AN ABSTRACT OF THE THESIS OF

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Title: Identification and Systematics of Larvae of Artedius, Clinocottus, and Oligocottus (Scorpaeniformes:Cottidae).

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Abstract approved: _____

Complete, identified, developmental series of larval cottids Artedius fenestralis, A. creaseri, A. meanyi, Oligocottus snyderi, Clinocottus embryum, and C. globiceps are described for the first time. In addition, redescriptions of four species, Artedius harringtoni, A. lateralis, Oligocottus maculosus, and Clinocottus acuticeps are included that provide new and comparative information on larval development. Partial developmental series of two species, Artedius Type 3 and Clinocottus analis, are also described and illustrated for the first time.

Using the methods of phylogenetic analysis proposed by Hennig (1966), characters of the larvae of 13 species of Artedius, Clinocottus, and Oligocottus are examined in terms of synapomorphic states. Number and pattern of preopercular spines, gut diverticula, body shape, and a bubble of skin at the nape are identified as synapomorphic characters useful in systematic analysis of this group.

The synapomorphic character, multiple preopercular spines, provides strong evidence that Clinocottus acuticeps, C. analis, C. embryum, C. globiceps, C. recalvus, Oligocottus maculosus, O. snyderi, Artedius

fenestralis, A. harringtoni, A. lateralis, and A. Type 3 form a monophyletic group within the Cottidae. Within this group, the species of Clinocottus and Oligocottus are very closely related; however, each genus appears to be monophyletic. Larvae of all species of Clinocottus possess the synapomorphy, auxiliary preopercular spines. Larval Oligocottus maculosus and O. snyderi share two derived characters, dorsal gut bumps and a bubble of skin at the nape. Artedius fenestralis, A. harringtoni, A. lateralis, and A. Type also form a monophyletic group closely related to Clinocottus and Oligocottus on the basis of a unique multiple preopercular spine pattern.

Synapomorphic characters of the larvae provide strong evidence that A. creaseri and A. meanyi are more closely related to Icelinus than to species of Clinocottus, Oligocottus maculosus, O. snyderi, Artedius fenestralis, A. harringtoni, A. lateralis, and A. Type 3. Characters of the larvae strongly indicate that the genus Artedius as defined by Bolin (1934, 1947) is not monophyletic and that A. creaseri and A. meanyi should be placed separately from the other species of Artedius. Clarification of the exact position of these two species in relation to Icelinus and the Artedius-Clinocottus-Oligocottus group must await identification of larvae of all species of Icelinus and reexamination of characters of adult Icelinus and Artedius.

Identification and Systematics of larvae of *Artedius*, *Clinocottus*, and *Oligocottus* (Scorpaeniformes:Cottidae)

by

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IDENTIFICATION AND SYSTEMATICS OF LARVAE OF ARTEDIUS, CLINOCOTTUS, AND OLIGOCOTTUS (SCORPAENIFORMES:COTTIDAE)

I. INTRODUCTION

The Cottidae are a large, morphologically diverse family of fishes composed of nearly 67 genera and 300 species (Nelson 1976). Most of these species are marine and are generally distributed in coastal waters of all oceans except the Indian Ocean. Cottids are most speciose in the North Pacific. Members of three of the 40 Northeast Pacific genera reported to occur between Baja, California and the Aleutian Islands, Alaska are common intertidal and subtidal inhabitants. These are Artedius, Clinocottus, and Oligocottus and the identification and systematics of the larvae of these genera are the subject of this study (Table 1).

Members of Artedius, Clinocottus, and Oligocottus employ a variety of reproductive strategies with both internal and external fertilization (Clemens and Wilby 1961; Morris 1951, 1955; Breder and Rosen 1966). Demersal egg masses are spawned in crevices and protected locations in both subtidal and intertidal areas. Eggs range in size from 1.0 to 1.5 mm in diameter with up to several hundred eggs in each mass (Morris 1966; Stein 1972). Larvae hatch in approximately two to three weeks and are primarily pelagic during the first four to eight weeks of life. Subsequently, larvae undergo a marked transformation and develop juvenile morphology and pigmentation. Simultaneously, transforming larvae settle from the plankton and assume a benthic existence.

Although larvae of most species of Artedius, Clinocottus, and Oli-cottus are frequently collected in nearshore plankton samples in the Northeast Pacific, larvae of few species have been described. Of the 16 nominal species, developmental series of identified larvae have only been described for A. harringtoni, A. lateralis, C. acuticeps, C. recalvus, and O. maculosus. Other forms which belong to this group based on larval morphology, but not identified to species, were described by Richardson and Washington (1980) as Artedius Type 2, Cottidae Type 1, Type 2, and Type 3. Previous descriptions of A. lateralis and O. maculosus are inadequate for specific identification. Descriptions by Richardson and Washington (1980) were based on incomplete developmental series and too few specimens for specific and/or generic identification.

Systematic treatments of Artedius, Clinocottus, and Oligocottus have yielded confusing and contradictory results. Different workers have placed members of these genera in various subfamilies and families within the suborder Cottoidei.

The objectives of this study were: 1) to identify and describe developmental series of larvae of as many species of Artedius, Clinocottus, and Oligocottus as possible; and 2) to evaluate phylogenetic relationships of Artedius, Clinocottus, and Oligocottus within the Cottidae using shared, derived characters (synapomorphies) of the larvae.

