

# CONTRIBUTIONS TO A GUIDE TO THE CYPRINIFORM FISH LARVAE OF THE UPPER COLORADO RIVER SYSTEM IN COLORADO 



## CONTRIBUTIONS TO A

## GUIDE TO THE CYPRINIFORM FISH LARVAE

 OF THE UPPER COLORADO RIVER SYSTEMIN COLORADO
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## DEDICATION

I dedicate these contributions and the planned guide to my wife Maryann B. Mulhall Snyder and to
my associates at Colorado State University; their assistance and encouragement was and continues to be vital to my work on fish larvae.

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The information provided in these contributions is a combination of original and previously published data and illustrations; the sources of published information are cited in the text and species accounts. Aside from my own efforts and supervision of all other work, the original contributions herein are the result of many long hours by a multitude of Colorado State University (CSU) students either conducting independent study or graduate research or serving as laboratory volunteers or employees. Most original illustrations were prepared by Lynn Bjork; others were drawn by Mark Jones, including the final preparation of all figures not part of the species accounts, and by Gail Ridlon. Those assisting with the acquisition of morphometric and meristic data from hundreds of specimens (some data not yet ready for inclusion herein) were: James Barrowman, Mark Castagneri, Linda Deutsch, William Emerson, Lyndon Evans, Marty Hayden, Robert Hufziger, Carol Jefferson, Eric Leitzinger, Leo Lentsch, Robert Muth, Martin Ogle, Florence Richey, Gail Ridlon, Robert Upton, Edmund Wick, and especially Stephanie Salyer. Tim Hill assisted in the clearing and staining of specimens. John Hawkins assisted in developing photographic techniques. Still others including Al Davis, Phil Harrison, David Herbet, Jeff Pearson, Dale Brown and Keith Fulsos assisted in the organization and/or culture of specimens for study (the latter two were local high school students in the summer CETA Youth Program).

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## PREFACE

The Upper Colorado River Basin includes a vast area of federal land under the stewardship of the Bureau of Land Management. With a rapidlyexpanding energy industry and ever-increasing agricultural, industrial, municipal, and recreational demands on the waters of the basin, impacts on the aquatic systems of the basin are particularly critical. Six endemic fishes are already in danger of extinction.

To make environmentally-sound management decisions, the Bureau of Land Management, and other federal, state, and local agencies with similar responsibilities, must have an understanding of the ecosystems potentially impacted, the organisms included in the systems, and the requirements for survival of all life history stages. Unfortunately, we are just now learning to recognize the larvae of many of the fish we must study, understand, and manage. This assemblage of developmental data, based on work by many university students, is intended to alleviate the problem. The information has already facilitated work on the early life history stages of fish in selected river reaches in western Colorado.

However, much remains to be done. Some species still await morphometric and meristic analysis and/or illustration. A few studies await acquisition of sufficient specimen material. Much data already obtained have yet to be summarized in the form of standardized tables and graphs. When this work is completed, a relatively-comprehensive guide will be possible. The planned guide will include most of the background text presented herein, keys by developmental phase, and a species account consisting of Larval Fish Laboratory Identification Circulars. In the interim, this publication is intended to make as much prepared information on larval fish identification and the cypriniform larvae of the Upper Colorado River System available to potential users as is possible under current temporal and financial constraints. Editorial comments, suggestions, and notices of observed errors are solicited and will be appreciated by the author.

## INTRODUCTION

Fish eggs and larvae are a principal focus of many ecological studies. Their sensitivity to environmental changes and susceptibility to entrainment are major concerns of siting, environmental impact, and monitoring surveys now required of many industries and utilities. Their distributions and densities are indicative of spawning and nursery areas, spawning seasons, larval behavior, and year-class strength. Even in baseline surveys designed to determine the presence and relative abundance of fishes, larval collections can often fill gaps in fish collection caused by gear selectivity, behavior, or habitats that make certain species difficult to collect or observe as adults. Studies of fish larvae can also provide information on morphological development, systematics, growth rates, survival rates, food habits, predation and various other ecological relationships (Snyder 1976a).

One of the major obstacles to including fish larvae in studies of the Upper Colorado River System, as well as in most other waters of the country, is the lack of adequate descriptions, keys, or guides to facilitate identification. In the report of a workshop group chaired by Snyder (1976a) it was estimated that of about 700 species of fish found in North America's freshwaters, the eggs or larvae of only about 15\% had been described and illustrated in the published literature. The report also discussed the limited number of regional keys and guides that included freshwater species, and noted that most were far from complete in coverage. The illustrated guides cited were Fish (1929a, 1929b and 1932, Lake Erie), Winn and Miller (1954, "postlarval" cypriniforms of the Lower Colorado River Basin), Mansueti and Hardy (1967, Chesapeake Bay Region), May and Gasaway (1967, Oklahoma), Taber (1969, Lake Texoma, Oklahoma) and Lippson and Moran (1974, Potomac River Estuary). Since that report, numerous descriptions have been added to the published literature as well as several major works including the following illustrated guides or keys: Lippson (1976, family characteristics, Great Lakes); Hogue, Wallus and Kay (1976, Tennessee River); Loos and Fuiman (1977, numerous species of the genus Notropis); Fuiman (1978 and 1979, Northeastern catostomids); Conner (1979, centrarchids, Louisiana); Loos et al. (1979, cyprinids, Upper Potomac River); Perry and Menzel (1978, cyprinids, Iowa); Wang and Kernehan (1979, Delaware Estuaries); Drewry (1979, punch card key to families of larvae with yolk, Great Lakes); and three of the six volumes of the Mid-Atlantic Bight series, Jones, Martin, and Hardy (1978), Hardy (1978a) and Hardy (1978b). The latter series is the most comprehensive synthesis of previously-published descriptive information and illustrations on the eggs, larvae, and juveniles of the species covered that is currently available; it also includes some original work. Unillustrated works such as Snyder (1971, preliminary family key, lower Susquehanna River), Nelson and Cole (1975, many species, western end of Lake Erie) and Dorr, Jude, Tesar and Thurber (1976, several species, southeastern Lake Michigan) are generally less useful than illustrated guides and keys. Many, perhaps the majority, of species described in published literature, theses, and reports are not covered in the keys and guides cited above. Bibliographies of early life history literature by Mansueti (1954), Werner (1976) and Kernehan (1976, up-date in progress) are most valuable in recognizing much, but by no means all, of this widely scattered and often obscure literature.

Not all of the information in the published literature is entirely reliable. Some published descriptions are based on misidentified specimens. For example, the $7.0,7.7,8.4$, and 9.7 mm TL specimens illustrated as Micropterus salmoides in Taber (1969) and reprinted as such in Lippson and Moran (1974) and Wang and Kernehan (1979) are a Lepomis species, possibly L. megatotis. Also, some guides include errors in transcription of certain information from the original descriptions (e.g. lengths of illustrated Morone americana in Lippson and Moran 1974 and Wang and Kernehan 1979). Some of these misidentifications and transcription errors have been reported in the published literature (Snyder and Douglas, 1978) while others await publication or discovery.

Of the 20 cypriniform fishes found in the Upper Colorado River System in Colorado, only Catostomus commersoni, Cyprinus carpio, Pimephales promelas, Notropis Lutrensis and Richardsonius balteatus, all non-natives, were adequately described and illustrated as larvae for identification purposes when work on the planned guide was begun in 1977. The descriptions of the latter two species were only marginally adequate. None of the native species were adequately described throughout a major portion of their larval development. Until work on the guide is completed, these contributions are intended to provide additional descriptive information useful in identification of the basin's cypriniform fish larvae.

## THE UPPER COLORADO RIVER SYSTEM AND ITS FISHES

All of Colorado west of the Continental Divide is drained by the Colorado River System. For water management purposes, the system has been politically divided at Lee Ferry, Arizona (just below the Glen Canyon Dam and Lake Powell) into upper and lower systems or basins. The Upper Colorado River Basin consists of three hydrologic subbasins, the Green River Basin, the Upper Main Stem Colorado River Basin, and the San Juan-Colorado River Basin, each of which is significantly represented in Colorado (Fig. 2). The nature of the Upper Colorado River System, its aquatic inhabitants and man's impact on it were summarized by Joseph et al. (1977).

Historically, the river system has provided rigorous aquatic environments typified by great fluctuation in flow, velocity, turbidity and temperature. Joseph et al. (1977) described three major habitat zones within the river system: 1) an upper zone of cold, high mountain streams; 2) an intermediate zone of small and medium-sized streams or rivers; and 3) a lower zone of larger, more turbid rivers. The latter includes both steepgradient canyon areas and meandering river stretches in flat terrain with low-gradient canyons. The numerous reservoirs constructed in relatively-recent years in all three zones should be considered a fourth habitat zone. All habitat zones are represented in Colorado.

Man has dramatically changed and continues to alter the nature of the Colorado River System physically, chemically and biologically. Due to his need to provide potable water to distant cities and to make small portions of the desert and semiarid regions of the Southwest green with lawns, orchards, and other agricultural crops, the once
mighty Colorado River System no longer flows, as it had for eons, into the Gulf of California. Man's reservoirs, diversions, and agricultural practices (including overgrazing and removal of natural riparian vegetation) have resulted in considerable reduction of habitat suitable for the long-term survival of many native species. This loss of habitat may be dramatically accelerated in the near future as streams are further modified with still more dams and reservoirs for water storage and hydroelectric production, and with massive water withdrawals to support the exploitation of vast coal and oil shale energy resources within the Upper Colorado River System.

Only a little over a century ago, the fish fauna of the Upper Colorado River System consisted of only 13 species; all but four of these native fishes are cypriniforms (Table 1). Due to the long and effective isolation of the Colorado River System, six of these species are unique forms endemic to only this river system, i.e., they are found nowhere else in the world. In addition two subspecific forms of more wide-spread species are also recognized as being endemic to the upper portion of the svstem, but one is not represented in the state of Colorado (Rhinichthys oscutus thermalis is known only in the outflow of Kendall Warm Springs in Wyoming).

Compared with the fish communities in river systems to the east, the original fish communities in the rivers of western Colorado, in fact, the
entire Colorado River System, were indeed depauperate with respect to the number of species represented. Without much consideration of long-term impacts, man set about to quickly rectify this flaw of nature by the introduction of other fishes, usually with the intention of establishing a fishery of famitiar game fishes. In recent years, at least 46 species, 33 of which are non-native and exotic, have been reported in Colorado's portion of the river system.

The modification and loss of suitable habitat as well as competition with non-native and exotic fishes has resulted in a general decline in the populations of most, perhaps all, native fishes. of the seven endemic fishes present or formerly found in Colorado's portion of the system, five are considered in danger of extinction: the Colorado squawfish (Ptychocheilus lucius, largest cyprinid in North America), the bonytail chub (Gila elegans), the humpback chub (Gila cypha), the razorback sucker (Xyrauchen texanus), and the Colorado cutthroat trout (Salmo clarki pleuriticus) (Deacon et al. 1979). Behnke and Benson (1980), as well as Joseph et al. (1977), summarized much of what is known about the habitat, behavior, distribution, and causes for decline of the threatened or endangered species in the Upper Colorado River System. The status of Cottus beldingi and Catostomus platyrhynchus in Colorado is still in need of study. Considering their apparent distribution and abundance, they should probably be considered for addition to the state list of threatened or endangered species.


Fig. 1. The Upper Colorado River System in Colorado. The three major basins or subbasins represented are further divided into twelve subregions.

Table 1. Status and recent distribution of fishes within 12 subregions of the Colorado River System in Colorado (Fig. 2). Relative abundance refers to abundance within at least one principal habitat zone within the subregion of concern and is designated on the basis of available reports and communications* as: C - generally common ( $\geq 1 \%$ of all fish collected), 0 - only occasionally common or generally less common ( $<1 \%$ of all fish but regularly collected), and R - rare (rarely or infrequently collected).**

$1 H$ - headwater streams and lakes, cold and clear; I - intermediate rivers and streams, cool to tepid and occasionally turbid; L - large rivers, warm and usually turbid; and R - major reservoirs.
${ }^{2} N$ - native, natural inhabitant of the system; $E$ - endemic, native species found only in the Colorado River System; threatened or in danger of extinction (endangered) as per Deacon et al. (1979) or the federal or Colorado lists Subspecies $S$. e. pleuriticus only.
"Includes relatively pure populations of the endemic subspecies which are common only in Trappers Lake (subregion 5) and mountain lakes in other subregions stocked with Trappers Lake fish.
${ }^{5}$ Reported only in Piceance Creek by Pettus (1974); probably $C$. Tatipinnis misidentified as c. commersoni.
${ }^{6}$ many of these specimens were previously identified as Funduzus kanaae. The two presumed forms are now recognized as being conspecific and are listed by Robbins et al. (1980) as Fundulus zebminas, the senior synonym.
Reproducing populations in Shadow Mountain Reservoir
Assuming the few specimens reported in Colorado were indeed Cottue betiangi and not variants of $C$. bairdi, this assumed native species should be placed on the state list of endangered species.

* Literary Sources: Baxter and Simon (1970); Behnke and Benson (1980); Carlson et al. (1979); Colorado River Fishery Recovery Team (1978 and 1979); Eiserman (1958); Goettl and Edde (1978); Holden and Crist (1979 and 1980); Holden and Stalnaker (1975a and b); Joseph (1978); Joseph et al. (1977); Koster (1957); Lanigan and Berry (1979); McAda (1977); McAda and Wydoski (1980); 01son and McNall (1965); Prewitt et al. (1978); Seethaler (197t); Seethaler et al. (1979); Sublette (1976); Vanicek et al. (1970); Wiltzius (1978) and Wick et al. (1979 and 1981). Personal Conmunications: Robert J. Behnke, Paul B. Holden, John P. Hubbard, David Langlois, Steven H. Lamigan, David L. Propst, Richard Valdez, William C. Weiler, Edmund J. Wick, and William J. Wiltzius.
**Information for certain fishes in many areas was limited and errors or misjudgnents are possible. please send any corrections or suggested changes to the author.


EARLY EMBRYOS
Fig. 2. Selected anatomical features of cypriniform fish eggs and embryos. (Modified from
Long and Ballard 1976 with permission of authors and publisher.)
PROTOLARVA
Caudal Fin
Principal Rays Hypurals of Lower Plate Upper Hypural Plate Secondary (Procurrent) Upturned Notochord and Analage of Urostyle
Median Finfold


- Ventral Portion
Urogenetal Du
Vent (Anus)
Myomere
- Myosepta
-Horizontal Skeletogenous Septa
- Preanal Finfold
Pelvic Fin Bud
Yolk within Yolk-sac Notochord Dorsal Fin
Principal Rays
Pterygiophore
Secondary or
Rudimentary Ray Coiled or Folded Gut Gas (Air) Bladder Stomach Region Heart Region Pectoral Opercle Melanophore Pigment Pectoral Fin Bud
Otolith
Auditory (Otic) Vessicle Gill Primordia (exposed)
d)
Heart
Pericardial Cavity Choroid Fissure of Eye Lens of Eye 01 factory Placode
Nares Lower or Mandibular Jaw Upper or Maxillary Jaw Region of Fore-, Mid-, and Hindbrain


## anatomical features of eggs and larvae

Figures 2 and 3 identify most of the more obvious morphological structures of cypriniform fish eggs and larvae.

## TERMINOLOGY OF DEVELOPMENTAL INTERVALS

## Classification of Developmental Intervals

The development of a fish is a continuous and somewhat gradual process, but there are differential and frequently varying rates of development for specific structures or physiological processes, and certain events occur rather suddenly. In the study of larval fish ecology and development, as in the preparation of formal descriptions and keys, it is most convenient and useful to divide the developmental continuum into specific recognizable intervals. Balon (1971 and 1975) suggested a four-tier hierarchy of developmental intervals, the period, phase, step or threshold, and stage. In fish, we typically recognize the largest intervals as the embryonic, larval, juvenile and adult periods. Balon also suggested a senescent period--an interval usually considered part of the adult period. Each period can be divided into two or more phases, each of which can be further subdivided into steps. Balon (1979) characterized steps as "natural intervals of ontogeny during which changes in form and function represent no significant alteration in the animal's environmental relationships. Only certain combinations of synchronous qualitative change will result in the attainment of a threshold, which is an abrupt functional change in ontogeny that produces a new environmental (external or internal) relationship, and therefore, a new step. In this manner, development occurs by a process of saltation." Stage is defined as a specific point in the developmental continuum and in this sense is misused by many fisheries biologists. This guide will use specifically-defined intervals of the period and phase type as a framework for presentation of developmental information.

