	8	10	13
Total																	24	5	23	28
Total																				
External row																	54	4	53	59
Internal row																	58	6	57	62
Total																	112	3	110	120

[a]For juveniles, vertebra counts on 12 cleared and stained specimens; counts include the four vertebrae of the Weberian complex and the urostylar vertebra. [b]N=2. [c]N=8. [d]For postflexion mesolarvae, counts were based on pterygiophores using whole specimens examined with polarized light or cleared and stained specimens. [e]N=3. [f]Counts were made on gill arches excised from the left side of 12 cleared and stained specimens (four gill arches per specimen).

TABLE D-2. Summary of selected meristics by developmental phase for Gila elegans X G. cypha cross cultured from brood stock collected from Lake Mohave, Nevada side, or from the Colorado River, Colorado (Figure 1, Methods). See Figures 4-6 for definitions of abbreviations and methods of counting. N_i is number of specimens out of the total number (N) having modal count. Developmental-interval terminology for fish early-life stages as defined by Snyder and Muth (1988, in press, see Methods).

	Protolarvae (N=26)			Flexion Mesolarvae (N=20)			Postflexion Mesolarvae (N=2)			Metalarvae (N=4)			Juveniles (N=8)		
	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max	Mode	N_i	Range Min Max
SL,mm			6 8			7 9			11 12			13 16			26 54
TL,mm			6 9			8 10			13 14			15 21			33 67
Myomeres or vertebrae[a]:															
to OP2									16 16	16	3	15 16	16	4	16 16
OD										18	3	18 19	19	3	19 20
PV	29	10	27 31	29	9	28 30			29 30	29	2	28 30	28	3	28 29
Postvent	17	8	16 18	17	12	17 19			17 18	17	3	17 18	19	4	19 19
Total	46	9	45 49	46	12	45 48			47 48	47	3	45 47	47	3	47 48
Principal fin rays:															
P1												15 15[b]	15	5	15 16
P2												9 9[b]	9	8	9 9
D[c]									9 9	9	3	9 10	9	7	9 10
A[c]									9 10	9	3	9 10	10	5	9 10
C									19 19	19	4	19 19	19	8	19 19
Gill rakers[d]:															
1st gill arch															
External row													10	2	10 12
Internal row													16	2	15 17
Total													26	2	26 29
2nd gill arch															
External row													15	2	12 16
Internal row													16	2	14 16
Total													31	2	28 31
3rd gill arch															
External row													16	2	15 17
Internal row													14	2	14 16
Total													31	3	30 31
4th gill arch															
External row													11	2	10 15
Internal row													11	3	10 11
Total													22	2	20 26
Total															
External row															49 59
Internal row													57	2	54 58
Total															105 117

[a]For juveniles, vertebra counts on 4 cleared and stained specimens; counts include the four vertebrae of the Weberian complex and the urostylar vertebra. [b]N=2. [c]For postflexion mesolarvae, counts were based on pterygiophores using whole specimens examined with polarized light or cleared and stained specimens. [d]Counts were made on gill arches excised from the left side of 4 cleared and stained specimens (four gill arches per specimen).

APPENDIX E

CLEARING AND STAINING PROCEDURES

Chemicals

Alcian blue (powder)
Alizarin red S (powder)
Distilled water
Ethanol (absolute or denatured)
Formalin (concentrated)
Glacial acetic acid
Thymol (crystals)
Glycerin (glycerol)
Potassium hydroxide (KOH)
Sodium borate (powder)
Sodium phosphate monobasic
Sodium phosphate dibasic
Trypsin (at least 1-100 activity)

Stock Solutions

Fixative: 10% solution of formalin in distilled water; buffer with 1.8 g sodium phosphate monobasic and 1.8 g sodium phosphate dibasic/L formalin solution.

Preservative: 3% solution of formalin in distilled water; buffer with 1.8 g sodium phosphate monobasic and 1.8 g sodium phosphate dibasic/L formalin solution.

Ethanol solution: 50% solution of ethanol in distilled water.

Saturated sodium borate solution: Excess of sodium borate powder in distilled water; mix well and allow excess sodium borate to settle.

Enzyme buffer solution: 30% of supernate from saturated sodium borate solution in distilled water.

KOH solution: 1% solution KOH in distilled water.

Alcian blue stain solution: 30% glacial acetic in ethanol; to every 100 ml add 20 mg alcian blue powder (solution will keep at room temperature for 3-4 weeks).

Saturated alizarin red solution: Excess of alizarin red powder in small amount (e.g., 20 ml) of distilled water; mix well and allow excess alizarin red powder to settle.

Alizarin red stain solution: To every 100 ml of 1% KOH solution add 1-2 ml of supernate from saturated alizarin red solution (solution will keep for 1 week).

Glycerin solutions: 25, 50, and 75% solutions of glycerin in distilled water.

Trypsin solution: To every 500 ml of enzyme buffer solution, add about 1 g of trypsin powder; mix well but do not allow to froth (make just prior to use).

Cartilage Staining Procedure

1. Place live or freshly killed specimens in fixative for at least 24 h; transfer specimens to preservative for storage.

2. Place preserved specimens directly in ethanol solution for 24 h then in absolute (or denatured) ethanol for another 24 h.

3. After alcohol dehydration, place specimens in alcian blue stain solution for 24 h.

4. After staining, place specimens in supernate from saturated sodium borate solution for 12 h.

5. Remove specimens from saturated sodium borate solution and place in trypsin solution (volume 10-40 times that of specimens) and leave until 80-90% of the muscle tissue is cleared. Completely change trypsin solution every 3 d.

6. After clearing, place specimens in distilled water for 1 h.

7. Work specimens through glycerin series (25-50-75%); 24 h in each solution. Store specimens in 100% glycerin with a few thymol crystals to prevent fungus growth.

Bone Staining Procedure

1. Place live or freshly killed specimens in fixative for at least 24 h; transfer specimens to preservative for storage.

2. After preservation, the skin of juveniles with scales or thick integument should be carefully removed using fine-pointed forceps.

3. Place specimens in trypsin solution (volume 10-40 times that of specimens) and leave until 80-90% of muscle tissue is cleared. Completely change trypsin solution every 3 d.

4. After clearing, place specimens in distilled water for 1 h.

5. Place specimens in alizarin red stain solution. Staining time depends on specimen size and will typically range 1-5 d (remove specimens from stain solution periodically and check on progress).

6. After staining, soak specimens in distilled water for 1-2 h. If after 2 h, specimens still retain much stain in soft tissues, place specimens back in trypsin solution for about 2 h (periodically check on progress), then soak again in distilled water for 1 h.

7. Work specimens through glycerin series (25-50-75%); 24 h in each solution. Store specimens in 100% glycerin with a few thymol crystals to prevent fungus growth.

Note: If semitransparent soft tissue covers cartilaginous or bony structures to be studied, it can be removed with fine-pointed scissors and forceps.