Review of Cottid Systematics

Cottoids are generally considered to be derived from an ancestral stock of scorpaenids, the most generalized group in the order Scorpaeniformes (Taranets 1941; Bolin 1947). Quast (1965) proposed that the

Table 1. Species of Artedius, Clinocottus, and Oligocottus and their meristics.[1]

Species	Dorsal fin spines	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Branchiostegal rays	Total vertebrae
Artedius corallinus[5]	VIII-IX	15-16	12-13	14-16	3	6	31-33
*Artedius creaseri	IX-X	12-14	9-11	15-17	3	6	30-31
*Artedius fenestralis	VIII-IX	16-18	12-14	14-16	3	6	32-35
*Artedius harringtoni	IX	15-18	10-14	13-15	3	7	32-34
*Artedius lateralis	VII-X	15-17	12-14	14-16	3	6	32-34
*Artedius meanyi	IX-X	14-17	10-12	14-16	2[2] or 3	6	33-35
Artedius notospilotus[5]	IX-X	14-16	11-13	14-17	3	6	32-34
*Clinocottus acuticeps	VII-IX	13-17	9-13	13-15	3	6	31-33
*Clinocottus analis	IX-X	14-18	11-14	14-15	3	6	31-35
*Clinocottus embryum	VIII-X	14-17	9-12	12-15	3	6	33-35
*Clinocottus globiceps	VIII-X	13-17	11-12	13-15	3	6[2] or 7[6]	32-34
Clinocottus recalvus[4]	VIII-IX	14-16	9-13	13-15	3	6	32-33
*Oligocottus maculosus	VIII-IX	15-18	12-14	12-15	3	6	33-34
Oligocottus rimensis	VIII-X	16-19	13-15	13-15	3	6	34-37
Oligocottus rubellio	VIII-IX	15-17	12-14	13-15	3	6	32-35
*Oligocottus snyderi	VII-IX	17-20	12-15	12-15	3	6	34-37

[1]From compilation by Howe and Richardson (1978) which incorporated counts from the literature and original counts.

[2]Most frequent count.

[3]Includes hypural.

[4]Described by Morris (1955).

[5]Artedius Type 3 larvae are either A. corallinus or A. notospilotus: see text for explanation.

[6]Counts observed in present study.

*Species for which larvae are described in this study.

suborder Cottoidei contained at least three separate evolutionary lines - Scorpaenidae, Anoplopomatidae, and Hexagrammidae - Cottidae. The Hexagrammidae and Zaniolepidae are considered to be primitive offshoots of the evolutionary line leading to the Cottidae. The Agonidae and Cyclopteridae are generally considered to be the closest allies of the cottids and have been placed in the same suborder Cottoidei (Taranets 1941; Quast 1965). Each of these latter two families is characterized by a unique derived attribute. All agonids possess specialized bony plates that cover the body, and cyclopterids possess a modified ventral sucking disc. In contrast, the Cottidae comprise a widely divergent group of genera which do not appear to share a single derived attribute.

The limits of the family Cottidae are poorly defined. Early workers provided several classifications at the family level with the number of proposed families ranging from 1 to 15 (Gill 1888; Jordan and Evermann 1898; Regan 1913; Jordan 1923; Berg 1940; Taranets 1941). Generally, these classifications have been superficial treatments that include only lists of cottid taxa with little or no discussion of intrageneric relationships. Currently, workers have taken two approaches to the taxonomy of the cottoids at the family level. Greenwood et al. (1966) and Nelson (1976) have basically followed the classification of Berg (1940) and Regan (1913). They recognized seven cottoid families: Icelidae, Cottidae, Psychrolutidae, Cottunculidae, Normanichthyidae, Comephoridae, and Cottocomephoridae. Others have combined all of these forms under the family Cottidae, until further study can redefine family limits (Bailey et al. 1970; Howe and Richardson 1978).

Much of the confusion in cottoid systematics has risen because; 1) the cottoids are a morphologically diverse group which exhibit a confusing array of divergent and convergent characters, 2) many of the characters used in defining systematic relationships have been regressive (undergoing reduction or loss throughout the cottoids) and, as such, may have been attained independently by two or more lineages, and 3) no group of genera within this large family has been recognized as monophyletic on the basis of a shared, derived character. This problem is especially pronounced among the relatively specialized genera Artedius, Clinocottus, and Oligocottus, which have been characterized and defined largely on the basis of regressive and primitive characters.

Systematic treatment of the genera Artedius, Clinocottus, and Oligocottus has been confused and in disagreement. Jordan and Evermann (1898), in a study of the fishes of North America, stated that cottoids could not easily be split into subgroups and recognized only two families of cottoids. They included Artedius, Clinocottus, and Oligocottus in the Cottidae. Regan (1913) based his classification on that of Gill (1888), and included Artedius and Oligocottus in the Cottidae. He did not mention Clinocottus in his work. Berg (1940) modified Regan's classification, placing Artedius, Clinocottus, and Oligocottus in the Cottidae. Neither Regan (1913) nor Berg (1940) discussed characters used in their classifications. Later, Jordan (1923) split the cottoids into 15 families. He placed Artedius in the family Icelidae along with Icelinus, Hemilepidotus, and other scaled sculpins. Clinocottus and Oligocottus were assigned to the scaleless family, Cottidae.

Bolin (1934, 1947) provided a detailed review of the marine cottoids of California including Artedius (six species), Clinocottus (five species), and Oligocottus (four species), all of which he placed in the family Cottidae. Bolin proposed that Artedius, Clinocottus, and Oligocottus were relatively specialized genera that evolved from an evolutionary line of cottids tending toward a reduction in gills, pelvic fin rays, preopercular spines, and squamation. Bolin (1947:159) suggested that "certain details of the more primitive members, particularly the scales, indicate that, while these forms undoubtedly did not spring from the modern genus Hemilepidotus, they shared a common and not particularly remote ancestor with the fishes of that genus." He further suggested that the evolutionary line leading to Artedius, Clinocottus, and Oligocottus gave rise to two major branches. The first branch was characterized by retention of hemilepidotoid-type scales (in various degrees of reduction), a large head, unadvanced anus, and "normal structure of pelvic fins" (Bolin 1947:161). This branch gave rise to the genus Artedius. He further subdivided Artedius into four subgenera: Ruscariops (A. creaseri), Axyrias (A. harringtoni), Astrolytes (A. fenestralis and A. notospilotus), and Artedius (A. lateralis and A. corallinus). Ruscariops was considered the most primitive because of its retention of continuous, dense squamation over the dorsal surfaces of the body, the retention of a pore behind the last gill, and only a slight reduction in the lower preopercular spines. The remaining three subgenera differed in having the lower preopercular spines greatly reduced and in a greater reduction in squamation. Axyrias was considered relatively primitive because of only a slight reduction in

squamation. However, this line was distinguished by the development of prominent secondary sex characters in the males. The remaining two subgenera, Astrolytes and Artedius, were considered to be very closely related, differing mainly in the degree of squamation.