## Need for a Standard Terminology

In past literature, over 60 different but often synonomous terms have been applied to periods and phases of development between hatching or parturition and attainment of sexual maturity (Snyder 1976b). Snyder (1976b) called for standardization of the terms and definitions used with respect to the larval period and its phases of development to better facilitate comparability of descriptions, keys, and reports of studies on fish larvae. Though the need had been expressed many times in the past, the call had remained largely unheeded. To promote such standardization, he reviewed, compared, and pointed out the difficulties in application of 15 candidate terminologies including those proposed and used by Hubbs (1943), Faber (1963), Mansueti and Hardy (1967),

Balon (1975), and Ahlstrom (Pers. Comm., 1968, and et al. 1976), and one that he and Maryann Mulhall Snyder had developed after several years of experimentation with various modifications of existing terminologies. The following criteria were suggested for selecting a standard: 1) "a standard terminology should be practical, precise, and easy to use without requiring intricate or time consuming techniques." 2) "the terminology should provide intervals indicative of relative age and state of development. It should therefore be based on a sequence of developmental characters which follow nearly the same course in all fishes." And 3) "the intervals must facilitate the production of comparable formal descriptions of fish larvae, keys to their identity, and reports of pertinent field and laboratory studies..."

The terminology proposed by the Snyders has proven to be useful to many larval fish biologists and is gaining acceptance for standard usage in descriptions and keys. Its use has been promoted by general, though not exclusive, usage in the Transactions of the American Fisheries Society and by agreement among many of the participants in the Second Symposium on Larval Fishes which was sponsored by TVA in Knoxville, Tennessee, 21-22 February 1978. Accordingly, it will be used exclusively in this guide.

## Terms and Definitions

The following discussion and definitions are paraphrased from Snyder (1976b).

The larval period is defined arbitrarily to consist of three distinct sequential phases: protolarva, mesolarva and metalarva. These phases, and therefore the period, are based on one of the most consistent and obvious sequences of development in all, or nearly all, bony fishes--the morphogenes is of the median finfold and fin elements (spines and rays). In addition, paired fins (pectoral and pelvic) are included in defining the last or metalarval phase. The definitions specify structures or features readily observed under low range magnification (less than 30x) and do not require dissection, clearing or staining. Not all fish pass through all three phases; salmon (Salmonidae), catfish (Ictaluridae) and certain killifish (Byprinodontidae), for example, hatch as mesolarvae. It is likely that some fish may hatch or be born as juveniles, lacking a larval period entirely. However, no examples of such are known among North America's freshwater or anadromous fishes (Snyder 1976b erroneously gave the mosquitofish, Combusia affinis, as an example; since that fish lacks pelvic fins at birth, it by definition has both a mesolarval and a metalarval phase).

The specific definitions of the larval period and its phases are as follows:

Larval Period - The period of bony fish development characterized by obvious fin morphogenes is following hatching or parturition. Transition to the juvenile period is based on the following three criteria, each of which must be met: 1) finfold and atrophying fins, if any (very rare), must be absorbed beyond recognition; 2) the full adult complement of fin spines (actinotricha) and rays (lepidotrichia), including secondary rays, must be distinctly formed (visually well defined) in all fins; and 3) segmentation must be evident in at least a few of the rays of each fin that is characterized by segmented rays in the adult.

Protolarval Phase - The larval phase of bony fish development characterized by the absence of distinct spines or rays associated with the future median fins (dorsal, anal or caudal fins). Transition to the mesolarval phase is based on the appearance of at least one distinct spine or ray in any of the median fins. Pectoral and pelvic fins or fin buds may be present.

Mesolarval Phase - The larval phase of bony fish development characterized by the morphogenesis of distinct principal rays in the median fins.
Transition to the metalarval phase is based on the following two criteria, each of which must be met, except in species lacking pelvic fins: 1) the full adult complement of principal rays must be distinctly formed in the median fins; and 2) the pelvic fins or fin buds must be evident.

## Metalarval Phase - The larval phase of bony fish

 development characterized by the full adult complement of principal rays in the median fins and the presence of pelvic fins or fin buds (except in species lacking pelvic fins). Transition to the juvenile period is as specified in the definition for the larval period.The median fin elements in most fishes appear first in the caudal portion of the finfold. For these species the protolarval phase is essentially synonymous with Ahlstrom's preflexion phase (except when a yolk sac is present) (Ahlstrom et al. 1976) and Faber's (1963) straight-notochord phase. For the remaining fishes, those in which the first median fin elements usually appear in the developing dorsal or anal fin, the protolarval phase terminates before the preflexion or notochord phase (e.g., the larvae of lined sole, Achirus Iineatus, described by Houde et al. 1970).

The metalarval phase is defined so as to allow in description and key preparation the use of principal ray counts of the dorsal, anal and caudal fins, as well as the relative positions of these fins and the pelvic fins, assuming the species has pelvic fins. In some fishes, the pelvic buds form as or after the full adult complement of distinct principal rays in the median fins is attained. For these the distinction between mesolarvae and metalarvae is exceedingly simple. In other fishes, the pelvic fin buds make their appearance during the mesolarval phase, prior to the appearance of the full complement of principal median fin rays, or they may be even more precocious and appear during or before the protolarval phase (e.g., the lanternfish Symbolophoms califomiensis described by Moser and Ahlstrom 1970).

For fishes in which part of the finfold is still present upon attainment of the other two criteria for transition to the juvenile period, distinction between the larval and juvenile periods is particularly easy. Recently-transformed juvenile fish, based on this terminology, may or may not yet resemble the adult. However, for most fishes, the appearance will be very adult-like.

In meeting the three criteria suggested for a standard terminology, this terminology, unlike most others, avoids the difficulties inherent in using the transition from endogenous to exogenous nutrition as a phase or period boundary. Although this transition is of tremendous physiological, ecological and behavioral significance, the various criteria previously used for determining a boundary between intervals based on it are frequently difficult to
discern with precision on preserved material and are no less arbitrary than criteria for other interval boundaries. Like hatching or parturition, the transition from endogenous to exogenous feeding, largely a physiological change, does not correlate well with the more obvious morphological features of larval development such as fin morphogenesis. In many fishes, yolk absorption is completed during the protolarval phase; in others, such as salmon and catfishes, yolk is still present in the metalarval phase. If it is desirable to indicate the presence of yolk, the phase name can be modified by the prepositional phrase "with yolk" (as per Faber 1963; e.g. mesolarva with yolk).

## CHARACTERISTICS USEFUL IN THE IDENTIFICATION

 OF CYPRINIFORM FISH LARVAEThe identification of fish larvae is in part a process of elimination. Even before examination of a single specimen, the range of possibilities can be narrowed by knowledge of the adult species which occur within or near the source of the specimens to be identified (possible incidental transport of the eggs or larvae from far upstream or distant tributaries must also be considered). Knowledge of spawning seasons, temperatures, habitats, and behavior coupled with information on egg deposition and larval nursery grounds and behavior are also useful in delimiting the possibilities.

In the following discussions of useful characters, generalizations with respect to the order Cypriniformes refer specifically to North American species of the families Cyprinidae and Catostomidae. The generalizations might not apply to other members of the order.
"Although species of a genus may vary from one geographical area to another, generally the larval forms of closely related species (and sometimes of genera and even families) look alike. At the same time, the larvae of distantly related forms may be closely similar in gross appearance." (Berry and Richards 1973). Cypriniform larvae as a group are distinctive and generally easy to distinguish from larvae of other families. The beginning worker is advised to become familiar with the general larval characteristics of each family likely to be encountered. The various guides and keys cited in the introduction are most useful in this respect. Lippson (1976), Lippson and Moran (1974), Wang and Kernehan (1979) or Drewry (1979) are particularly recommended for the variety of families covered. Faber (1963), May and Gasaway (1967), Scotton et al. (1973) and Berry and Richards (1973), discuss the types of characters useful in the identification of larval fishes; the latter, strongly influenced by the late Elbert H. Ahlstrom, is especially recommended.

In the Upper Colorado River Basin, cypriniform larvae are readily categorized as cyprinids or catostomids. But elsewhere, if members of the cyprinid subfamily Cyprininae (the carps) and the catostomid subfamily Ictiobinae (the carpsuckers and buffalofishes) or tribe Erimyzontini (chubsuckers, Catostominae), are present, identification at the family level may become more difficult for the inexperienced.

Within their respective families, and especially at the subfamily level, cypriniform larvae are very homogeneous in gross structure and appearance and, therefore, may be especially difficult to discriminate
at the genus or species levels. Specific identification relies largely on meristics such as myomere and fin ray counts, morphometrics such as snout to vent lengths, and melanistic (brown or black) pigment patterns. In addition, the size at which certain developmental events occur and the form of various structures can be useful. There is often a noticeable amount of intra- as well as inter-regional variability in many of the characters to be discussed. Awareness of this variability or its possible presence, and use of several diagnostic characters, if possible, will increase confidence in identification while reducing the probability of error.

Myomeres: Myomeres, because they are obvious morphological features and relatively consistent in number and position, are one of the most useful characters available for identification of larvae above (and sometimes at) the specific level, especially for protolarvae and mesolarvae. They begin as part of the embryonic somites and are usually formed in their full complement prior to hatching. Throughout the protolarval and much of the mesolarval phase, myomeres are chevron-shaped but by the beginning of the metalarval phase they evolve to their typical three-angled adult form. Fish (1932) and many subsequent authors indicated that there is a nearly direct, one-to-one correlation between total myomeres and total vertebrae. Snyder (1979), including or assuming inclusion of the Weberian ossicles in total vertebra counts, provided considerable data on cypriniform fishes in support of this generalization.

The most anterior and posterior myomeres are frequently difficult to distinguish. The most anterior myomeres are apparent only in the epiaxial or dorsal half of the body; the first is often deltoid in shape and is located immediately behind the occiput. The most posterior myomere is defined as lying anterior to the most posterior complete myoseptum. Siefert (1969) describes a "false (partial) myoseptum" posterior to the last complete myoseptum which adds to the difficulty of discerning the last myomere. Early in the larval period, myomeres are most readily observed using transmitted light. Polarizing filters, depending on the thickness and certain other qualities of the preserved tissues, can often be used to dramatically increase the contrast between the muscle tissue of the myomeres and the myosepta that separate them. Surface staining (i.e., dipping momentarily in Alizarin Red, or perhaps another dye, then rinsing) or submergence in glycerin might also be useful in helping to distinguish individual myomeres. The myomeres of some metalarvae and juveniles are often difficult to observe; reflected light at a low angle from one side and higher magnification sometimes facilitates observation.

Typical counts used in taxonomic work include total, preanal, and postanal counts. Partial counts are frequently used to reference the location of various structures in addition to the vent. The most generally accepted method of making partial counts is that described by Siefert (1969) for distinguishing preanal and postanal myomeres:
"postanal myomeres include all [entire] myomeres posterior to an imaginary vertical line drawn through the body at the posterior end of the anus Remaining myomeres, including those bisected by the line, are considered preanal."

The technique is equally applicable to other structures or points of reference such as the origins of various fins or finfolds. Another approach used by Snyder et al. (1977), Snyder and Douglas (1978), Loos and Fuiman (1977) and, according to the latter authors, Fish (1932) is essentially the opposite; only entire myomeres are included in the count anterior to the structure of reference. As counts resulting from Siefert's methods are expected to more nearly approximate the number of vertebrae to the point of interest, that approach will be accepted as the standard for this guide and future Identification Circulars.

Snyder (1979) reported: "The range of total vertebra and/or myomere counts for 70 cyprinid species, 28 to 51, is larger and essentially includes that for 27 catostomids, 32 to 52. Preanal and postanal myomere counts ranged from 19 to 31 and 10 (9?) to 18, respectively, for cyprinids and 25 to 42 and 5(3?) to 12(14?) for catostomids. The two families can be readily distinguished by the proportion of postanal to preanal myomeres, about 1/2 or greater for cyprinids and 1/3 or less for catostomids; or preanal to total myomeres, about $2 / 3$ or less for cyprinids and $3 / 4$ or more for catostomids. The genera of each family are characterized by distinctive ranges of total myomeres or vertebrae which can be used to help determine the identity of unknown cypriniform larvae."

Fins and Finfolds: Fin ray meristics and fin positions, usually determined from older juveniles and adults or gleaned from published descriptions of adults, are among the most useful characters for later mesolarvae and metalarvae, especially among the cyprinids. The sequence and timing (relative to larval length) of fin development as well as fin lengths and basal lengths of the dorsal and anal fins are also useful.

The median finfold, one of the most obvious of larval structures in protolarvae and early mesolarvae, is a continuous structure originating on the dorsal surface, usually well behind the head, and extending posteriorly to and around the end of the notochord then anteriorly along the ventral surface to the posterior margin of the vent. During the mesolarval phase, this finfold differentiates at the sites of the future median fins then, as the fins develop, it recedes or diminishes before and between the fins until it is no longer apparent, usually at or near the end of the metalarval phase.

The preanal finfold, a second median finfold, may or may not be present upon hatching, depending upon the size and shape of the yolk sac. In the burbot (Lota lota) and its marine relatives (Gadidae), the preanal finfold is initially continuous with the ventral portion of the median finfold, the vent opening to one side of the finfold; they later separate. In cypriniforms, the preanal finfold is typically absent or barely apparent upon hatching. As yolk is consumed and the yolk sac is reduced in size, either during the late embryonic phase or the protolarval phase, a small finfold appears just anterior to the vent. As more yolk is consumed and the larva grows, the preanal finfold enlarges and extends anteriorly, usually well in advance of the origin of the dorsal finfold. The preanal finfold remains prominent throughout the mesolarval phase and slowly diminishes in a posterior direction during the metalarval phase. It is typically the last of the finfolds to completely disappear.

The caudat fin is the first fin to differentiate from the median finfold in many fishes. Such is always the case in cypriniforms. The portion involved first thickens along the ventral side of the posterior end of the notochord, then begins to differentiate into the hypural elements of the caudal skeleton. Immediately thereafter, the first caudal rays become apparent, marking the beginning of the mesolarval phase, and the posterior portion of the notochord begins to bend or flex upward. Care must be taken not to confuse striations or folds in the finfold with developing rays. As the fin develops and the notochord continues to flex upward, the hypurals and developing caudal rays, all of which are ventral to the notochord, are moved to a posterior or terminal position. The first principal rays are medial; subsequent principal rays are progressively added posteriorly above and anteriorly below. The principal caudal rays, which are the first to attain their full adult complement, articulate with the hypural bones of the caudal structure and include all branched rays plus one unbranched ray on each side. Branching and segmentation can be observed as or shortly after the full complement of rays becomes evident.

The number of principal caudal rays is typically very consistent within major groupings of fish. Cyprinids, for example, generally have 19 principal rays (ten based on the superior hypurals) while catostomids usually have 18 principal rays.

Secondary or procurrent caudal rays, which are added in an anterior direction, begin forming immediately after the principal rays are formed or nearly formed. They are often the last group of rays to attain the full adult complement. Accordingly, they are often ignored in larval work though they may be of taxonomic value in juveniles and adults.

The dorsal and anal fins, which typically form either simultaneously (many cyprinids) or dorsal first (most catostomids), usually begin development prior to the attainment of the full complement of principal caudal rays. Tissue first aggregates in the vicinity of the future fin, and the basal structures or pterygiophores soon become evident. The latter structures permit limited use of dorsal and anal fin position and meristics about midway through the mesolarval phase. The anterior principal rays develop first with subsequent rays added in a posterior direction; the first of the secondary rays (anterior to the principal rays) are frequently evident before all the principal rays are formed; secondary rays are added in an anterior direction.