Bolin (1934) believed that the remaining evolutionary branch of the Artedius, Clinocottus, and Oligocottus group split into two lines, one leading to Oligocottus, the other to Clinocottus. Both of these lines were distinguished by the loss of scales. The members of Oligocottus were characterized by the possession of a long, slender penis, modification of the anterior anal fin rays in the male, and an unadvanced anus. Bolin (1934, 1947) recognized two evolutionary lines within this genus. The first consisted of the subgenus Rusciculus containing O. rimensis. This line was considered more primitive because of retention of minute prickles covering the body and a retractile penis. The second line consisted of the subgenus Oligocottus containing the three more specialized species O. maculosus, O. snyderi, and O. rubellio. All of these species were characterized by loss of all but the lateral line scales, a greatly modified anal fin in males, and a permanently external penis.

The evolutionary line leading the Clinocottus, on the other hand, was characterized by an advanced anus, a heavy, blunt penis, and an unmodified anal fin in males. Bolin (1934, 1947) recognized three lines of evolution in Clinocottus represented by the subgenera Clinocottus (C. analis), Blennicottus (C. embryum, C. recalvus, and C. globiceps) and Oxycottus (C. acuticeps). Clinocottus was considered the most primitive because of the retention of minute prickles over the body.

Blennicottus was characterized by possession of a round, rotund head and the retention of a pore behind the last gill. Oxycottus was the most specialized with a penis with a tri-lobed tip and pelvic fins strongly adnate to the belly.

Bolin (1947) considered Oligocottus to be equally related to both Artedius and Clinocottus. Unfortunately, most of his decisions about evolutionary relationships of this group were based on reductive and primitive characters, both of which are poor indicators of evolutionary relationship. As Bolin (1934:42) stated, primitive characters such as high number of pelvic fin rays, heavy squamation, and retention of a pore behind the last gill are, "...evidently due to a conservative retention of an ancestral character and the relationship indicated may, therefore, be as broad as the family itself."

Bolin (1934, 1947) made no mention of Artedius meanyi because it was not reported to occur off California at the time of his work. Rosenblatt and Wilkie (1963) described A. meanyi as being very close to A. creaseri and therefore placed A. meanyi in the same subgenus Ruscariops, along with A. creaseri.

Taranets (1941) reviewed the cottoids, including Artedius, Clinocottus, and Oligocottus, in some detail, recognizing 11 families on the basis of morphological and osteological characters. He placed Artedius, Clinocottus and Oligocottus together in the family Cottidae. However, he assigned all of Clinocottus, Oligocottus, and four species of Artedius (A. corallinus, A. fenestralis, A. harringtoni, and A. lateralis) to the subfamily Oligocottinae, which was characterized by the presence of vomerine and palatine teeth, weakly developed spines on the preopercle,

and two plates of pharyngeal teeth on each side of the mouth. Taranets (1941) further divided the subfamily into two generic groupings, the Artediini and Oligocottini. Oligocottus and Clinocottus were placed in the Oligocottini on the basis of an absence of scales and the presence of an "anal papillae" (penis). In contrast, the four species of Artedius mentioned above, were assigned to the Artediini because of the presence of rows of scales above the lateral line and the absence of an "anal papillae." Artedius creaseri and A. meanyi were placed in a separate subfamily, the Icelinae. The Icelinae were characterized by an enlarged upper preopercular spine and two rows of scales, one along the lateral line and the other below the dorsal fins.

Recent workers generally have followed the classification of Berg (1940) and placed Artedius, Clinocottus, and Oligocottus in the family Cottidae. Greenwood et al. (1966) and Nelson (1976) assigned Artedius, Clinocottus, and Oligocttus to the family Cottidae, however neither mention the criteria for their decision. Howe and Richardson (1978) further proposed that within the family Cottidae, Artedius, Clinocottus, and Oligocottus are closely related, but that the latter two are most closely related. They do not discuss the characters on which their decision is based.

Use of Larval Characters in Systematics

The search for unique, derived characters has been one of the greatest problems in systematic ichthyology. Osteological and morpholocical characters of adult fishes, usually have provided the basic criteria for classifications (Regan 1913; Berg 1940; Greenwood et al. 1966. Recently, new characters are being considered that are contributing

to our understanding of phylogeny, e.g., cytogenetics, biochemistry, behavior, and ontogeny (e.g., De Ligny 1969; Ohno 1970; Moser and Ahlstrom 1972, 1974; Kendall 1977).

The use of characters of larvae in elucidating systematic relationships has been demonstrated in several groups. Bertelsen (1951), in his systematic revision of the ceratioids, used distinctive morphology and pigmentation of the larvae, along with characters of the adults, to clarify the phylogeny of the group at the specific and generic levels. Morphology and pigment patterns of larvae were also useful in discerning generic relationships in the Paralepididae (Ege 1953), the Scopelarchidae (Johnson 1974) and the Myctophiformes (Okiyama 1974). Moser and Ahlstrom (1970, 1972, and 1974) used specialized morphological features of the larvae such as eye shape, fin length and shape, and photophore pattern, to clarify relationships of the myctophids at the subgeneric, generic, and subfamilial levels. Characters such as head spines, fin spines, and body shape of larval serranids, enabled Kendall (1979) to postulate phylogenetic relationships at subfamilial and generic levels. Okiyama and Ueyanagi (1978) used a variety of pigmentation, morphological, and osteological characters of larvae to evaluate relationships within the scombrids. They coded these characters for primitiveness in order to construct a dendrogram of relationships between the genera. This was the first time characters of larvae had been evaluated in a rigorous manner. Richardson (in press) in a phenetic study of cottid larvae, found six groups of genera using similarities in pigmentation, morphology, and spination of the larvae.

Most of these studies based on larval characters have been in remarkable agreement with classifications based on characters of the adults. Discrepancies between the two sets of classifications have arisen in groups where characters examined in adults have been primitive, convergent, or regressive. In these cases, specialized characters of the larvae have been particularly useful in clarifying relationships. These studies have also demonstrated that characters of larvae frequently are functionally independent of adult characters. This is particularly true in fishes with ecologically independent and/or prolonged larval stages in which selection acts independently on the larval and adult stages. In addition, characters of larvae appear to equal adult characters in number and magnitude and to display the same range of primitive to advanced states (Moser and Ahlstrom 1974). Hence, characters of larvae provide another set of independent characters with which to evaluate phylogenetic relationships.

II. METHODS AND MATERIALS

Specimens

Traditionally, there have been two approaches to establishing early life history series of eggs and larvae (Ahlstrom and Moser 1979). One is to start with fertilized eggs of known parentage and to rear larvae through early life history stages. The other is to use ichthyoplankton collections to construct developmental series of larvae that are connected with juveniles and adults using characters such as meristics, morphology, and pigmentation. Both methods were used to assemble series of larval cottids.

Ripe female and male specimens of Clinocottus globiceps, C. acuticeps, Oligocottus maculosus, and O. snyderi were collected in tidepools along the central Oregon coast during winter-spring of 1979 and 1980. These adults were held in 10-gal, 30°/oo seawater, aerated aquaria in a cold room maintained at 12 to 13°C with a 16-hr photoperiod. Broken bricks were stacked in the corners of the aquaria to provide suitable substrate for spawning.

Newly spawned egg masses were incubated between two glass plates separated by a glass rod and held together by rubber bands, following the method of Morris (1955). These plates were then suspended in 1-liter beakers and aerated by a gentle stream of bubbles from an airstone situated just below the eggs.

Newly hatched larvae were immediately transferred to glass 1-gal jars of fresh 30°/oo seawater in which a bloom of the green flagellate, Tetraselmis, and the naked flagellate, Gymnodinium, were maintained.

Seawater was changed daily and aeration was provided by a gentle stream of bubbles from an airstone suspended in each jar. Larvae were fed to excess with newly hatched Artemia nauplii twice daily.

In addition to the reared specimens, developmental series of larvae were put together with larvae obtained from over 1100 plankton and neuston samples collected off Oregon between 1969 and 1978. Additional material was obtained from estuarine and coastal collections of the Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service; Scripps Institute of Oceanography; Los Angeles County Museum; Marine Ecological Consultants; California Academy of Sciences; Humboldt State University; Northwest Fisheries Center, Seattle Laboratory, National Marine Fisheries Service; and University of Washington. Reared specimens of Artedius lateralis from University of British Columbia and Oligocottus maculosus and Clinocottus acuticeps from Vancouver Public Aquarium were also utilized. Transforming and juvenile specimens were also collected monthly from 1977 to 1980 from tidepools along the central Oregon coast.

All specimens were preserved in 5 or 10% buffered Formalin and some material was subsequently transferred to 36 or 40% isopropyl alcohol.

Developmental series of larvae and juveniles were assembled for 12 of the 16 species of Artedius, Clinocottus, and Oligocottus. The number of specimens examined in each series varied from 13 to 37 according to availability of material. Developmental series were formed utilizing field-caught larvae, except as noted below, because of the large amounts of variation in morphology and pigmentation in laboratory-reared larvae. Newly hatched reared larvae were included in series of Artedius

fenestralis, A. lateralis, Clinocottus acuticeps, C. globiceps, Oligocottus maculosus, and O. snyderi. In addition, reared larvae were used to supplement incomplete developmental series of field-caught larvae of Clinocottus globiceps and Oligocottus maculosus (see Tables 12 and 21). Marked differences between developmental series based on field specimens and laboratory-reared specimens are noted in the descriptions.

Developmental Terminology

Following Ahlstrom et al. (1976), the larval period is divided into three stages: preflexion, flexion, and postflexion. Preflexion is defined as the period before the upward bending of the notochord tip. Flexion is defined as the period during the upward bending of the notochord tip. Initiation of notochord flexion is accompanied by a thickening of tissue in the forming hypural region just ventral to the notochord tip. Postflexion is defined as the period when the hypural plates are formed and the notochord is fully flexed.

Cottids undergo a marked transformation from the larval to juvenile form. This transition usually begins in postflexion larvae between 8 and 12 mm long and is accompanied by ossification of the fin rays, the development of juvenile pigmentation on the head, and formation of cirri. Although this transition may occur while specimens are in the plankton, they are considered to be postflexion larvae while they remain in the water column.

Transition to the juvenile stage is accompanied by a marked increase in juvenile pigmentation particularly over the head and in saddles along the dorsum, reduction in number and size of preopercular spines,

ossification of the pelvic fin spine and rays, and by the formation of scales. Specimens are referred to as juveniles when they settle from the plankton and assume a benthic existence.

Morphometrics

Measurements of selected body parts were made to the nearest 0.1 or 0.01 mm using an ocular micrometer in a stereo-microscope. Measurements were made following the definitions of Richardson and Laroche (1979) except as follows: body depth at anus = vertical distance from the dorsal to ventral body margin at the anus; snout to pelvic fin origin = horizontal distance from the tip of the snout to a vertical through the origin of the pelvic fin; and origin of pelvic fin to anus = horizontal distance from a vertical through the origin of the pelvic fin to the anus.