The first or most anterior principal ray in both dorsal and anal fins remains unbranched, while all others branch shortly after or as segmentation becomes evident. The last or most posterior principal ray in each fin is considered to be divided at the base and therefore usually consists of two elements that, except for their close proximity and association with the same pterygiophore, might be mistaken for separate rays.

Principal dorsal and anal ray counts between and within certain genera vary sufficiently to often be of use in identification at the specific level, especially the anal rays of cyprinids and the dorsal rays of catostomids. The position of the dorsal fin origin (anterior insertion) and
insertion (posterior insertion) relative to the origin of the pelvic fins or fin buds and the vent varies considerably among the cyprinids and is useful in identification at the genus or species levels. These position characters are relatively more constant among the catostomids (e.g., dorsal fin origin is always well in advance of the pelvic fins), especially at the subfamily level, and therefore of less value in larval identification.

The pelvic fins begin as buds at some stage prior to or at the very beginning of the metalarval phase. In cypriniform fishes, they originate in an abdominal position along each side of the preanal finfold. They may erupt shortly after dorsal and anal fin development begins or be delayed until just before or shortly after all principal rays are present in the median fins. Pelvic rays begin to form shortly after the buds make their appearance; the adult complement of segmented rays quickly ensues. Within the cypriniform fishes, pelvic ray counts are seldom used diagnostically. However, both the position of the pelvic fin or fin bud relative to other structures and its position in the sequence of developmental events can be useful in identification, especially in the family Cyprinidae.

The pectoral fins typically begin as buds immediately behind the head during the late embryonic phase. However, pectoral buds are not evident on some species (including some cypriniform fishes) until shortly after hatching. Though strongly striated and occasionally with membraneous folds and breaks, they typically remain rayless in cypriniforms until late in the mesolarval phase when most of the principal median fin rays are present. With the exception of secondary caudal rays, the rays of the pectoral fins are often the last to establish their full complement. For this reason and because the number of pectoral rays is usually relatively large and difficult to count without excision (especially the smaller ventral rays), pectoral ray counts are generally of little value in larval identification.

Other Countable Structures. Other characters that may be treated meristically (and in some cases morphologically) include branchiostegal rays, gill rakers, pharyngeal teeth and scales. Branchiostegal rays form early in larval development but counts are usually constant within major taxon groups. Within the order cypriniformes, all members of the superfamily Cyprinoidea, which includes the Cyprinidae and Catostomidae, have three branchiostegals (McAllister 1968). Due to later development, small size and/or internal location, the other characters are seldom used, and then usually only on later metalarvae and juveniles. Gill rakers form gradually with numbers increasing throughout much of the larval period and the early portion of the juvenile period. Pharyngeal teeth form relatively early but may not be sufficiently well developed to be readily removed and observed until late in the larval period or early in the juvenile period. Detailed study of gill rakers and pharyngeal teeth might reveal some useful diagnostic qualities, including size, shape, and number; however, in most cases, species can be more easily distinguished by use of external characteristics. Scales typically become apparent late in the larval period or early in the juvenile period, but all are not typically present until a short time later. First scales on
cypriniforms typically appear mid-laterally on the posterior half of the body and from there spread anteriorly, dorsally and ventrally toward adult coverage. The scales of larger-scaled species are sometimes obvious by late in the metalarval phase and may be used to separate or help distinguish certain species or genera.

Morphology: The shape or form of larvae and specific anatomical structures, which change as the fish grow and develop, provide some of the most obvious characters for identification purposes, particularly at the family and subfamily levels, occasionally at the species level. Much of this shape or form-related information can be quantified to some degree via proportional measurements or morphometrics. The shape and form of structures such as the gut, air bladder, yolk sac, and mouth, especially as they change during development, can be diagnostic.

Morphometric data emphasizes the relative position and relative size of various body components and body dimensions, and may be critical to species identification of certain larvae. Such measurements may be allometric, changing in proportion as the fish grow; thus morphometric data should be related to size, at least for protolarvae and mesolarvae. Some morphometric data, particularly body depths and widths, may be directly affected by the condition of individual specimens and the volume and form of food items in their digestive tracts. The source of the specimens and the nature of the solution in which they are stored should also be considered in the use of this data. Shrinkage and deformation are greater in alcohol than in formalin.

Morphometric data in this guide are reported as a percentage of standard length. Use of standard length avoids the allometric influence of caudal fin growth included in percentages based on total length. As explained later (Methods), conversion of certain data to percent total length for comparison with other works is relatively simple. Prior to hypural plate formation and completion of notochord flexion, herein correlated with the acquisition of the adult complement of principal caudal fin rays, standard length is defined as notochord length (snout to the posterior end of the notochord). Thereafter, it is defined as the length from the anterior margin of the snout to the most posterior margin of the hypural plates (usually the superior plate or hypurals). Use of notochord length for protolarvae and early mesolarvae gives the appearance of greater allometric growth differences than may really exist, at least in comparison with subsequent measures based on the posterior margin of the hypural plates. This undesirable effect is a result of the upward bending or flexing of the notochord and the switch from use of the end of the notochord to the posterior margin of the hypurals as the basis for length measurement. These factors must be taken into account when reviewing the morphometric data given herein.

Measurement of body lengths and various parts thereof, in contrast to the procedures recommended by Hubbs and Lagler (1958) for larger juveniles and adults, is generally done along a line parallel to the horizontal axis of the fish. Exceptions are fin lengths, which in studies conducted for this guide were measured from the origin of the fin base to the most distal margin of the fin rays. Typical measures include total, standard, snout-to-vent preanal, predorsal, prepelvic, head, eye, snout and fin lengths.

Snout-to-vent length, which is measured to the posterior margin of the vent or anus, reflects the position of the vent. The term preanal length should be reserved specifically for the length measure from the snout to the origin of the anal fin; in many fishes, including the cypriniforms, the latter point is often the same or nearly the same as the posterior margin of the vent. The snout-to-vent length is a primary diagnostic character for many species, especially at the family and sometimes subfamily level. Except for most larvae of the common carp (Cyprinus carpio) and an occasional mesolarva of the Colorado squawfish (Ptychocheilus Zucius), cyprinid larvae in the Upper Colorado River System are readily differentiated from catostomid larvae by snout-to-vent lengths of less than $72 \%$ SL.

Head length is typically measured to the posterior margin of the operculum in juveniles and adults, but the operculum may be absent or incomplete throughout much of the larval period. Accordingly, many biologists have redefined head length to be measured to the posterior end of the auditory vesicle or the anterior or posterior margin of the cleithrum, one of the first bones to ossify in fish larvae (Berry and Richards 1973). Unfortunately, the auditory vesicle and cleithrum are not always easily observed, especially later in larval development. Also, resultant measures from the auditory vesicle are considerably anterior to the eventual posterior margin of the operculum. Snyder et al. (1977) and Snyder and Douglas (1978) measured larval head length to the anterior insertion or origin of the pectoral fin. The base of the pectoral fin is readily observed throughout the larval period (except in the few species that hatch prior to pectoral bud formation), somewhat approximates the position of the cleithrum (part of its supporting structure), and more nearly approximates the posterior margin of the operculum than does the posterior margin of the auditory vesicle. Accordingly, head length is defined herein as the length from the anterior margin of the snout to the anterior-most margin or origin of the base of the pectoral fin and is used, for purposes of consistency, for juveniles as well as larvae. The measure is most precisely determined while examining the specimen from above or below and, if necessary, holding the fin away from the body.

Body depths and widths are measured in planes perpendicular to the horizontal axis of the fish. Many biologists report these as maximum or minimum measures (e.g., greatest head depth, greatest body depth, and least caudal peduncle depth). However, it seems more logical for comparative purposes to specify specific locations as standard reference points for such measures, as per Moser and Ahlstrom (1970), Fuiman (1978) and Snyder and Douglas (1978). Five specific locations, four corresponding to specific length measurements, are used herein: 1) immediately posterior to the eyes, 2) origin of the pectoral fin, 3) origin of the dorsal fin, 4) immediately posterior to the vent and 5) at the anterior margin (mid-lateral apex) of the most posterior myomere. Neither fins nor finfolds are included in depth measurements.

Other morphological characters such as the position, size, and form of the mouth and the gut, and related changes can be among the more useful characters for identification to the species level. The size of the mouth, as well as its position and angle of inclination, and the form of specific
mouth structures are diagnostic for some cypriniforms, especially later in the larval period. The timing of mouth migration from a terminal to an inferior position is particularly useful during a portion of the metalarval period in catostomids. The length, timing of the occurrence of the first loop, and eventual degree and form of the loops or coils of the gut can be important diagnostic characters for many fish. They are among the more obvious characters used to distinguish the late mesolarvae, metalarvae and early juveniles of the bluehead and flannelmouth suckers (Catostorms discobolus and $C$. Latipinnis respectively).

Pigmentation: The basic patterns of chromatophore distribution, and changes in these patterns as fish grow and advance developmentally, are characteristic at the species level (for some fishes at the subspecies level). Used with caution, preferably in combination with other characters if feasible, and with an awareness of both intra- and inter-regional variation, the chromatophore distribution and patterns of many fishes are among the most useful characters available for identification at the species level. However, in some instances, differences are so subtle that use of pigmentation is impractical and may be misleading.

Pigmental variation, for a specific developmental stage within a species, exists largely in the number of chromatophores exhibiting pigment, either in general or in specific areas, rather than differences in the basic pattern. Complete loss of pigment in an area, of course, eliminates that portion of the overall pattern. In addition, the pigment in chromatophores can be variously displayed from tight, contracted spots, giving a relatively light appearance, to widely expanded, reticular networks which gives a dark or more brilliant appearance to the area affected. Differences in environmental conditions and food can significantly affect the appearance of pigmentation. Cultured specimens accordingly, can appear quite different from field-collected material.

In cypriniform fishes, as well as most other fishes, chromatophores other than melanophores have not been sufficiently studied for identification purposes, in part because they are typically neither as numerous nor as obvious, and because of the difficulty in preserving these pigments over a period of time. Melanin, the amino acid breakdown product responsible for the dark, typically black, appearance of melanophores (Lagler et al. 1977), remains relatively stable in preserved specimens. Melanophores are, however, subject to fading and loss of pigment if specimens are stored or studied extensively in bright light or if subjected to changing concentrations in the fluids in which they are stored or studied. To minimize the latter effects, as well as shrinkage and deformation, dilute formalin solutions ( $3-5 \%$, preferably buffered) are strongly recommended over alcohol solutions as storage media. Most of the following discussion refers to chromatophores in general, but in this guide, as well as previous guides to freshwater species in North America, pigmentation typically refers to melanophores only.

According to Orton (1953), pigment cells originate in the neural crest region (dorsal portion of body and tail) and migrate in amoeboid fashion in waves to their eventual position. The first wave of chromatophores occurs late in the embryonic period or early in the larval period and establishes a relatively fixed basic or primary pattern of
chromatophore distribution. In a few (mostly marine) species, the cells become pigmented prior to migration and the actual migration can be observed and documented. But in cypriniform fishes, as in most other freshwater species, pigment is not present (or appears not to be present) in the chromatophores until some time after the cells have reached their ultimate destinations.

Pigmentation often changes considerably as fish grow and develop. Most of the change is due to the increased numbers and spread of chromatophores. Observable pigmentation may also be lost from certain areas, usually through either a loss of the pigment or chromatophores themselves, or, in the case of subsurface or internal chromatophores, by the thickening and increasing opacity of covering tissues. Internal melanophore pigmentation can be observed more readily by careful clearing of the larva.

## COMMENTS ON THE IDENTIFICATION OF FISH EGGS

Identification of fish eggs or embryos has received very little attention in the published literature, especially for freshwater species. Due to lack of distinctive features for most freshwater forms, all but the latest stages of the late-embryo (tail-free) phase of most fishes are very difficult, if not nearly impossible, to identify to species. The latest embryonic stages can sometimes be identified to species or designated as belonging to one of several related species by use of diagnostic characters for the recently-hatched larvae.

Certain egg and embryo characteristics are sufficiently distinctive to allow most specimens to be identified as belonging to one or more specific families or subfamilies. Characteristics useful in this respect are egg diameter and shape; nature of the chorion (e.g., smooth or patterned); projections or invaginations; attachment threads, filaments, or stalks; presence and form of an obvious micropyle; number and thickness of chorionic membranes; gelatinous or adhesive coatings; homogeneous or segmented (granular) yolk; type of cleavage; and at specific stages the number, position and size of oil globules in the yolk, and the size of the perivitelline space.

Size of the egg and perivitelline space and the presence and nature of oil globules (coupled with time of year, location, and apparent nature of egg deposition) are characteristics particularly useful in identifying the eggs of freshwater species. Most freshwater fish eggs, including those of the cypriniforms, are round, relatively smooth, and without distinctive surface features, stalks, filaments or coatings; cleavage is typically meroblastic. Exceptions in North America include Lepisosteus species, Notropis girardi, Ictalurus punctatus and Perca flavescens with special coatings or outer envelopes; Osmemus mordax with an attachment stalk; Labidesthes sicculus and Menidia audens with chorionic filaments or threads; and Acipenseridae, Polyodontidae, Lepisosteidae and Amiidae with semiholoblastic cleavage. Cypriniform eggs are typically demersal with moderate to little perivitelline space and no oil globules, though most are readily transported if dislodged in moderate to strong currents. Exceptions include Notropis atherinoides and $N$. amoenis which have pelagic or semipelagic eggs with expanded chorions enlarging the egg diameter to about 3 mm and providing for a large perivitelline
space (Loos and Fuiman 1977). Cyprinid eggs, except as noted above, are typically $1.0-2.0 \mathrm{~mm}$ in diameter, while catostomid eggs are typically 2.5-3.5 mm in diameter except in the subfamily Ictiobinae and tribe Erimyzantini in which eggs measure around 2.0 mm . Cyprinid eggs are deposited in a variety of ways from broadcast with no parental care to attachment in masses under submerged rocks or other objects with intimate parental care. Catostomid eggs are broadcast with no parental care.

## METHODS \& MATERIALS

Most of the specimens studied were collected from the Yampa, White, Colorado and Gunnison Rivers in Colorado from 1976 through 1979 as part of Bureau of Land Management and Colorado Division of Wildlife Surveys (Carlson et al. 1979, Prewitt et al. 1978, Wick et al. 1979, and Wick et al. 1980). Unrecognized larval specimens were originally segregated into like groups. Continua were then established with identifiable juveniles. Once distinguishing characters were determined for the various species, most larvae and early juveniles were assembled into developmental study series based on size. Several series of specimens were reared from artifi-cially-fertilized eggs during the spring and summer of 1978 through 1981, and from collected larvae during the summer of 1977 . Additional specimens or series were loaned or donated by outside sources (see Acknowledgments).

Most of the collected and reared specimens were killed and fixed in 10\% formalin, then stored in 3\% buffered formalin. Some borrowed specimens were stored in ethyl or isopropyl alcohol.

Figure 4 illustrates the various measurements, fin ray counts, and myomere counts that were made on at least two or three specimens, if available, in each $1-\mathrm{mm}$ total-length (TL) interval throughout the larval period of each species. One or more specimens in each 3- to $4-\mathrm{mm}$ interval were similarly processed thereafter to a length of about 50 mm TL. Juveniles for each species, for which specimens were available, were cleared with trypsin, potassium hydroxide, and glycerin and stained with Alizarin Red (modifications of methods by Taylor 1967) to enable the recording of internal meristics such as vertebra counts and verify fin meristics. Specimens were studied under low power stereo-zoom microscopes with measuring eyepiece reticles and various combinations of reflected, transmitted and polarized light. Magnification was adjusted before each series of measurements to calibrate the scale in the eyepiece against a stage micrometer for direct measurement. Measurements were made to the nearest tenth of a millimeter and occasionally to half that unit. Remeasurement of selected specimens by a second observer indicated that most measurements are repeatable to within 0.1 mm . Most measurements are reported as a percentage of standard length but are readily converted to percent total length by dividing the length of interest, in terms of SL, by total length, in terms of SL, and multiplying by 100 .