All body lengths given in this study refer to either NL (notochord length), which is defined as snout tip to notochord tip preceding development of the caudal fin, or SL (standard length), which is defined as snout tip to the posterior margin of the hypural plates.

Meristics

Following the methods of Dingerkus and Uhler (1977), several larvae were cleared and stained with Alcian Blue and Alizarin Red S for each species when specimens were available in sufficient numbers. Counts were made of dorsal fin spines and rays, anal fin rays, pelvic fin spines and rays, principal caudal rays, branchiostegal rays, preopercular spines, and vertebrae. Vertebral counts always included the urostyle.

All meristic elements[1] were counted if they absorbed Alizarin stain. Principal caudal rays are defined as the number of caudal fin rays that articulate with the upper and lower hypural plates.

Counts of meristic elements were also made on unstained larvae from the developmental series used in the morphometric examination. All fin rays and spines, branchiostegal rays, preopercular spines, and myomeres were counted when visible under magnification. In this study, all fin rays and spines were counted, regardless of whether they arose from the same pterygiophore.

Spination

Head spination is poorly defined in cottid larvae, partly because spination varies considerably among larvae of different species, and partly because not all spines present in the larvae are found in adults. Spine terminology generally follows Richardson and Washington (1980) in which spines are named for the bones from which they originate. However, all spines occurring in the parietal region are called parietal spines and are numbered in an anterior to posterior sequence.

Systematic Approach

In the past decade, three basic schools or methodological approaches to systematics have been recognized: numerical taxonomy, phylogenetic systematics, and evolutionary systematics. Numerical taxonomy, described by Sneath and Sokal (1973), is a phenetic approach in which taxa are

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[1]Meristic elements are considered to be all countable characters.

clustered by overall similarity. Phylogenetic systematics, based largely on the methodology of Hennig (1966), is a phyletic approach in which shared, derived character states are used to define monophyletic taxa. The third approach, evolutionary systematics, combines both phyletic and phenetic information in the study of relationships (Mayr 1969; Simpson 1961).

Early ontogenetic characters have received little study in systematic ichthyology and our understanding of the evolution of many of the characters of larvae is incomplete or lacking. The few studies which have used larval characters have not incorporated current systematic theory or methodology. The investigation of systematic relationships in this study follows the phylogenetic approach of Hennig (1966) because 1) it is a phyletic approach; 2) it is a well-defined, repeatable methodology in regard to character evaluation, and 3) it is becoming the most widely used approach in phylogenetic studies.

The phylogenetic approach of Hennig (1966) is based on the premise that morphological character states are progressively modified or transformed during the course of evolution. The successive stages of character states of a particular character constitute a transformation series (Hennig 1966). The original or ancestral state from which the transformation series evolved is considered to be the primitive (plesiomorphic) condition. All other character states are derived (apomorphic) relative to the primitive state. The designation of primitiveness or derivedness to each character state is relative to the entire transformation series. Each character state will be derived relative to all preceding or ancestral states and primitive relative to all more advanced or derived states.

The basic tenet of Hennig's approach is that the shared possession of derived character states is the only valid criterion for establishing phylogenetic relationships. The probability of two or more distantly related taxa evolving similar complex, derived structures is extremely rare (Mayr 1969; Simpson 1961). Shared, primitive (symplesiomorphic) characters are not used because primitive character states inherited from an ancestral taxon may remain unchanged in various divergent lineages and may not be evidence of close relationship.

Hennig's methodology maintains that the first step in constructing a dendrogram of phylogenetic relationships for a group of organisms is to find a monophyletic group. Hennig (1966) defines a monophyletic group as a group in which all members are descended from a single stem. The common possession of one or more derived characters is the only conclusive evidence that a group is monophyletic. Monophyletic groups that arose from a common stem by the same splitting process are called sister groups. Every monophyletic group, together with its sister group, constitutes a monophyletic group of higher taxonomic rank. Hence, a dendrogram of phylogenetic relationships of a group is determined by finding monophyletic groups (those sharing at least one derived character) of sequentially higher taxonomic rank.

Estimation of Primitive and Derived Character States

Since only derived character states should be used in determining phylogenetic relationships, the direction of change of character states in a transformation series must be determined. In this study, direction

of change of transformation series was determined through outgroup comparisons utilizing the following criteria of Kluge and Farris (1969:5).

(1) "The primitive state of a character for a particular group is likely to be present in many of the representatives of closely related groups.

(2) A primitive state is more likely to be widespread within a group than is any one advanced state.

(3) The primitive state is likely to be associated with states of other characters known from other evidence to be primitive."

The uniqueness criteria of Marx and Rabb (1970:530) was also utilized in determining derived character states.

(4) "The group which represents the ancestral phenetics unequivocally determines the direction of change in any character having a state unique to the descendent group. Such a unique state is derived."

The immediate ancestral group of Artedius, Clinocottus, and Oligocottus is not known. Bolin (1934, 1947) postulated that Scorpaenichthys marmoratus retained many primitive characters, hence was similar to the ancestral cottid. However, Taranets (1941) did not consider Scorpaenichthys as a cottid. Bolin also suggested that the evolutionary line leading to Artedius, Clinocottus, and Oligocottus evolved from a "hemilepidotoid-like" ancestor. The out-groups used in this study consisted of larvae of seven different cottid genera. These genera include: Scorpaenichthys marmoratus, Hemilepidotus spinosus, Leptocottus armatus,

Enophrys bison, Myoxocephalus sp., Icelinus sp., and Radulinus asprellus. Members of these genera are quite varied and represent several divergent lineages within the Cottidae (Bolin 1934, 1947; Taranets 1941; Howe and Richardson 1978). In this way, a wide range of phenotypic characters present in the family Cottidae were considered. These characters are assumed to represent the phenotypic pool of characters available for evolution of larvae belonging to Artedius, Clinocottus, and Oligocottus. Larvae of several other scorpaeniform families also were examined for outgroup comparisons. These taxa included: Sebastes flavidus (Scorpaenidae), Hexagrammos sp. (Hexagrammidae), Cyclopteridae Type 1 (Cyclopteridae), and Stellerina (Agonidae). The scorpaenids are generally considered to be the most generalized scorpaeniform. The cyclopterids and agonids are considered to be very close allies of the cottids (Quast 1965; Bolin 1947; Matsubara 1943; and Taranets 1941). Character states that are present in most of the cottid outgroup taxa, and also in Sebastes are considered to be primitive. Character states that are unique to members of Artedius, Clinocottus, and Oligocottus are considered to be derived.

Selection of Characters for Analyses

A variety of characters were examined in Artedius, Clinocottus, and Oligocottus larvae including meristics, morphology, pigmentation, spination, and developmental osteology. However of the 50 characters initially examined, many were deleted from final analyses. The criteria used in deleting characters are as follows:

(1) Characters that exhibit a large amount of variability were deleted from analysis. Highly variable characters are poor indicators of phylogenetic relationships (Bolin 1947; Simpson 1961; Mayr 1969). Variable characters are head pigmentation and number of post-temporal-supracleithral spines.

(2) Characters that exhibited the same state in all larvae of Artedius, Clinocottus, and Oligocottus were excluded. These characters are of little use in delimiting intragroup relationships (Zehren 1979). Characters dealing with the form and shape of many bones of the cranium were included in this category.

(3) Derived character states found in only one species were deleted. Again characters of this nature are of no value in determining intragroup relationships. Hindgut diverticula of Clinocottus acuticeps are an example of a specific character.

(4) Characters in which the sequence of change or the primitive and derived states could not be identified were deleted from the analysis. Many of the morphometric and pigmentation characters fell into this category.

Wagner Analysis

The unrooted Wagner network was used in analyzing the data (Farris 1970; Farris et al. 1970). This program uses a phylogenetic method of uniting taxa on the basis on synapomorphies. The Wagner method forms a network or phyletic tree by connecting all the operational taxonomic units (OTU) using a minimum number of steps or the minimum length between OTU's. This has been called the most parsimonious criterion of Camin and Sokal (1965).

This program has several advantages over other phylogenetic and phenetic clustering methods. The Wagner analysis yields the most stable classifications (Mickevich 1978; Presch 1980). In addition, it allows for all types of homoplasy (parallelism, convergence, and reversals). Other phylogenetic techniques allow for parallelisms and convergences, but not reversals. Phenetic clustering techniques do not allow for homoplasy of any kind. Phenetic clustering techniques also require a very large number of characters in order to yield stable classifications. Finally, the Wagner method is probably the most widely used phylogenetic technique in recent years.

III. RESULTS AND DISCUSSION

Taxonomic Descriptions

Larvae of Artedius, Clinocottus, and Oligocottus have been difficult to identify at both the specific and generic levels because of their striking similarities. Many of the diagnostic characters useful in separating these larvae are transient features which are present during only a part of larval development (i.e., head spines, nape bubble). Hence, frequently a combination of several characters is necessary for identification of the larvae. A dichotomous key is of little utility in identification of the larvae because it does not allow for simultaneous use of several characters. In addition, larvae of three species (Artedius notospilotus, Oligocottus rimensis, and Oligocottus rubellio) in this group are still unknown and characters presented in the form of a dichotomous key may not be adequate to separate them from described species. Therefore, to facilitate identification, larval descriptions are arranged in species groups formed by the shared presence of diagnostic characters (Table 2).

Larvae of Artedius fenestralis, A. harringtoni, A. lateralis, A. Type 3, Clinocottus acuticeps, C. analis, C. embryum, C. globiceps, C. recalvus, Oligocottus maculosus, and O. snyderi (Groups A, B, and C) are very similar in morphology, pigmentation, and spination. They are all relatively lightly pigmented with melanophores present on the nape, dorso-lateral surface of the gut, and in a series on the ventral midline of the tail. Presence and amount of head pigmentation is variable within the group. All of these larvae possess blunt, rounded snouts, stubby

bodies, and a bulging gut which trails somewhat below the rest of the body. These larvae are readily distinguished from all other known cottid larvae by the presence of multiple preopercular spines ($\geq$5).

Larvae in Group A, Artedius fenestralis, Artedius harringtoni, Artedius lateralis, and Artedius Type 3, all have a distinctively stubby shape, a rounded snout, and a humped appearance in the nape region. They are further distinguished by a series of ventral midline melanophores posterior to the anus that extend onto the ventral finfold as characteristic pigment slashes in flexion and postflexion larvae. These Artedius larvae possess distinctive preopercular spination with postflexion larvae having a relatively high number ($\geq$14) of preopercular spines. The dorsalmost, middle, and ventralmost spines are larger than the other spines creating the "Artedius" spine pattern unique to larvae of this group. Characters such as number of preopercular spines, number of ventral midline melanophores, size at formation of head pigmentation, presence of gut diverticula, and number of branchiostegal rays distinguish larvae of each of these species of Artedius.

Larvae in Group B include Oligocottus maculosus and O. snyderi. These larvae may be distinguished by the presence of a distinctive bubble of skin situated just anterior to the origin of the dorsal finfold in preflexion and early flexion larvae. Larvae of both species are more slender than larvae in Groups A and C and have a relatively short, compact gut. In contrast to larvae of Group A, the dorsalmost preopercular spine becomes larger than other spines in flexion and postflexion larvae. Characters useful in distinguishing larvae of the

two species of Oligocottus are number and position of ventral midline melanophores, number of preopercular spines, number of parietal spines or prickles, and presence of melanophores on the nape bubble.

Group C includes Clinocottus acuticeps, C. analis, C. embryum, and C. globiceps. Larvae of C. recalvus, described by Morris (1955), also belong to Group C based on morphology. This is the least cohesive group in that larvae vary more in morphology and pigmentation than in the other groups.