Drawings, including dorsal, lateral and ventral views were prepared for a recently transformed and later stage of each larval phase available and for the juvenile period. Enlarged photographs were traced to assure accurate body proportions. Various structures were checked and additional detail was added to the drawings while the specimens were examined under a microscope. Final drawings were idealized (e.g.,
closed or frayed fins opened and smoothed and curved bodies straightened). If necessary, melanophore distribution was modified to represent a more typical pattern.

## RESULTS

The remainder of these "contributions to a guide" consists of three parts: a preliminary key to the metalarvae, the species accounts, and a pair of comparative summary tables. Unfortunately, information on the development of certain species remains incomplete and many characters exhibit a large degree of overlap among the various species considered. Accordingly, it might not always be possible to trace the identity of a specimen to the species level with the degree of confidence desired. Still, with the information provided, the vast majority of collected specimens can be accurately identified.

The key is not absolute and does not cover all contingencies, but it should prove to be satisfactory for determining the identity of most metalarvae. In many instances, the key will also work for early juveniles. Specimens with atypical morphometry or fin ray or myomere counts might not key-out properly. Upon reaching a conclusion via the key, the identity should be varified with the data and illustrations provided in the species accounts. Median fin ray counts given in the key are for the principal rays only.

Most species accounts consist of a page of tabulated data and two pages of illustrations. Some accounts currently consist of only one or the other. A few species have not been sufficiently studied or the information adequately assembled to provide either tabulated data or illustrations. Previously published illustrations are used where originals are not yet available.

Most of the developmental studies upon which this material is based are still underway. The planned guide will include detailed coverage of additional species; the addition of background information, verbal descriptions and commentary, graphed morphometric length data, and more original illustrations to the species accounts; a summary table of reproductive information; and refinement to the metalarvae key and the addition of keys to the protolarvae and mesolarvae. Users of the key, species accounts and summary tables are asked to make known any errors, problems, or suggestions for improvement.

 measures but fins and finfolds are not. "B" in BPE and BPV means immediately behind, i.e. not including the eye or vent, respec-
tively. AMPM is the anterior margin of the most posterior myomere. Location of width and depth measures at 0D prior to D formation is approximated to that of later larvae. Once the dorsal fin is formed, length to ODF is measured only as long as finfold remains anterior to it. PHP is measured to the end of the notochord until the adult complement of principal caudal rays are observed. For fish in which PV and OA approximate each other, OA is often deleted and assumed to be the same. Fin lengths of the median fins are darkened and the number given in arabic while secondary rays are outlined and given in lower case Roman numerals; when counted, the rays of paired fins are not so divided. The first and last myomeres, as well as the last myomeres in counts to specific points of reference, are shaded.

## Preliminary Key to the Cypriniform Metalarvae of the Upper Colorado River System in Colorado

1. 

a. Snout-to-vent length $72 \%$ or greater. Dorsal fin (principal) ray count 10 or more (rarely 9), anal fin ray count less than 9 , typically 6 or 7; and caudal fin ray count typically 18 or 19.
2.
2.
a. Dorsal fin very long with a ray count greater than 17 and an insertion well posterior to the vent. Caudal ray count typically 19. Robust body with greater proportional widths, depths, and head lengths than for other metalarvae. . . Cypminus carpio (Cyprininae, Cyprinidae).
3.
a. Anal rays typically 7 , dorsal rays typically 8. . . . . . . . . . . . . . . . . . . . 4
4.
a. Dorsal fin origin posterior to pelvic fin origin. Dark area of melanophore pigmentation on lateral surface of the snout and late in the phase in the form of a lateral band on the body. Myomeres 23-27 to vent, typically 24-27, and 36-41 total, typically 38-41.
5. (Rhinichthys)
5.
a. Groove between upper lip and the rest of the snout broken by frenum along its most anterior junction. Myomeres $24-27$ to the vent, typically 25-27, and 37-41 total, typically 40-41. Rhinichthys cataractae.
6.
a. Peritoneum usually dark laterally, sometimes ventro-laterally. Pigment under dorsal and anal fins but not as an "intense" dash. Dorsal fin origin located somewhat beyond $1 / 2$ the standard length ( $53-56 \%$ SL), usually over or slightly behind pelvic fin origin. Mouth oblique. Myomeres to the vent typically 23-24. . . . . . . . Pimephales promeZas.
7.
a. Anal rays typically 8 . Insertion of dorsal fin well forward of vent. 8.
8.
a. Dorsal and pelvic rays typically 9. No series of melanophores along the lower margin of the opercula.
ciza atraria.
9.
a. Dorsal fin origin over or anterior to pelvic fin origin. Myomeres about 24-26 to the vent and 35-39 total. Mid-ventral surface anterior to the vent pigmented with a single line of melanophores. No lateral band of melanophores. Metalarvae about 8 mm SL ( 9 mm TL ) or larger.

Hybognathus hankinsoni.
10.
a. Dorsal rays typically 8. Myomeres 19-24 to vent, typically 21-23, and 34-37 total, typically 35-36. Metalarvae about $8-10 \mathrm{~mm}$ SL ( $9-13 \mathrm{~mm} \mathrm{TL}) . . . . . . . N o t r o p i s$ Iutrensis.
b. Snout-to-vent length Tess than $72 \%$ SL. Dorsal fin rays less than 10 , typically 8 , or 9 , rarely 11 ; anal ray count rarely less than 7 or more than 12; caudal fin ray count typically 19. . . . . . . . 3. (Leuciscinae, Cyprinidae).
b. Dorsal fin shorter with ray count less than 17 and insertion well anterior to the vent. Caudal ray count typically 18. . . 15. (Catostominae, Catos tomidae).
b. Anal and dorsal rays typically 8 or more each. 7.
b. Dorsal fin origin over, slightly anterior, or slightly posterior to pelvic fin origin. No concentration of pigment on lateral surface of snout or in the form of a lateral band on the body. Myomeres 20-25 to vent, typically 21-24, and 33-38 total, typically 34-36. . . . . . 6
b. Groove between upper lip and the rest of the snout continuous, no frenum. Myomeres 23-27 to the vent, typically 24-25, and $36-40$ total, typically 38. . . . . . Rhinichthys oscalus.
b. Peritoneum light. "Intense" dash of melanophores usually under middle of both dorsal and anal fins. Dorsal fin origin located at or before 1/2 the standard length ( $46-50 \% \mathrm{SL}$ ), usually over or slightly anterior to pelvic fin origin. Mouth nearly horizontal. Myomeres to the vent typically 21-23. . . . . Notropis stramineus.
b. Anal rays typically 9 or greater. Insertion of dorsal fin variable.
10.
b. Dorsal and pelvic rays typically 8 . Series of melanophores along the lower edge of the opercule. 9.
b. Dorsal fin origin posterior to origin of pelvic fins. Myomeres about 26-29 to the vent, typically 27-29, and 40-44 total, typically 40-42. No mid ventral line of melanophores anterior to the vent. Prominent lateral band of melanophores on the body and continued on the snout. Metalarvae about 11 mm SL (13 mm TL) or larger. Semotilus atromaculatus.
b. Dorsal rays typically 9 or greater. Myomeres typically 24 or greater to vent and 37 or greater total. Metalarvae about 10 mm SL (12-13 mm TL) or larger. 11.
a. Anal rays $10-13$, typically 11 or 12 . Dorsal rays $8-10$, typically 9 . Myomeres 23-26 to the vent, typically 24-25, and $36-41$ total, typically 37-39. Dorsal fin origin far behind pelvic fin origin, nearly $6 \%$ SL difference in position. Metalarvae as small as 10 mm SL (11 mm TL). . . . . . Richardsonius balteatus.
12.
a. Dorsal and anal rays typically 10 , rarely 9 , 11 or 12. Myomeres, based on adult vent position and vertebra counts, probably 30 or less to the vent and 48-50 total.
. . . . . . . . . . . . . . . . Giza elegans (speculative, could be $G$. cypha or $G$. robusta).
13.
a. Myomeres typically 21 or more to the dorsal fin origin, 31 or more to the vent, and 48 or more total. Anal fin rays typically 9, rarely 10. . . . . . . . . . . Ptychocheilus Zucius.
14.
a. Anal rays usually 9, sometimes 10. . . . . . . . . . . Giza robusta, possibly Giza cypha.
15.
a. Dorsal rays 15-16. . . . . Xyrauchen texanus.
16.
a. Dorsal rays 14.
either
Catostomus Zatipinnis or Xyrauchen texanus.
17.
a. Peritoneum dark, well pigmented with melanophores. Gut with one or two loops crossing from side to side. . . Catostomus discobolus or Catostomus platyrhynchus (subgenus Pantosteus; latter species usually restricted to headwater streams).
18.
a. Dorsal rays typically 12 or 13 , with rare extremes of 11 and 14. Gut "S" shaped throughout metalarval phase. Ventral surface without a mid-ventral line of melanophores from pectoral fins to vent or with only a short series. . . . . . . . . . . . Catostomus Zatipinnis.
19.
a. Eye diameter less than $6 \%$ SL. Body depth at vent from dorsal surface to ventral surface of the vent itself less than $7 \%$ SL (Fuiman and Witman, 1979). . . Catostomus commersoni.
20.
a. Eye diameter greater than $6 \%$ SL. Body depth at vent, including vent, greater than $7 \% \mathrm{SL}$ (Fuiman and Witman, 1979).
. . . . . . . . . . . . Catostomus catostomus.
b. Dorsal and anal rays typically 9 or 10 , rarely 11 or 12. Myomeres 26 or greater to the vent, typically 28 or greater, and 42 or greater total, typically 44 or greater. Dorsal fin origin less posterior to pelvic fin origin, only about 2-4\% SL difference in position. Metalarvae no smaller than 12 mm SL (14 mm TL). . . . . . . . . . 12.
b. Dorsal rays typically 9, rarely 8 or 10 . Total myomeres typically less than 48 or if 48 or more, preanal myomeres greater than 30. . . . . . 13.
b. Myomeres typically 20 or less to the dorsal fin, 30 or less to the vent and 47 or less total. Anal fin rays typically 9 or 10. . . . . . 14.
b. Anal rays usually 10 , sometimes 9. . . . . . . Gita cypha, possibly Gila robusta (G. cypha not expected outside canyon areas).
b. Dorsal rays 14 or less. . . . . . . . . . 16 .
b. Dorsal rays 13 or less.
b. Peritoneum essentially unpigmented on ventral surfaces. Gut either "S" shaped or with one, rarely two, loops crossing from side to side in later metalarvae. . . I8 (subgenus Catostomus).
b. Dorsal rays typically 10 or 11 , with rare extremes of 9 and 13. Gut "S" shaped in earlier metalarvae and with one, rarely two, loops crossing from side to side in later metalarvae. Ventral surface with distinctive mid-ventral line of melanophores from pectoral fins to vent, sometimes incomplete. . . . . . . . . . . . . . 19.
b. Eye diameter $6 \%$ SL or greater. Body depth at vent, including vent, $7 \%$ SL or greater. . . 20
b. Eye diameter about $6 \%$ SL. Body depth at vent, including vent, about 7-8\% SL. Catostomus catostomus or Catostomus conmersoni.

MEANS AND RANGES OF SELECTED MORPHOMETRICS, EXPRESSED AS PERCENT STANDARD LENGTH, AND MYOMERE COUNTS for each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.


SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. 1

D rays: ii-iii, (16)18-22(24)* Pl rays: (13)15-18(19)
A rays: ii(iii),5-6-7* Branchiostegal rays: 3
C rays: (iii)vi-x,(18)19(20),(iii)vi-ix
P2 rays: (6) $8-\overline{9}$

Gill rakers: 21-29
Pharyngeal teeth: 1,1(2),3/3,1(2),1

Vertebrae: (32)3538(40)
Scales, lateral series:
32-35-38-41
*first principal ray is spine-like and serrated on posterior margin.

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses. ${ }^{2}$

Hatching: (3)4-5(6) / (3)4-5(7)
Eyes pigmented: typically prior to hatching Pl bud formation: prior to hatching P2 bud formation: 9-11(12) / 10-12(15) Yolk completely absorbed: 6-7(8) / 6-8 Finfold completely absorbed: 16-19(20)/20-23(24) Gut coil or loop formation, as evidenced by at least a $90^{\circ}$ bend: $10-11 / 12-13$
Segmentation evident in the principal rays of all fins: 15-16 / 18-19

| Fin ra | First observed | Adult complement |
| :---: | :---: | :---: |
| Principal C: | 7-8/ (7)8 | 8-9/9-10 |
| Secondary C: | 9-11/10-13 | 15-16(17) / 18-19(20) |
| Principal D: | (8)9-11/(9)10-12(1.3) | 13-16(18) / 16-19(21) |
| Principal A: | 10-11/11-13 | 12-13 / 15-16 |
| All Pl: | 11-12/13-15 | (14)16-17/ (17)19-21 |
| All P2: | 12/14-15 | (15)17-19 / (19)21-23 |

Scales: initial appearance: 13-15/16-18
full coverage: 18-21 / 22-25

[^0]

Mesolarva, $13.0 \mathrm{~mm} \mathrm{TL}, 10.8 \mathrm{~mm} \mathrm{SL}$.
(From Taber 1969 with author's permission.)


Mesolarva, recently transformed, $8.5 \mathrm{~mm} \mathrm{TL}, 8.1 \mathrm{~mm} \mathrm{SL}$.
(From Taber 1969 with author's permission.)


Protolarva, recently hatched, $5.6 \mathrm{~mm} \mathrm{TL}, 5.3 \mathrm{~mm}$ SL.
(From Wang and Kernehan 1979 with authors' permission. (From Taber 1969with author's permission.)

Metalarva, recently transformed, $15.0 \mathrm{~mm} \mathrm{TL}, 12.5 \mathrm{~mm} \mathrm{SL}$.
(From Bragensky 1960)

Juvenile, recently transformed, $24.5 \mathrm{~mm} \mathrm{TL}, 20.8 \mathrm{~mm} \mathrm{SL}$.
(From Taber 1969 with author's permission.)