In general, larvae have a long gut, the posteriormost portion of which trails below the rest of the body. Larvae of all species except C. embryum have melanistic pigmentation on the head and nape. The dorsalmost preopercular spine is larger than other preopercular spines in postflexion larvae. Characters such as number of preopercular spines, number and spacing of ventral midline melanophores posterior to the anus, and presence of hindgut diverticula or bulges are useful in separating larvae of each of these Clinocottus species.

Group D consists of Artedius creaseri and A. meanyi. These larvae differ from all other larvae of Artedius, Clinocottus, and Oligocottus species listed above in morphology, pigmentation, and spination. They have pointed snouts and large heads, light pigmentation, and four preopercular spines. These characters bind them more closely with Icelinus larvae.

In addition, A. creaseri and A. meanyi larvae are further distinguished by large blotch-like melanophores situated along the ventral midline posterior to the anus. Snout to anus length, meristics, finfold

pigmentation, and nape pigmentation are useful characters in separating larvae of the two species.

Table 2. Groupings of *Artedius*, *Clinocottus*, and *Oligocottus* larvae based on certain diagnostic characters.

	Taxa	Preopercular spinea[1]	'Artedius' apine pattern[2]	'Clinocottus' spine pattern[3]	Ventral midline melanophores	Branchiostegals	Gut diverticulae	Nape bubble	Hindgut diverticulae	Head pigment: preflexion	Head pigment: flexion	Head pigment: postflexion	Nape pigment	Finfold pigment	Lateral pigment[6]
A.	*Artedius fenestralis*	18-22	+	-	21-23	7	-	-	-	-	-	-	+	-	-
	Artedius harringtoni	18-22	+	-	13-19	6	+	-	-	-	-	-	+	-	-
	Artedius lateralis	14-16	+	-	22-31	6	+	-	-	-	+	+	+	-	-
	Artedius Type 3	22-24	+	-	9-13	6	+	-	-	-	-	-	+	-	-
B.	*Oligocottus maculosus*	9-11	-	+	16-36[4]	6	-	+	-	-	+	+	+	-	-
	Oligocottus snyderi	18-22	-	+	3-7	6	-	+	-	-	+/-	+/-	+	-	-
C.	*Clinocottus acuticeps*	11-13	-	+	2-10	6	-	-	+	+	+	+	+	-	-
	Clinocottus analis	9-11	-	+	16-22	6	-	-	-	+	+	+	+	-	+
	Clinocottus embryum	13-14	-	+	15-21	6	-	-	-	-	-	+	+	-	-
	Clinocottus globiceps	16-19	-	+	4-8	6 or 7	-	-	-	+	+	+	+	-	-
	Clinocottus recalvus[5]	5-9	-	+	14-24	6	-	-	-	+	+	+	+	-	-
D.	*Artedius creaseri*	4	-	-	7-11	6	-	-	-	-	+	+	-	-	-
	Artedius meanyi	4	-	-	8-13	6	-	-	-	-	+	+	+	+	-

[1] Number at height of development.
[2] Upper, middle, and lower preopercular apines largest.
[3] Upper preopercular spine largest.
[4] Reared larvae from California and Oregon have 14-20 melanophores; reared larvae from British Columbia have 26-36 melanophores.
[5] Based on Morris 1951.
[6] In postflexion larvae.

Artedius fenestralis

(Figures 1, 2, 3; Tables 3, 4, 11)

Literature

Blackburn (1973) illustrated an 8.5 mm SL larva similar to Artedius fenestralis, which he described at Cottid 4. Eldridge (1970) and White (1977) briefly described and illustrated 3.2 mm and 3.9 mm larvae, respectively, which are similar to A. fenestralis. These illustrations also closely resemble Artedius lateralis larvae. Richardson and Pearcy (1977) listed these larvae as Artedius sp. 2. Richardson and Washington (1980) described and illustrated 3.0, 4.7, 6.0, 7.2, 9.9, and 11.8 mm specimens as Artedius Type 2.

Identification

Juveniles and adults were identified by the following combination of characters: high dorsal fin ray counts (16-18), absence of nasal and preorbital cirri, and the presence of scales on the head under the entire orbit and in a dense patch on the caudal peduncle. The developmental series was linked together primarily by pigmentation, body shape, gut diverticula, and preopercular and parietal spination. Identification of larvae was further confirmed through comparison with larvae reared from known eggs. Postflexion and transforming larvae were linked with juveniles using pigmentation, cirri patterns, spination, and meristics.

Distinguishing Features

A combination of characters is useful in distinguishing preflexion A. fenestralis larvae including prominent gut diverticula protruding

from the dorsal surface of the abdominal cavity, melanistic nape pigmentation, lack of head melanophores, and a series of 13 to 19 ventral midline melanophores posterior to the anus.

Late flexion and postflexion larvae are further distinguished by the presence of 18 to 22 preopercular spines with the dorsalmost, middle, and ventralmost spines being larger than the others. Postflexion larvae also have a cluster of five or six spines situated on the posterior margin of each parietal bone.

Juvenile A. fenestralis are distinguished by meristics, dark pigmentation over the dorsolateral surface of the body, and 13 to 16 ventral midline melanophores posterior to the anus. Other useful characters include the absence of a nasal and preorbital cirrus, the presence of one or two small cirri on the eyeball, and two frontoparietal cirri.

Pigmentation

Newly hatched larval Artedius fenestralis reared in the laboratory have no melanistic pigmentation on the head or nape. Intense melanophores are scattered over the dorsolateral surface of the gut. These ventral gut melanophores are frequently faded and difficult to see in field-collected larvae. Posterior to the anus, a series of 13 to 19 melanophores originates under the third to fourth postanal myomere and extends posteriorly along the ventral body midline. An additional one or two melanophores extend onto the ventral finfold near the notochord tip. These ventral midline melanophores are evenly spaced approximately one every other myomere.