MEANS AND RANGES OF SELECTED MORPHOMETRICS, EXPRESSED AS PERCENT STANDARD LENGTH, AND MYOMERE COUNTS for each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.

|  | Protolarvae | $N=11$ | Mesolarvae | $N=11$ | Metalarvae | $N=2$ | Juveniles | $N=1$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range |
| $\underset{\substack{\text { mmTL }}}{\text { Size, }}$ | $-5.3 \pm 7.0$ | 4.2-6.5 | $7.8 \pm 0.8$ | 6.7-9.7 | $11 \pm 2.0$ | 9.3-12.0 | 19.0 |  |
|  | - $5.6 \pm 1.0$ | 4.4-6.8 | $8.7 \pm 1.3$ | 7.1-10.7 | $12.7 \pm 2.1$ | 11.2-14.1 | 23.6 |  |
| Lengths, anterior margin of the snout to: |  |  |  |  |  |  |  |  |
| AE | $-3 \pm 1$ | 2-5 | $3 \pm 1$ | 2-4 | $4 \pm 1$ | 3-4 | 5 |  |
| PE | $-9 \pm 1$ | 7-11 | $11 \pm 2$ | 8-13 | $12 \pm 0$ | 12-12 | 14 |  |
| OP1 | $-18^{10} \pm 2$ | 14-20 | $22 \pm 3$ | 18-26 | $26 \pm 1$ | 25-26 | 28 |  |
| OP2 | - |  | $50^{3} \pm 1$ | 50-51 | $49 \pm 0$ | 49-49 | 50 |  |
| OD | - |  | $53^{6} \pm 0$ | 52-54 | $52 \pm 1$ | 51-53 | 53 |  |
| ID | - |  | $63^{3} \pm 1$ | 62-63 | $61 \pm 1$ | 60-62 | 64 |  |
| PV | $-69 \pm 2$ | 66-72 | $69 \pm 2$ | 66-72 | $68 \pm 0$ |  | 65 |  |
| IA | - |  | $76^{3} \pm 1$ | 76-77 | $77 \pm 1$ | 76-77 | 76 |  |
| AFC | - |  | $109^{4} \pm 2$ | 106-110 | $112 \pm 1$ | 111-112 | 113 |  |
| PC | - $105 \pm 2$ | 102-108 | $111 \pm 5$ | 104-118 | $120 \pm 2$ | 118-121 | 124 |  |
| Fin lengths: |  |  |  |  |  |  |  |  |
| P1 | $-6 \pm 4$ | 0-11 | $13 \pm 1$ | 10-14 | $14 \pm 1$ | 13-14 | 16 |  |
| P2 | - |  | $1 \pm 1$ | 0-4 | $6 \pm 3$ | 4-8 | 13 |  |
| D | - |  | $14^{3} \pm 2$ | 12-15 | $16 \pm 0$ | 16-16 | 22 |  |
| A | - or just |  | $9^{3} \pm 1$ | 9-10 | $12 \pm 1$ | 11-12 | 17 |  |
| Body depths at or just behind ( $B-$ ): |  |  |  |  |  |  |  |  |
| BPE | - $12 \pm 1$ | 10-14 | $13 \pm 1$ | 11-15 | $17 \pm 1$ | 16-17 | 17 |  |
| OP1 | $-16^{10} \pm 5$ | 11-24 | $14 \pm 2$ | 11-18 | $19 \pm 2$ | 17-20 | 22 |  |
| OD | - |  | $10^{6} \pm 2$ | 7-12 | $14 \pm 3$ | 12-16 | 23 |  |
| BPV | $-6 \pm 1$ | 4-7 | $6 \pm 1$ | 5-8 | $11 \pm 2$ | 9-12 | 16 |  |
| AMPM | - $3 \pm 1$ | 2-4 | $4 \pm 1$ | 3-6 | $7 \pm 1$ | 6-7 | 9 |  |
| Body widths at or just behind ( $B-$ ): |  |  |  |  |  |  |  |  |
| BPE | - $11 \pm 1$ | 9-13 | $13 \pm 2$ | 11-15 | $16 \pm 1$ | 15-16 | 15 |  |
| OP1 | $-12^{10} \pm 5$ | 7-22 | $8 \pm 1$ | 7-10 | $12 \pm 2$ | 10-13 | 14 |  |
| OD | - |  | $5^{6} \pm 1$ | 4-7 | $9 \pm 2$ | 7-10 | 12 |  |
| BPV | $-4 \pm 1$ | 2-5 | $4 \pm 1$ | 3-5 | $6 \pm 1$ | 5-7 | 9 |  |
| AMPM | $-2 \pm 0$ | 1-2 | $2 \pm 1$ | 1-2 | $4 \pm 1$ | 3-4 | 4 |  |
| Myomere counts: |  |  |  |  |  |  |  |  |
| to OP2 | - |  | $15^{3} \pm 0$ | 15-15 | $16 \pm 1$ | 15-17 | 15 |  |
| to OD | - |  | $16^{4} \pm 2$ | 13-17 | $18 \pm 1$ | 17-18 | 17 |  |
| to PV | $-27^{10} \pm 1$ | 26-28 | $26 \pm 1$ | 25-27 | $27 \pm 1$ | 26-27 | 25 |  |
| PV-MPM | - $13 \pm 1$ | 11-14 | $13 \pm 1$ | 12-14 | $14 \pm 0$ | 14-14 | 14 |  |
| total | $-40^{10} \pm 1$ | 39-41 | $39 \pm 1$ | 38-40 | $41 \pm 1$ | 40-41 | 39 |  |

SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. ${ }^{1}$

| rays: | i-ii,8-9-10 |
| :---: | :---: |
| A rays: | i-ii,7-8-9 |
| C rays: | vii-viii, 19,vi-vii |
| P2 rays: | 8-9 |


| Pl rays: 16 | Vertebrae: 39 |
| :--- | :--- |
| Branchiostegal rays: 3 |  |
| Gill rakers: $8-16$ | Scales, lateral series: |
| Pharyngeal teeth: $2,5 / 4,2$ | (45) $50-59-65$ |

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses.

Hatching: 4/4
Eyes pigmented: upon or shortly after hatching
Pl bud formation: upon or shortly after hatching
P2 bud formation: 8-9 / 10
Yolk completely absorbed: 6-7 / 7
Finfold completely absorbed: > $12 / 14$, < $19 / 24$
Gut coil or loop formation, as evidenced by at least a $90^{\circ}$ bend: $9 / 10-11$
Segmentation evident in the principal rays of all fins: > $12 / 14$, < $19 / 24$

| Fin rays | First observed | Adult complement |
| :---: | :---: | :---: |
| Principal C: | 7/7 | 9/10 |
| Secondary C : | 8 / 8-9 | $>12 / 14,<19 / 24$ |
| Principal D: | $8 / 9-10$ | (8)9 / 10-11 |
| Principal A: | 8/9-10 | $9 / 11$ |
| All PI: | $9 / 11$ | > $12 / 14,<19 / 24$ |
| All P2: | > $9 / 11,<12 / 14$ | $>12 / 14,<19 / 24$ |

Scales: initial appearance: 16? / ?
full coverage: > 19 / 24

[^1]mm SL.
mm SL.
mm TL,
Mesolarva,

Mesolarva, recently transformed, $7.4 \mathrm{~mm} \mathrm{TL}, 6.9 \mathrm{~mm} \mathrm{SL}$.

Notes

MEANS AND RANGES OF SELECTED MORPHOMETRICS, EXPRESSED AS PERCENT STANDARD LENGTH, AND MYOMERE COUNTS for each larval phase and the early juveniles. See figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.

| Protolarvae $\quad N=26$ |  | Mesolarvae | $N=21$ | Metalarvae | $N=4$ | Juveniles | $N=16$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range |
| Size,mmSL - 8.2 0.6 | 7.2-9.4 | $9.8 \pm 1.0$ | 8.7-12.9 | $15.2 \pm 1.5$ | 13.6-17.1 | $29.3 \quad 6.3$ | 20.9-43.0 |
| $\mathrm{mmTL}-8.5 \pm 0.7$ | 7.5-9.6 | $10.5 \pm 1.3$ | 9.3-15.4 | $18.8 \pm 2.1$ | 16.5-21.1 | 36.6810 | 26.4-53.2 |
| Lengths, anterior margin of the snout to: |  |  |  |  |  |  |  |
| AE - $3 \pm 1$ | 2-5 | $4 \pm 2$ | 2-5 | $5 \pm 1$ | 4-6 | $6 \pm 1$ | 5-7 |
| PE - $9 \pm 1$ |  | $10 \pm 1$ | 8-12 | $13 \pm 1$ | 11-14 | $12 \pm 1$ | 10-14 |
| OP1 - $17^{23} \pm 4$ |  | $21 \pm 2$ | 18-24 | $26 \pm 2$ | 25-28 | $25 \pm 2$ | 21-28 |
| OP2 - |  | $45^{1}$ |  | $47 \pm 1$ | 46-47 | $45 \pm 1$ | 42-46 |
| OD |  | $50^{3} \pm 0$ | 50-50 | $50 \pm 1$ | 49-51 | $49 \pm 1$ | 46-50 |
| ID |  | $61^{3} \pm 1$ | 61-62 | $64 \pm 1$ | 62-65 | $62 \pm 1$ | 61-64 |
| PV - $65 \pm 1$ | 62-68 | $66 \pm 2$ | 62-70 | $66 \pm 1$ | 65-67 | $64 \pm 1$ | 62-66 |
| IA |  | $74 \pm 1$ | 73-74 | $75 \pm 1$ | 74-75 | $75 \pm 1$ | 74-77 |
| AFC - |  | $110 \pm 1$ | 109-112 | $112 \pm 1$ | 111-113 | $112 \pm 1$ | 111-114 |
| PC - $104 \pm 1$ | 102-106 | $109 \pm 4$ | 104-119 | $123 \pm 2$ | 121-126 | $125 \pm 2$ | 121-128 |
| Fin lengths: |  |  |  |  |  |  |  |
| P1 - $9^{2 l} \pm 2$ | 5-12 | $12 \pm 1$ | 10-14 | $14 \pm 1$ | 13-15 | $17 \pm 1$ | 15-19 |
| P2 |  | 71 |  | $10 \pm 3$ | 7-12 | $15 \pm 2$ | 14-16 |
| D |  | $15 \pm 3$ | 12-18 | $20 \pm 2$ | 18-23 | $23 \pm 1$ | 21-25 |
| A |  | $11 \pm 1$ | 10-12 | $15 \pm 2$ | 13-17 | $18 \pm 3$ | 14-21 |
| Body depths at or just behind (B-): |  |  |  |  |  |  |  |
| BPE - $12 \pm 1$ | 10-14 | $14 \pm 1$ | 12-17 | $18 \pm 1$ | 17-18 | $16 \pm 1$ | 14-19 |
| OP1 - $15^{22} \pm 3$ | 13-21 | $14 \pm 2$ | 12-19 | $21 \pm 1$ | 20-22 | $23 \pm 1$ | 22-26 |
| OD - $14 \pm 1$ | 10-17 | $13 \pm 2$ | 10-17 | $19 \pm 4$ | 16-24 | $26 \pm 3$ | 23-28 |
| BPV - $8 \pm 1$ | 6-12 | $8 \pm 1$ | 7-11 | $14 \pm 2$ | 12-16 | $17 \pm 1$ | 15-19 |
| AMPM - $4 \pm 1$ | 3-5 | $5 \pm 1$ | 3-8 | $8 \pm 1$ | 7-9 | $8 \pm 1$ | 6-9 |
| Body widths at or just behind ( $\mathrm{B}-)$ : $\quad 10$ |  |  |  |  |  |  |  |
| BPE - $12 \pm 1$ | 10-13 | $14 \pm 1$ | 12-18 | $17 \pm 1$ | 16-18 | $17 \pm 1$ | 15-18 |
| OP1 - $9^{22} \pm 1$ | 7-10 | $12 \pm 1$ | 10-17 | $18 \pm 1$ | 17-19 | $18 \pm 3$ | 15-20 |
| OD - $7 \pm 1$ | 5-9 | $6 \pm 1$ | 5-11 | $13 \pm 4$ | 10-18 | $19 \pm 2$ | 16-24 |
| PBV - $5 \pm 1$ | 4-6 | $5 \pm 1$ | 4-9 | $10 \pm 1$ | 9-11 | $13 \pm 1$ | 12-14 |
| AMPM - $2 \pm 0$ | 2-3 | $2 \pm 1$ | 2-3 | $4 \pm 1$ | 4-5 | $4 \pm 1$ | 3-5 |
| Myomere counts: |  |  |  |  |  |  |  |
| to OP2- |  | $16^{1}$ |  | $15 \pm 1$ | 14-16 | $15^{7} \pm 1$ | 14-16 |
| to OD - |  | $18^{3} \pm 1$ | 17-19 | $18 \pm 1$ | 18-19 | $18^{7} \pm 0$ | 18-19 |
| to PV - $29 \pm 1$ | 26-30 | $29 \pm 1$ | 27-30 | $29 \pm 1$ | 28-30 | $28^{7} \pm 1$ | 27-29 |
| PV-MPM- $16 \pm 1$ | 15-19 | $16 \pm 1$ | 15-20 | $17 \pm 1$ | 16-18 | $17^{7} \pm 1$ | 17-18 |
| total - $45 \pm 1$ | 43-48 | $45 \pm 1$ | 44-49 | $46 \pm 1$ | 45-46 | $46^{7} \pm 1$ | 45-46 |

SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. 1

| D rays: | ii, (8) $\overline{9}-10$ | P1 rays: (15) $\overline{\overline{6-17}-18-(19)}$ | Vertebrae: 45-46-47- |
| :---: | :---: | :---: | :---: |
| A rays: | ii,9-10-11 | Branchiostegal rays: 3 | 48(49) |
| ${ }^{\text {C }}$ rays: | xi-x,19,xi-x | Gill rakers: 20-24-28 | Scales, lateral series: |
| P2 rays: | (8) $\overline{9}-10$ | Pharyngeal teeth: 2,5/4, 2 | 73-76-87-90 |

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses.

Hatching: 6-7 / 7
Eyes pigmented: prior to hatching
Pl bud formation: 7-8/8
P2 bud formation: <13/15
Yolk completely absorbed: 8-9 / 9
Finfold completely absorbed: 21-22 / 26-27
Gut coil or loop formation, es evidenced by at least a $90^{\circ}$ bend: > $14 / 17$, < $17 / 21$
Segmentation evident in the principal rays of all fins: 16-17 / 20-21

| Fin rays | First observed | Adult complement |
| :---: | :---: | :---: |
| Principal C: | 9/9-10 | $<14 / 17$ |
| Secondary C: | 10-11 / 11-12 | < 16 / 20 |
| Principal D: | $10 / 11$ | < $13 / 15$ |
| Principal A: | 10/11 | < $14 / 17$ |
| All Pl: | 10-11/12 | $17 / 21$ |
| All P2: | 11-12/13 | 16/20 |

Scales: initial appearance:
full coverage:

[^2] Suttkus and Clemmer (1977).


Mesolarva, $11.7 \mathrm{~mm} \mathrm{TL}, 10.6 \mathrm{~mm} \mathrm{SL}$.


Protolarva, recently hatched, $6.6 \mathrm{~mm} \mathrm{TL}, 6.3 \mathrm{~mm} \mathrm{SL}$.


Mesolarva, recently transformed, 9.3 mm TL, 8.9 mm SL .


MEANS AND RANGES OF SELECTED MORPHOMETRICS, EXPRESSED AS PERCENT STANDARD LENGTH, AND MYOMERE COUNTS fOr each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.


SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. I
D rays: i- $\bar{i}-\mathrm{i} i \mathrm{i},(8) \overline{9} \quad$ P1 rays: $12-\overline{14-15}-16 \quad$ Vertebrae: (42)43- $\overline{46}-48(49)$

A rays: i-ii-iii, (7) $\overline{9}-10 \quad$ Branchiostegal rays: $3 \quad$ Scales, lateral series:
$C$ rays: (ix)x-xi,19(20),(ix)x-xi Gill rakers: 20-23-28 Scales, lateral series:
P2 rays: 8-9
Pharyngeal teeth: $2,5 / 4,2$

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses.

Hatching:
Eyes pigmented:
P1 bud formation:
P2 bud formation: 10-11 / 12
Yolk completely absorbed: $10 / 10-11$
Finfold completely absorbed: 19-20/21-25
Gut coil or loop formation, as evidenced by at least a $90^{\circ}$ bend: $13 / 15-16$
Segmentation evident in the principal rays of all fins: $14 / 17-18$

full coverage:

Adult complement
10/10-11
16-19 / 20-23
(10)12 / (11)14 $12 / 14$
14-16 / 16-20
15-16 / 18-19

[^3]
Mesolarva, $12.0 \mathrm{~mm} \mathrm{TL}, 10.8 \mathrm{~mm} \mathrm{SL}$.

 (From Perry 1979 with author's permission.)

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$E$

## Notes

MEANS AND RANGES OF SELECTED MORPHOMETRICS, EXPRESSED AS PERCENT STANDARD LENGTH, AND MYOMERE COUNTS for each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.


SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. ${ }^{1}$

D rays: ii-iii,(7) $\overline{8}-9 \quad$ Pl rays: (12) $\overline{14-15-16}$
A rays: ii-iii, (7) 8- $\overline{9}-10 \quad$ Branchiostegal rays: 3
C rays: v-x-xiii,(18)19,vi-x-xi
P2 rays: $8-\overline{9}$

Gill rakers:
Pharyngeal teeth: $\overline{0}-1,4 / 4, \overline{0}-1$

Vertebrae: 35-36
Scales, lateral series:
31-33-37-40

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses. ${ }^{2}$

Hatching: 3-4(5) / (3)4(5)
Eyes pigmented: typically prior to hatching Pl bud formation: prior to hatching
P2 bud formation: 7-8 / 8-9
Yolk completely absorbed: (4)5/5
Finfold completely absorbed: (9) 10 / (10)12-13
Gut coil or loop formation, as evidenced by at least a $90^{\circ}$ bend: $10 / 11-12$
Segmentation evident in the principal rays of all fins: 10 / 11-12
$\frac{\text { Fin rays: }}{\text { Principal C: }}$
Secondary C:
First observed

Principal D:
Principal A:
All Pl:
All P2:
Scales: initial appearance: 12-13/15-16
full coverage: (15)16/19-20

[^4]
Metalarva, recently transformed, $9.2 \mathrm{~mm} \mathrm{TL}, 7.9 \mathrm{~mm}$ SL. (From Perry 1979 with author's permission.)

Juvenile, recently transformed, $16.4 \mathrm{~mm} \mathrm{TL}, 13.7 \mathrm{~mm} \mathrm{SL}$.
(From Saksena 1962 with author's and publisher's permission.)
means and ranges of selected morphometrics, expressed as percent standard lengit, and myomere counts for each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.

|  | Protolarvae | $N=4$ | Mesolarvae | $N=8$ | Metalarvae | $N=20$ | Juveniles | $N=54$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range |
| Size,mmSL | - $5.1 \pm 0.5$ | 4.4-5.5 | $6.6 \pm 0.5$ | 5.8-7.2 | $10.1 \pm 1.7$ | 7.1-13.1 | $23.1 \pm 8.3$ | 12.7-38.1 |
| mmTL | $-5.3 \pm 0.6$ | 4.5-5.9 | $7.3 \pm 0.7$ | 6.2-8.0 | $12.3{ }^{19} \pm 2.3$ | 8.9-16.0 | $29.4 \pm 10.5$ | 16.2-48.4 |
| Lengths, | anterior margi | n of the snoun | ut to: |  |  |  |  |  |
| AE | $-3 \pm 1$ | 2-4 | $4 \pm 1$ | 3-5 | $5 \pm 1$ | 3-6 | $6 \pm 1$ | 4-7 |
| PE | - $10 \pm 1$ | 9-11 | $11 \pm 1$ | 10-13 | $13 \pm 1$ | 12-14 | $14 \pm 1$ | 11-16 |
| OP1 | $-19 \pm 1$ | 18-20 | $23 \pm 2$ | 21-27 | $26 \pm 1$ | 23-28 | $26 \pm 1$ | 23-29 |
| OP2 | - |  |  |  | $49 \pm 1$ | 47-51 | $49 \pm 1$ | 46-52 |
| OD | - |  | $50^{6} \pm 2$ | 48-52 | $49 \pm 1$ | 46-50 | $49 \pm 1$ | 46-52 |
| ID | - |  | $60^{6} \pm 2$ | 58-63 | $62 \pm 1$ | 59-64 | $61 \pm 1$ | 58-64 |
| PV | - $62 \pm 2$ | 59-64 | $65 \pm 2$ | 62-68 | $65 \pm 1$ | 63-68 | $63 \pm 1$ | 61-66 |
| IA | - |  | 771 |  | $75 \pm 1$ | 73-77 | $74 \pm 1$ | 72-77 |
| AFC | - |  | $110^{2} \pm 1$ | 109-111 | $11419 \pm 2$ | 110-116 | $117 \pm 2$ | 113-122 |
| PC | - $104 \pm 2$ | 102-107 | $111 \pm 2$ | 108-113 | $121^{19} \pm 3$ | 116-125 | $127 \pm 2$ | 122-132 |
| Fin lengt |  |  |  |  |  |  |  |  |
| P1 | - $11 \pm 1$ | 10-13 | $13 \pm 1$ | 12-15 | $16 \pm 2$ | 13-19 | $18 \pm 1$ | 16-21 |
| P2 | - |  |  |  | $8 \pm 3$ | 2-12 | $15 \pm 1$ | 12-17 |
| D | - |  |  |  | $21 \pm 2$ | 16-23 | $23 \pm 1$ | 21-26 |
| A | - |  |  |  | $14 \pm 2$ | 10-17 | $19 \pm 1$ | 17-20 |
| Body depth | s at or just | behind ( $\mathrm{B}-$ ) |  |  |  |  |  |  |
| BPE | - $11 \pm 2$ | 10-13 | $13 \pm 1$ | 11-14 | $15 \pm 1$ | 13-17 | $16 \pm 1$ | 14-18 |
| OP1 | - $12 \pm 1$ | 11-13 | $14 \pm 1$ | 12-16 | $17 \pm 2$ | 14-19 | $20 \pm 1$ | 18-22 |
| OD | $-10 \pm 1$ | 9-11 | $13 \pm 1$ | 11-15 | $17 \pm 2$ | 13-21 | $21 \pm 2$ | 18-24 |
| BPV | $-7 \pm 1$ | 6-8 | $9 \pm 1$ | 8-10 | $12 \pm 2$ | 9-15 | $16 \pm 1$ | 13-19 |
| AMPM | $-4 \pm 1$ | 2-5 | $5 \pm 1$ | 3-7 | $8 \pm 1$ | 6-10 | $9 \pm 1$ | 8-11 |
| Body width | s at or just | behind ( $\mathrm{B}-$ ) |  |  |  |  |  |  |
| BPE | - $12 \pm 2$ | 10-13 | $13 \pm 1$ | 12-15 | $16 \pm 1$ | 14-18 | $15 \pm 1$ | 13-17 |
| OP1 | $-8 \pm 1$ | 6-9 | $10 \pm 1$ | 8-11 | $13 \pm 2$ | 10-17 | $16 \pm 1$ | 13-18 |
| OD | - $5 \pm 1$ | 4-6 | $7 \pm 1$ | 6-8 | $11 \pm 3$ | 7-15 | $15 \pm 1$ | 13-18 |
| BPV | - $5 \pm 1$ | 4-5 | $6 \pm 1$ | 5-6 | $8 \pm 1$ | 5-10 | $11 \pm 1$ | 9-15 |
| AMPM | - $2 \pm 1$ | 1-2 | $3 \pm 1$ | 2-3 | $3 \pm 1$ | 2-5 | $5 \pm 1$ | 3-7 |
| Myomere coun | unts: |  |  |  |  |  |  |  |
| to OP2 | - |  |  |  | $13^{19} \pm 1$ | 11-15 | $13^{39} \pm 1$ | 12-14 |
| to OD | - |  | $13^{6} \pm 1$ | 12-14 | $13^{19} \pm 1$ | 10-14 | $13^{39} \pm 1$ | 12-14 |
| to PV | - $21 \pm 1$ | 21-22 | $21 \pm 1$ | 20-22 | $2119 \pm 1$ | 20-23 | $20^{39} \pm 1$ | 19-22 |
| PV-MPM | - $14 \pm 1$ | 13-15 | $14 \pm 1$ | 13-14 | $1319 \pm 1$ | 12-15 | $14^{39} \pm 1$ | 12-15 |
| total | - $35 \pm 1$ | 34-36 | $35 \pm 1$ | 34-36 | $35^{19} \pm 1$ | 33-36 | $34 \pm 1$ | 33-36 |

SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. 1

```
D rays: (i)ii,8(9)
A rays: ii(iii),(6)7(8)
C rays: viii-\overline{x}-xi,(18)19(20),viii-\overline{ix}-xi
P2 rays: 7- 
```

Pl rays: $12-\overline{13-14}-16$
Branchiostegal rays: 3
Gill rakers:
Pharyngeal teeth: 0,4 / 4,0

Vertebrae: (33) 34- $\overline{35}-36$
Scales, lateral series:
(31) $-34-36-38(39)$

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses. ${ }^{2}$

| ching: 3-4/ | Fin rays: | First observed | Adult complement |
| :---: | :---: | :---: | :---: |
| Eyes pigmented: ? prior to hatching or $4 / 4$ | Principal C: | $6 / 6$ | $7 / 8$ |
| Pl bud formation: ? prior to hatching or $4 / 4$ | Secondary C: | 7-8 / 8-9 | (12)13 / 16 |
| P2 bud formation: 8/9 | Principal D: | $6 / 6(7)$ | 7 / 8 |
| Yolk completely absorbed: 4(5) / 4(5) | Principal A: | 6-7 / 7 | 7 / 8 |
| Finfold completely absorbed: (12)13/16 | All Pl: | 8/9-10 | 10-11(12) / 12-14 |
| Gut coil or loop formation, as evidenced by at least a $90^{\circ}$ bend: (9) $10-11$ / (11)12-13 | All P2: | $8 / 9(10)$ | 12-13/15-16 |
| ```Segmentation evident in the principal rays of all fins: 11 / 13``` | Scales: in | appearance: verage: about | $\begin{aligned} & 15-16 / 19-20 \\ & / 23-25 \end{aligned}$ |

[^5]
Protolarva, recently hatched, $4.2 \mathrm{~mm} \mathrm{TL}, 4.0 \mathrm{~mm} \mathrm{SL}$.

## (From Perry 1979 with author's permission.)


Mesolarva, recently transformed, $7.0,7.0, \& 6.6 \mathrm{~mm} \mathrm{TL}$, $6.8,6.8, \& 6.4 \mathrm{~mm} \mathrm{SL}$.
(From Perry 1979 with author's permission.)

> (From Perry 1979 with author's permission.)



$$
\text { Juvenile, } \quad m \mathrm{~mL}, \quad \mathrm{~mm} \text { SL. }
$$



[^6]
Juvenile, recently transformed, $19.6 \mathrm{~mm} \mathrm{TL}, 16.0 \mathrm{~mm} \mathrm{SL}$.
(From Snyder et al. 1977 with publisher's permission.)

Notes

## $\bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet \bullet$

MEANS AND RANGES OF SELECTED MORPHOMETRICS, EXPRESSED AS PERCENT STANDARD LENGTH, AND MYOMERE COUNTS for each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.


SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. 1

```
C rays: viii-ix-x-xi,19,ix-x
```

D rays: ii-iii,9(10) Pl rays: (14)16-17(18)
A rays: ii-iii, (8) $\overline{9}-10 \quad$ Branchiostegal rays: 3
Gill rakers:

Vertebrae: 47- $\overline{48-49}$
Scales, lateral series:
(79) $80-84-93-95(98)$

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses. ${ }^{2}$

Hatching: 6-7 / 6-7
Eyes pigmented: Prior to hatching
Pl bud formation: Prior to hatching or (6/6)
P2 bud formation: 10-11 / 11-13
Yolk completely absorbed: (7)8/8(9)
Finfold completely absorbed: 19-20/(24)25
Gut coil or loop formation, as evidenced by at least a $90^{\circ}$ bend: 15-17 / 19-22
Segmentation evident in the principal rays
of all fins: 15 / 18

Fin rays:
Principal C:
Secondary C:
Principal D:
Principal A:
All Pl:
All P2:

First observed
(7) $8 / 8$
(7) $8-9(10) / 8-9(10)$
$8 / 9$ $9-10 / 10$
11-12 / 13-15
11-12/13-15

Adul't complement 8/8(9)
$17 / 21$
(10)11/12(13)

11-12/13-15
16-17 / 20-21
15/18-19

Scales, initial appearance: ~27-31/35-40 full coverage:

[^7]






Metalarva, recently transformed, $14.0 \mathrm{~mm} \mathrm{TL}, 12.1 \mathrm{~mm} \mathrm{SL}$.
(From Buynak and Mohr 1979a with authors' permission.)
Juvenile, recenty transformed, 17.8 mm TL , 14.8 mm SL.
(From Buynak and Mohr $1979 a$ with authors' permission.)

MEANS AND RANGES OF SELECTED MORPHOMETRICS, EXPRESSED AS PERCENT STANDARD LENGTH, AND MYOMERE COUNTS for each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.

| Protolarvae $\quad N=1$ | Mesolarvae | $N=21$ | Metalarvae | $N=41$ | Juveniles | $N=53$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Mean $\pm$ SD Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range |
| Size,nm SL- 6.6 | $8.0 \pm 0.8$ | 6.4-9.6 | $\overline{12.4 \pm 1.9}$ | 9.0-15.9 | $\overline{25.1 \pm 8.4}$ | 14.6-42.1 |
| mm TL- 7.0 | $8.9 \pm 1.3$ | 6.7-11.2 | $14.8 \pm 2.5$ | 10.5-19.6 | $30.3 \pm 9.9$ | 17.6-50.4 |
| Lengths, anterior margin of the snout to: |  |  |  |  |  |  |
| AE - 2 | $4 \pm 1$ | 3-6 | $5 \pm 1$ | 4-6 | $6 \pm 1$ | 4-8 |
| PE -8 | $12 \pm 1$ | 11-15 | $13 \pm 1$ | 11-15 | $13 \pm 1$ | 11-15 |
| OP1 - 17 | $23 \pm 2$ | 20-27 | $25 \pm 1$ | 23-28 | $24 \pm 2$ | 21-28 |
| 0 P 2 | $48^{1}$ |  | $51 \pm 2$ | 48-54 | $50 \pm 2$ | 45-53 |
| OD | $53^{9} \pm 2$ | 51-56 | $55 \pm 2$ | 51-57 | $53^{52} \pm 2$ | 50-57 |
| ID | $64^{4} \pm 1$ | 64-65 | $67^{30} \pm 1$ | 65-70 | $65^{45} \pm 2$ | 62-69 |
| PV - 65 | $67 \pm 2$ | 63-71 | $65 \pm 2$ | 63-67 | $63^{52} \pm 2$ | 57-65 |
| IA |  |  | $75^{27} \pm 1$ | 72-77 | $73^{46} \pm 2$ | 70-77 |
| AFC |  |  | $112^{30} \pm 2$ | 106-114 | $112^{46} \pm 2$ | 109-115 |
| PC - 106 | $111 \pm 5$ | 105-122 | $119 \pm 2$ | 115-124 | $121 \pm 2$ | 117-126 |
| Fin lengths: |  |  |  |  |  |  |
| Pl - 9 | $13 \pm 1$ | 11-15 | $14 \pm 2$ | 11-18 | $17 \pm 1$ | 14-20 |
| P2 | $0 \pm 0$ | $0^{20-1}$ | $730 \pm 3$ | 2-13 | $13^{47} \pm 1$ | 10-16 |
| D |  |  | $18^{30} \pm 2$ | 13-22 | $2147 \pm 1$ | 18-24 |
| A |  |  | $15^{30} \pm 2$ | 10-20 | $19^{47} \pm 2$ | 16-22 |
| Body depths at or just behind ( $B-$ ) : |  |  |  |  |  |  |
| BPE - 11 | $14^{10} \pm 1$ | 12-15 | $17^{26} \pm 1$ | 15-18 | $16^{43} \pm 1$ | 13-18 |
| OP1 - 12 | $15, \pm 2$ | 12-21 | $20 \pm 1$ | 17-23 | $21 \pm 1$ | 18-24 |
| OD - 11 | $12^{13} \pm 1$ | 10-14 | $17^{30} \pm 2$ | 13-21 | $20^{47} \pm 1$ | 18-23 |
| BPV - 8 | $10 \pm 1$ | 8-12 | $13 \pm 2$ | 10-16 | $16 \pm 1$ | 13-19 |
| AMPM - 5 | $5 \pm 1$ | 4-7 | $8 \pm 1$ | 6-10 | $10 \pm 1$ | 9-12 |
| Body widths at or just behind ( $B-$ ): |  |  |  |  |  |  |
| BPE - 11 | $14^{11} \pm 1$ | 13-16 | $17^{26} \pm 1$ | 15-19 | $15^{43} \pm 2$ | 12-18 |
| OP1-8 | $11 \pm 3$ | 8-18 | $14 \pm 2$ | 12-18 | $16 \pm 2$ | 13-21 |
| $\begin{array}{ll}0 D & -6\end{array}$ | $7^{13} \pm 1$ | 6-9 | $10^{30} \pm 1$ | 7-13 | $14^{46} \pm 2$ | 1-18 |
| BPV - 3 | $6 \pm 1$ | 4-8 | $9 \pm 1$ | 6-11 | $12 \pm 2$ | 9-16 |
| AMPM - 2 | $3 \pm 1$ | 1-6 | $4 \pm 1$ | 2-5 | $6 \pm 1$ | 3-7 |
| Myomere counts: |  |  |  |  |  |  |
| to OP2 - | 171 |  | $16^{29} \pm 1$ | 14-17 | $16^{46} \pm 1$ | 13-17 |
| to OD | $19^{4} \pm 2$ | 17-21 | $19^{30} \pm 1$ | 16-20 | $18^{46} \pm 1$ | 16-20 |
| to PV - 26 | $25^{13} \pm 1$ | 23-26 | $24^{30} \pm 1$ | 23-27 | $23^{46} \pm 1$ | 21-25 |
| PV-MPM - 14 | $13^{13} \pm 1$ | 11-14 | $14^{30} \pm 1$ | 11-16 | $15^{46} \pm 1$ | 12-17 |
| total - 40 | $38 \pm 1$ | 37-40 | $38 \pm 1$ | 36-40 | $38^{46} \pm 1$ | 36-40 |

SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. 1

D rays: i- $\overline{\mathrm{i}}-\mathrm{i} i \mathrm{i}, 7-\overline{8}-9$
A rays: i-ī-iii,6-7-8
C rays: (v) $\overline{\mathrm{v} i \mathrm{i} i-\bar{x}-x i,(18) 19,(v i) v i i i-x}$
P2 rays: (6) $7-\overline{8}-9$

Pl rays: 12- $\overline{13-14}-15$
Branchiostegal rays: 3
Gill rakers:
Pharyngeal teeth: $1-\overline{2}, 4 / 4,1-\overline{2}$

Vertebrae: 37-40
Scales, lateral series:
(47)54-80(90)

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses.

Hatching: ? 5-6 / 5-6
Eyes pigmented: ? Prior to hatching
Pl bud formation: ? Prior to hatching
P2 bud formation: $9 / 10(11)$
Yolk completely absorbed: 6-7/7
Finfold completely absorbed: 15-16/18-19(20)
Gut coil or loop formation, as evidenced by at least a $90^{\circ}$ bend: $10-11 /(11) 12-13$ Segmentation evident in the principal rays
of all fins: 14-15(16) / 17-18(19)

| Fin rays: |  | First observed |
| :--- | :--- | :--- |
| PrincipalC: |  | $6-7 / 7$ |
| Secondary C: |  | $9-10 / 10-11$ |
| Principal D: |  | $7-8 / 8-9$ |
| Principal $A:$ |  | $8 / 9$ |
| A11 P1: |  | $12-13 / 13-14(15)$ |
| Al1 P2: |  | $11-12 / 13-14$ |

Adult complement
$8(9) / 9(10)$
15-16/18-19(20)
9-10/10-11
9-10 / 10-11
13-15(16)/16-18(20)
(12) $13-14 /(14) 15-17$

Scales: initial appearance:
full coverage:

[^8]Protolarva, recently hatched, $\mathrm{mm} \mathrm{TL}, \mathrm{mm}$ SL.

Mesolarva, recently transformed, $7.0 \mathrm{~mm} \mathrm{TL}, 6.5 \mathrm{~mm} \mathrm{SL}$.
$$
\mathrm{mm} \text { SL. }
$$

Mesolarva, $9.8 \mathrm{~mm} \mathrm{TL}, 9.0 \mathrm{~mm} \mathrm{SL}$


Juvenile, $38.0 \mathrm{~mm} \mathrm{TL}, 32.2 \mathrm{~mm}$ SL.


MEANS AND RANGES OF SELECTED MORPHOMETRICS, EXPRESSED AS PERCENT STANDARD LENGTH, AND MYOMERE COUNTS for each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.


SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. ${ }^{1}$

| D rays: | i-7̄-iji, 8 - $\overline{9}-10^{*}$ | P1 rays: (11) 12-15(17) | Vertebrae: (38)39-40(43) |
| :---: | :---: | :---: | :---: |
| A rays: | ii-iii, (9) $10-\overline{11}-12(16) *$ | Branchiostegal rays: 3 |  |
| C rays: | (vii) $\overline{\text { viii-x }}$-xi, 19, vii- $\overline{\text { viii-ix }}$ | Gill rakers: $6-9+6-9$ | Scales, lateral series: |
| P2 Rays: | 8-9 | Pharyngeal teeth: 2,5 / 4-5,2 | 49-55-63-67 |

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses. ${ }^{2}$

Hatching: ? 5 / 5
Eyes pigmented: ? Prior to hatching Pl bud formation: ? Prior to hatching P2 bud formation: 9-10 / 11 Yolk completely absorbed: $6 / 6$ Finfold completely absorbed: 19/23 Gut coil or loop formation, as evidenced by at least a $90^{\circ}$ bend: 11 / 13
Segmentation evident in the principal rays of all fins: 12/14

| Fin rays: | First observed | Adult complement |
| :---: | :---: | :---: |
| Principal C: | $6 / 6$ | 8-9/9-10 |
| Secondary C: | 9/10 | 14/17-18 |
| Principal D: | 8/9 | 9-10 / 11 |
| Principal A: | $8 / 9$ | 8-10 / 10-12 |
| All Pl: | 10-11/12-13 | ? 12-13/15-16 |
| All p2: | 12 / 14 | 14-15 / 17-18 |
| Scales: ini | ial appearance: coverage: ? | $\begin{aligned} & 7 / 23 \\ & 31 \end{aligned}$ |

[^9]

Protolarva, 8.0 mm TL, 7.5 mm SL.
(From Lindsey and Northcote 1963 with permission.)


Mesolarva, $9.1 \mathrm{~mm} \mathrm{TL}, 8.2 \mathrm{~mm} \mathrm{SL}$.

Protolarva, recently hatched, $5.3 \mathrm{~mm} \mathrm{TL}, 5.1 \mathrm{~mm} \mathrm{SL}$.
(From Weisel and Newman 1951 with permission.)

Mesolarva, recently transformed, 7.1 mm TL, 6.6 mm SL.



Protolarva, recently hatched, $6.1 \mathrm{~mm} \mathrm{TL}, 5.8 \mathrm{~mm} \mathrm{SL}$.
(From Buynak and Mohr 1979b with authors' permission.)


Mesolarva, recently transformed, $9.7 \mathrm{~mm} \mathrm{TL}, 9.1 \mathrm{~mm} \mathrm{SL}$.
(From Kranz et al. 1979 with authors' permission.)

Juvenile, $27.8 \mathrm{~mm} \mathrm{TL}, 23.8 \mathrm{~mm} \mathrm{SL}$.
(From Buynak and Mohr 1979b with authors' permission.)

Juvenile, recently transformed, $23.0 \mathrm{~mm} \mathrm{TL}, 19.6 \mathrm{~mm} \mathrm{SL}$.
(From Kranz et al. 1979 with authors' permission.)

(From Kranz et al. 1979 with authors permission.)

Metalarva, $19.2 \mathrm{~mm} \mathrm{TL}, 17.4 \mathrm{~mm} \mathrm{SL}$.
(From Kranz et al. 1979 with authors' permission.)

Protolarva, recently hatched, $\mathrm{mm} \mathrm{TL}, \quad \mathrm{mm} \mathrm{SL}$.
Mesolarva, recently transformed,
$\dot{3}$
E
‘71 шแ

Mesolarva, recently transformed,


$$
\text { Juvenile, } \quad m m T L, \quad m m S L .
$$


Protolarva, recently hatched, $8.0 \mathrm{~mm} \mathrm{TL}, 7.8 \mathrm{~mm}$ SL. (From Stewart 1926)


[^10]
Metalarva, $23.8 \mathrm{~mm} \mathrm{TL}, 19.8 \mathrm{~mm} \mathrm{SL}$.
(From Buynak and Mohr 1978 with authors' permission.)

Juvenile, $30.0 \mathrm{~mm} \mathrm{TL}, 24.6 \mathrm{~mm}$ SL.
(From Stewart 1926)

Mesolarva, recently transformed, $14.1 \mathrm{~mm} \mathrm{TL}, 13.2 \mathrm{~mm} \mathrm{SL}$.


means and ranges of selected morphometrics, expressed as percent standard lengit, and myomere counts for each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.

| Protolarvae | $N=9$ | Mesolarvae | $N=25$ | Metalarvae | $N=7$ | Juveniles | $N=22$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range |
| Size,mmSL - $\overline{11.5 \pm 0.8}$ | 10.3-12.8 | $16.2 \pm 2.3$ | 13.0-20.2 | $21.5 \pm 0.5$ | 20.5-22.2 | $30.3 \pm 6.2$ | 22.5-42.5 |
| mmTL - $11.9 \pm 1.0$ | 10.6-13.3 | $18.0 \pm 3.3$ | 13.6-23.6 | $25.8 \pm 1.0$ | 23.9-26.9 | $36.8 \pm 7.5$ | 27.7-51.2 |
| Lengths, anterior margin of the snout to: |  |  |  |  |  |  |  |
| AE $\quad-2 \pm 0$ | 2-3 | $5 \pm 2$ | 3-8 | $8 \pm 1$ | 6-9 | $8 \pm 1$ | 6-10 |
| PE $\quad-7 \pm 1$ | 6-9 | $11 \pm 2$ | 8-15 | $15 \pm 1$ | 13-16 | $14 \pm 1$ | 13-15 |
| OP1 - $15 \pm 1$ | 12-16 | $21 \pm 3$ | 16-27 | $26 \pm 1$ | 25-27 | $25 \pm 1$ | 22-28 |
| OP2 |  | $52^{9} \pm 1$ | 50-54 | $55 \pm 2$ | 52-57 | $55 \pm 1$ | 52-56 |
| OD |  | $49^{16} \pm 1$ | 48-50 | $49 \pm 2$ | 46-51 | $48 \pm 1$ | 45-50 |
| ID |  | $63^{3} \pm 2$ | 61-65 | $64 \pm 1$ | 63-65 | $63 \pm 2$ | 59-66 |
| PV - $79 \pm 1$ | 77-81 | $78 \pm 1$ | 75-81 | $76 \pm 1$ | 74-77 | $74 \pm 1$ | 72-76 |
| IA |  |  |  | $83 \pm 1$ | 82-85 | $83 \pm 1$ | 81-85 |
| AFC |  | $110^{12} \pm 1$ | 108-112 | $113 \pm 2$ | 111-115 | $112 \pm 2$ | 110-115 |
| PC - $104 \pm 1$ | 102-105 | $110 \pm 5$ | 104-118 | $120 \pm 3$ | 116-125 | $121 \pm 2$ | 117-124 |
| Fin lengths: |  |  |  |  |  |  |  |
| P1 - $6 \pm 2$ | 3-9 | $11 \pm 1$ | 9-15 | $14 \pm 2$ | 11-16 | $16 \pm 2$ | 13-19 |
| P2 |  | $2 \pm 3$ | 0-8 | $10 \pm 1$ | 8-11 | $12 \pm 1$ | 9-14 |
| D |  | $20^{3} \pm 1$ | 19-21 | $23 \pm 1$ | 20-24 | $24 \pm 1$ | 22-26 |
| A |  |  |  | $12 \pm 2$ | 9-14 | $13 \pm 1$ | 11-15 |
| Body depths at or just behind (B-): |  |  |  |  |  |  |  |
| BPE - $8 \pm 1$ | 7-9 | $12 \pm 2$ | 9-16 | $16 \pm 1$ | 15-17 | $16 \pm 1$ | 14-17 |
| OP1 - $9 \pm 1$ | 8-10 | $14 \pm 3$ | 10-19 | $19 \pm 2$ | 16-22 | $19 \pm 2$ | 16-22 |
| OD $-14 \pm 1$ | 13-15 | $13 \pm 2$ | 9-18 | $20 \pm 2$ | 16-24 | $19 \pm 2$ | 16-22 |
| $\mathrm{BPV}-5 \pm 1$ | 4-6 | $7 \pm 1$ | 5-10 | $11 \pm 1$ | 10-12 | $11 \pm 1$ | 10-13 |
| AMPM - $3 \pm 1$ | 2-3 | $5 \pm 1$ | 3-7 | $7 \pm 1$ | 6-8 | $7 \pm 1$ | 6-8 |
| Body widths at or just behind (B-): $12+2$ |  |  |  |  |  |  |  |
| BPE - $\quad- \pm 1$ | 6-9 | $12 \pm 2$ | 9-14 | $15 \pm 1$ | 14-16 | $15 \pm 1$ | 14-16 |
| OP1-7士1 | 6-9 | $9 \pm 2$ | 6-13 | $14 \pm 1$ | 12-15 | $15 \pm 1$ | 13-16 |
| 0 DV - $-10 \pm 1$ | 7-11 | $8 \pm 2$ | 5-13 | $12 \pm 1$ | 10-14 | $13 \pm 2$ | 10-15 |
| $\mathrm{BPV}-4 \pm 1$ | 3-4 | $6 \pm 2$ | 4-9 | $10 \pm 2$ | 8-13 | $10 \pm 2$ | 8-13 |
| AMPM - $2 \pm 0$ | 1-2 | $3 \pm 1$ | 1-5 | $4 \pm 1$ | 4-5 | $4 \pm 1$ | 4-5 |
| Myomere counts: 219 |  |  |  |  |  |  |  |
| to OP2 - |  | $21^{9} \pm 1$ | 19-23 | $22 \pm 1$ | 21-23 | $23 \pm 1$ | 21-24 |
| to OD - |  | $19^{16} \pm 1$ | 17-20 | $18 \pm 1$ | 17-18 | $17 \pm 1$ | 15-18 |
| to PV - $39 \pm 1$ | 38-40 | $39 \pm 1$ | 37-40 | $38 \pm 1$ | 37-39 | $37 \pm 1$ | 35-39 |
| PV-MPM - $9 \pm 1$ | 8-10 | $9 \pm 1$ | 8-11 | $10 \pm 1$ | 9-11 | $10 \pm 1$ | 8-12 |
| total - $48 \pm 1$ | 47-49 | $48 \pm 1$ | 47-49 | $48 \pm 1$ | 47-48 | $47 \pm 1$ | 46-48 |

SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses. ${ }^{1}$

| D rays: | ii- $\overline{\mathrm{i} i \mathrm{i}}$ (iv) , (10) $11-\overline{12}-13(14)$ | P1 rays: (12)14-17(18) | Vertebrae: 49-50 |
| :---: | :---: | :---: | :---: |
| A rays: | i-ī, (6) $7-8$ | Branchiostegal rays: 3 | Scales, lateral series: (89)90- |
| C rays: |  | Gill rakers: 25-27-31-33 | 99-107-116(120) |
| P2 rays: | (8) $9-10-11$ | Pharyngeal teeth: |  |

SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses. 2

Hatching: (9) 10-11 / (9)10-11 Fin rays. First observed Adult complement
Eyes pigmented: prior to hatching or 10-11/11
Pl bud formation: prior to hatching or (9) / (9)
P2 bud formation: (17)18 / 20
Yolk completely absorbed: 14-15 / 15-16
Finfold completely absorbed: 20-21/24
Gut coil or loop formation, as evidenced by
at least a $90^{\circ}$ bend: (20)21-22(23)
Segmentation evident in the principal rays
of all fins: 21 / 24-25

| Fin rays: | irst observed | Adult complen |
| :---: | :---: | :---: |
| Principal C: | 13/13-14 | 15/16 |
| Secondary C: | (16)17 / 18 | 22-23 / 27-28 |
| Principal D: | 15 / 16 | 19 / 21-22 |
| Principal A: | (16)17 / 18 | 20-21 / (23) 24 |
| All Pl: | 17 / 19-20 | 20-21/ 23-24(27) |
| All P2: | 19 / 22 | 21 / 24-25 |

Scales, initial appearance: ~21/~25
full coverage: $\sim 33 / \sim 40$
${ }^{1}$ Based in part on data from: Hubbs and Hubbs (1947), Hubbs and Miller (1953), LaRivers (1962), Prewitt (1977) and Sigler and Miller (1963).
${ }^{2}$ Based in part on data from: McAda (1977)

Mesolarva, recently transformed, $14.0 \mathrm{~mm} \mathrm{TL}, 13.0 \mathrm{~mm}$ SL.


Metalarva, $27.5 \mathrm{~mm} \mathrm{TL}, 22.7 \mathrm{~mm} \mathrm{SL}$.


Juvenile, $38.0 \mathrm{~mm} \mathrm{TL}, 31.6 \mathrm{~mm} \mathrm{SL}$.
 Metalarva, recently transformed, $24.5 \mathrm{~mm} \mathrm{TL}, 20.5 \mathrm{~mm} \mathrm{SL}$.


Juvenile, recently transformed, $32.0 \mathrm{~mm} \mathrm{TL}, 26.6 \mathrm{~mm} \mathrm{SL}$.



Notes
means and ranges of selected morphometrics, expressed as percent standard lengit, and myomere counts for each larval phase and the early juveniles. See Figure 4 for explanation of abbreviations and methodology of counts and measures. Superscripts in the table indicate the number of specimens on which the value is based if less than the number given in the column heading.

|  | Protolarvae | $N=6$ | Mesolarvae | $N=8$ | Metalarvae | $N=2$ | Juveniles | $N=$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range |
| Size, mmSL | $8.9 \pm 1.1$ | 7.4-10.5 | $12.6 \pm 1.1$ | 17.1-14.2 | $17.0 \pm 1.7$ | 15.8-18.2 |  |  |
| mmTL | $9.1 \pm 1.2$ | 7.5-11.0 | $13.7 \pm 1.6$ | 11.7-16.1 | $19.6 \pm 2.1$ | 18.1-21.1 |  |  |
| Lengths, anterior margin of the snout to: |  |  |  |  |  |  |  |  |
| AE | $2 \pm 1$ | 1-3 | $3 \pm 2$ | 2-6 | $7 \pm 1$ | 6-7 |  |  |
| PE | $9 \pm 1$ | 8-9 | $10 \pm 2$ | 8-13 | $13 \pm 1$ | 12-13 |  |  |
| OP1 | $17 \pm 1$ | 16-18 | $19 \pm 2$ | 17-23 | $24 \pm 1$ | 23-25 |  |  |
| OP2 |  |  | $53^{3} \pm 1$ | 52-53 | $54 \pm 1$ | 53-55 |  |  |
| OD |  |  | $50^{3} \pm 1$ | 49-50 | $51 \pm 0$ | 51-51 |  |  |
| ID |  |  | $62^{1}$ |  | $65 \pm 0$ | 65-65 |  |  |
| PV | $80 \pm 3$ | 77-84 | $78 \pm 2$ | 75-80 | $78 \pm 1$ | 77-78 |  |  |
| IA |  |  |  |  | $84 \pm 0$ | 84-84 |  |  |
| AFC |  |  | $108 \pm 3$ | 105-112 | $113 \pm 1$ | 112-114 |  |  |
| PC | $103 \pm 2$ | 101-105 | $108 \pm 3$ | 105-113 | $116 \pm 1$ | 115-116 |  |  |
| Fin lengths: |  |  |  |  |  |  |  |  |
| P1 | $5 \pm 3$ | 2-9 | $11 \pm 1$ | 10-12 | $13 \pm 1$ | 12-13 |  |  |
| P2 |  |  | $1 \pm 2$ | 0-4 | $7 \pm 1$ | 6-8 |  |  |
| D |  |  |  |  | $18 \pm 1$ | 17-19 |  |  |
| A |  |  |  |  | $9 \pm 1$ | 8-10 |  |  |
| Body depths at or just behind ( $\mathrm{B}-)$ : 13 |  |  |  |  |  |  |  |  |
| BPE | $10 \pm 1$ | 9-12 | $13 \pm 2$ | 11-16 | $17 \pm 1$ | 16-17 |  |  |
| OP1 | $13 \pm 4$ | 10-20 | $15 \pm 2$ | 12-18 | $18 \pm 0$ | 18-18 |  |  |
| OD | $13 \pm 2$ | 10-14 | $12 \pm 2$ | 10-16 | $17 \pm 1$ | 16-18 |  |  |
| BPV | $5 \pm 1$ | 3-6 | $7 \pm 1$ | 6-9 | $11 \pm 1$ | 10-12 |  |  |
| AMPM | $3 \pm 1$ | 2-3 | $5 \pm 1$ | 4-6 | $7 \pm 1$ | 6-7 |  |  |
| Body widths at or just behind ( $\mathrm{B}-$ ): 13 |  |  |  |  |  |  |  |  |
| BPE | $9 \pm 1$ | 8-10 | $13 \pm 2$ | 11-17 | $15 \pm 1$ | 14-15 |  |  |
| OP1 | $10 \pm 4$ | 7-16 | $10 \pm 2$ | 8-13 | $14 \pm 1$ | 13-14 |  |  |
| OD | $8 \pm 2$ | 6-11 | $7 \pm 2$ | 5-10 | $12 \pm 3$ | 10-14 |  |  |
| BPV | $4 \pm 1$ | 3-4 | $4 \pm 0$ | 4-5 | $6 \pm 0$ | 6-6 |  |  |
| AMPM | $2 \pm 0$ | 1-2 | $2 \pm 1$ | 2-3 | $3 \pm 0$ | 3-3 |  |  |
| Myomere counts: |  |  |  |  |  |  |  |  |
| to OP2 |  |  | $21^{3} \pm 1$ | 21-22 | $21 \pm 1$ | 20-21 |  |  |
| to OD |  |  | $19^{3} \pm 0$ | 19-19 | $18 \pm 0$ | 18-18 |  |  |
| to PV | $36 \pm 1$ | 34-37 | $37 \pm 1$ | 35-38 | $35 \pm 0$ | 35-35 |  |  |
| PV-MPM | $9 \pm 0$ | 9-10 | $10 \pm 1$ | 8-11 | $10 \pm 0$ | 10-10 |  |  |
| total | $45 \pm 1$ | 43-46 | $46 \pm 1$ | 45-47 | $45 \pm 0$ | 45-45 |  |  |

SELECTED ADULT MERISTICS. Mean or modal values are overlined, if significant, and rare or questionable extremes are enclosed by parentheses.*

| D rays: | (i) $\bar{i} \mathbf{i - \overline { i } \overline { i }}$, (8)9-70-11(13) | P1 rays: $14-\overline{15-16}$ | Vertebrae: $42-\overline{44-47-48}$ |
| :---: | :---: | :---: | :---: |
| A rays: | ii-īi, 7 | Branchiostegal rays: 3 |  |
| C rays: | ix-xii,(17)18,viii-xi | Gill rakers: 23-37 + 31-51 | Scales, lateral series: |
| P2 rays: | 9-10 | Pharyngeal teeth: | (60)75-92-100(108) |

## SIZE (mm SL / TL) AT THE APPARENT ONSET OF SELECTED DEVELOPMENTAL EVENTS. Based on structures observable under low power magnification; rare or questionable extremes are enclosed in parentheses.

Hatching: (7) $8 / 8$
Eyes pigmented: 8 / 8
Pl bud formation: prior to hatching P2 bud formation: 13/14
Yolk completely absorbed: $12 / 12-13$
Finfold completely absorbed: > $18 / 21$
Gut coil or loop formation, as evidenced by at least a $90^{\circ}$ bend: 14-15/16-17
Segmentation evident in the principal rays of all fins: 17-18 / 19-21

| Fin rays: | First observed |
| :---: | :---: |
| Principal C: | 11/11-12 |
| Secondary C: | 13-14/15 |
| Principal D: | 13/14-15 |
| Principal A: | 14 / 16 |
| All Pl: | $14 / 16$ |
| All P2: | 15-16/18 |

Adult complement
13/14-15
$>18 / 21$
15-16 / 18
15-16 / 18
$>18 / 21$
> 18 / 21
Scales: initial appearance:
full coverage:
*Based on original observations combined with values reported in: Baxter and Simon (1970), Beckman (1952), Hubbs et al. (1943), Jordan and Evermann (1896), La Rivers (1962), McAllister (1968), Moyle (1976), Scott and Crossman (1973), Sigler and Miller (1963), Simpson and Wallace (1978), Smith (1966), and Wydoski and Whitney (1979).



Table 2: Summary of fin ray, lateral line scale, vertebra and myomere counts of Cypriniform fishes in the Upper Colorado River System in Colorado. Some extreme values are deleted; mean or modal values overlined when significant

| Species | Principal Rays ${ }^{2}$ |  |  | Total Rays |  | Lateral Line Scales | Vertebrae | Myomeres ${ }^{3}$ |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Dorsal | Anal | Cauda ${ }^{-}$ | Pelvic | Pectoral |  |  | Preanal | Postanal | Total |
| Cyprinidae |  |  |  |  |  |  |  |  |  |  |
| Cyprinus Giza carpio | 18-22 | $5-\overline{6}-7$ | 19 | 8- $\overline{9}$ | 15-18 | 32-35-38-41 | 35-38 | 25-27-28 | 10-71-12-13 | 36-37-38-39 |
| Giza <br> atraria | 8-9-10 | 7-8-9 | 19 | $8 \cdot \overline{9}$ | 16 | 50-59-65 | 39 | 25-26-27-28 | 11-13-14 | 38-39-40-41 |
| Giza <br> cypha | 9-10 | $9-\overline{10}-11$ | 19 | 9-10 | 16-17-18 | 73-76-87-90 | 45-46-47-48 | 26-28-29-31 | 14-15-17-20 | 43-74-46-49 |
| Gila <br> elegans | $9-\overline{10}-11$ | 9-1-12-12 | 19 | 9-10 | 16 | 75-99 | 47-49-51 |  |  |  |
| robusta Hybognathus | 9 | 9-10 | 19 | 8- $\overline{9}$ | 12-74-15-16 | 65-80-94-99 | 43-46-48 | 25-28-29-31 | 15-76-17-19 | $42-\overline{45-46}-48$ |
| hankinsoni Notropis | 7- $\overline{8}$ | $6-\overline{8}-9$ | 19 | 8 | 13-15 | 32-35-39-41 | 35-37 | $24-\overline{25-26}$ | $\overline{11-12-13}$ | 36-38 |
| iutrensis <br> Notropis | $\overline{8}-9$ | 8-9-10 | 19 | 8- $\overline{9}$ | $\overline{14-15-16}$ | 31-33-37-40 | 35-36 | 19-21-23-24 | 12-73-14-15 | 34-35-36-37 |
| stramineus Pimephales | 8 | 7 | 19 | 7- $\overline{8}$ | 12-1 $\overline{3-14}-16$ | 34-36-38 | 34- $\overline{35}-36$ | $20-\overline{21-23}$ | 11-12-14-15 | 33-34-36 |
| promezas Ptychocheizus | $7-\overline{8}-9$ | 7 | 19 | 8-9 | 14- $\overline{15-16-17 ~}$ | 40- $\overline{44-48}-54$ | 35-36-37-38 | $20-\overline{23-24}-25$ | 11-12-14-15 | 34-35-37-38 |
| Lucius Rhinichthys | 9 | 9-10 | 19 | $8-\overline{9}$ | 16-17 | 80-84-93-95 | 47-48-49 | 31-33-34-35 | 14-75-17-18 | 48-49-50-51 |
| cataractae Rhinichthys | $7-\overline{8}-9$ | 7 | 19 | 7-8-9 | 12-73-14-15 | 58-63-70-72 | 37-38-40-42 | $24-\overline{25-27}$ | 14-15 | 37-40-41 |
| osculus Richardsonius | 7-8-9 | 6-7-8 | 19 | 7-8-9 | 12-13-14-15 | 47-54-80-90 | 37-40 | 23-24-25-27 | 11-13-14-16 | 36-38-40 |
| balteatus Semotilus | 8-9-11 | 10-TT-T2-13 | 19 | 8-9 | 13-15-17 | 49-55-63-67 | 38-43 | 23-24-25-26 | 13-14-17 | 36-37-39-41 |
| atromaculatus | 7-8-9 | 7-8-9 | 19 | 8 | 13-7 $\overline{6-17}-18$ | 50- $\overline{55-65-70}$ | 39-40-43-44 | $26-\overline{27-28-29}$ | 12-15 | $\overline{40-41-42-44 ~}$ |
| Catostomidae |  |  |  |  |  |  |  |  |  |  |
| Catostomus catostomus | 9- $\overline{10-11}-12$ | 7 | 18 | 9-11 | 16-18 | 90-95-110-120 | 45-47 | 36-37-38-40 | $5-\overline{8-9}-12$ | 44-46-48-50 |
| Catostomus commersoni | 10-17-13 | 6-7-8 | 18 | 9-11 | 16-18 | $55-\overline{60-75-85}$ | 44-48 | 35-36-39-42 | $5-8-9-12$ $5-8-9-11$ | 41-44-47-52 |
| discobozus Catostorms | 9-10-11-12 | 7 | 18 | 9-10 | 14-17 | 75-95-105-118 | 43- $\overline{45-49}-50$ | 33-35-39-40 | 8-70-13-14 | 46-48-50 |
| latipinnis Catostomus | 11-12-13 | 7-8 | 18 | 9-10-11 | 14-17 | 90-99-107-116 | 49-50 | 37-38-39-40 | $8-\overline{9-10}-11$ | 47-48-49 |
| platyrhynchus Xyrauchen | 9-10-11 | 7 | 18 | 9-10 | 14- $\overline{15-16}$ | 75-92-100 | 42-44-47-48 | 34-35-37-38 | 8-9-10-11 | 43- $\overline{45-46}-47$ |
| texanus | 14-15-16 | 7 | 18 | 10 | 15-16-18 | 68-73-87-95 | 45-47 | $35-\overline{37-39}$ | 7-8-9-11 | 45-4-46-48 |

2. Data summarized from that given in individual species accounts; based on original observations and/or previously published values. As per Hubbs and Laglar (1958) except that hardened lepidotrichia, as in Cyprinus carpio, are not separated by use of
Roman numerals.
3. Where known, data based on larval counts only
Table 3. Summary of typical diameters of fertilized eggs ( mm , water-hardened), and lengths of larvae ( $\mathrm{mm} \mathrm{SL} / \mathrm{mm} \mathrm{TL}$ ) at the beginning or completion of selected developmental events for cypriniform fishes in the Upper Colorado River System in Colorado. ${ }^{1}$
Beginning of:

${ }^{1}$ See species accounts for sources of data; some based on previously published data for different geographic areas and subspecies.

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    ${ }^{2}$ Based in part on data from: Jones et al. (1978).

[^1]:    ${ }^{1}$ Based in part on data from: Baxter and Simon (1970), LaRivers (1962), Minckley (1973), and Sigler and Miller (1963).

[^2]:    ${ }^{1}$ Based in part on data from: Holden and Stalnaker (1970), Minckley (1973), Sigler and Miller (1963) and

[^3]:    ${ }^{1}$ Based in part on data from: Baxter and Simon (1970), Beckman (1952), Holden and Stalnaker (1970), Jordan and Evermann (1896), Koster (1957), LaRivers (1962), Minckley (1973), Moore (1957), and Sigler and Miller (1963).

[^4]:    ${ }^{1}$ Based in part on data from: Beckman (1952), Clay (1975), Eddy and Underhill (1974), and Minckley (1973).
    ${ }^{2}$ Based in part on data from: Perry (1979), Saksena (1962) and Taber (1969).

[^5]:    ${ }^{1}$ Based in part on data from: Beckman (1952), Eddy and Underhill (1974), Jordan and Evermann (1896), Pflieger (1975), Scott and Crossman (1973) and Smith (1979).
    ${ }^{2}$ Based in part on data from: Perry (1979).

[^6]:    (From Snyder et al. 1977 with publisher's permission.)

[^7]:    ${ }^{1}$ Based in part on data from: LaRivers (1962), Moore (1957), Seethaler (1978), and Sigler and Miller (1963).
    ${ }^{2}$ Based in part on data from: Seethaler (1978) and Vanicek (1967).

[^8]:    ${ }^{1}$ Based in part on data from: Baxter and Simon (1970), Beckman (1952), LaRivers (1962), Minckley (1973), Moore (1957), Sigler and Miller (1963), and Scott and Crossman (1973).

[^9]:    *subspecies described herein is $R . b$. hydrophzox; $R . b$. balteatus is reported to have up to 12 dorsal and 22 anal rays, though the typical counts are 10 and 15 or 16 , respectively.
    ${ }^{1}$ Based in part on data from: Baxter and Simon (1970), Jordan and Evermann (1896), LaRivers (1962), Moore (1957), Scott and Crossman (1973) and Sigler and Miller (1963).

    2Based in part on data from: Weisel and Newman (1951).

[^10]:    Mesolarva, recently transformed, $14.6 \mathrm{~mm} \mathrm{TL}, 14.0 \mathrm{~mm} \mathrm{SL}$. (From Fuiman 1979 with author's and publisher's permission.)