During larval development, the head region remains unpigmented. Two to four melanophores are added on the nape in larvae 3.4 mm long and

become embedded in musculature over the notochord by ∿7 mm. By that size the posterior half of the series of ventral midline melanophores appear as distinctive slashes that extend onto the ventral finfold.

During transformation (planktonic specimens ∿12 to 14 mm long) juvenile pigmentation begins to develop. Melanophores are added on the dorsal surface of the head, on the tip of the lower jaw, and on the pectoral fin base. Gradually, melanophores develop on the anteriormost portion of the spinous dorsal fin, then extend ventrally as a band of pigment stretching from the fourth or fifth dorsal spines to the pigmentation over the dorsal surface of the gut just posterior to the pectoral fin base.

Juvenile pigmentation increases markedly in newly settled individuals 13 mm SL. Numerous melanophores are added over the dorsolateral surface of the head and become concentrated in the parietal-interorbital region. Additional melanophores extend down onto the snout and lips. Laterally, melanophores are added in the cheek region between the eye and the preopercle and the dorsal portion of the opercle. Several melanophores are clustered at the posterior edge of the lower jaw. The ventral surface of the head remains unpigmented. Pigmentation gradually extends from the head posteriorly across the dorsolateral surface of the body until it fuses with bands of pigment reaching from the middle of the spinous dorsal fin to the gut. Pigmentation increases on the anterior end of the dorsal fin creating a dark blotch of pigment across the first four dorsal spines. Melanistic pigmentation also increases on the pectoral fin base with melanophores extending onto the pectoral fin rays and eventually forming several bands of pigmentation. Several

irregular clusters of melanophores appear along the lateral midline and gradually form a band of pigment reaching from the gut to the caudal peduncle.

As juvenile pigmentation develops, saddles of pigment form along the dorsum in an anterior to posterior sequence. The first saddle or band of pigment forms under the fourth to seventh dorsal fin rays. Gradually, melanophores extend ventrally from the pigment saddle and merge with the lateral midline melanophores. Concurrently, a second saddle of pigment forms under the ninth to tenth dorsal fin rays, while a third saddle of pigment begins to develop under the 13th to 15th dorsal fin rays. Melanophores from these pigment saddles also extend ventrally and fuse with the lateral midline pigment. At the same time, melanophores are added on the dorsal fin forming three to four bands. Melanophores extend ventrally from the lateral midline band and form a series of five to eight scallops which reach just below the lateral midline. The rest of the ventrolateral surface of the body remains characteristically unpigmented until juveniles reach about 19 to 20 mm. As the dorsal pigment saddles are forming, the lateral midline melanophores extend posteriorly to the base of the caudal fin where they form a dark band. Gradually, melanophores extend onto the caudal fin rays forming three or five indistinct bands of pigment. Approximately 13 to 16 ventral midline melanophores remain visible in juveniles up to ∿20 mm long.

Morphology

Larvae of Artedius fenestralis hatch at ∿3.5 to 3.8 mm NL. The largest planktonic larva collected is 13.9 mm and is beginning to undergo

transformation. The smallest benthic juvenile examined is 13.1 mm. Thirty-four selected specimens, 3.2 to 21.2 mm, were examined for developmental morphology.

Larval A. fenestralis have stubby bodies with a humped appearance in the nape region. Distinctive diverticula extend dorsolaterally from the dorsal surface of the gut just posterior to the origin of the pectoral fin base. These diverticula are present in newly hatched larvae and remain prominent in the largest planktonic larvae. The diverticula completely disappear in benthic juveniles shortly after settling. The gut itself is moderately long and the posterior portion of the hindgut trails well below the rest of the body. Snout to anus length increases relative to standard length, from 43% in preflexion larvae to 45% in postflexion larvae and 49% in benthic juveniles. Relative body depth at the pectoral fin base and anus increases from 22% and 19% in preflexion larvae, respectively, to 28% SL in postflexion larvae. In juveniles, body depth decreases again to 26% at the pectoral fin base and 22% SL at the anus. Distance from the snout to the origin of the pelvic fins remains constant at 25% SL throughout larval development, as does the distance from the origin of the pelvic fin to the anus at 22% SL. However, length from the snout to the origin of the pelvic fin increases to 29% in benthic juveniles while distance from the pelvic fin origin to the anus decreases slightly to 20% SL.

Relative head length increases during larval development from 23% in preflexion larvae to 27% in postflexion larvae and then to 34% SL in juveniles. Snout length also increases from 15% HL in preflexion larvae to 23% HL in postflexion larvae and juveniles. Eye diameter increases

from 39% to 41% during larval development, then decreases to 26% HL in juveniles.

Fin Development

Caudal fin rays begin to form at ∿6 mm. The adult complement of principal caudal rays is present in larvae ∿7 mm long. The bases of the dorsal and anal fin rays appear in 7 to 7.5 mm larvae. The full complement of fin rays is formed by ∿8.5 to 9 mm. Dorsal fin spines begin to form at ∿8 mm and the full complement of spines is present by ∿9.5 mm. Although pectoral fin rays are visible by ∿7 mm, the adult complement is not formed until ∿9 mm. Pelvic buds form between 6.5 and 7 mm and the adult complement of I,3 pelvic fin rays is formed in larvae ∿10 mm long.

Spination

Seven to 13 tiny spines begin to form along the posterior margin of the preopercle in larvae ∿4.7 mm NL. The preopercle appears to develop in two arc-shaped sections which overlap slightly at the angle of the preopercle. Three to seven spines are present along the dorsalmost section and six to eight spines occur on the lower section. The two sections fuse together in postflexion 7 mm long. Two spines located at the site of fusion begin to increase in length relative to the other preopercular spines. Concurrently, the preopercular spines increase in number during larval development and range between 18 to 21 in larvae ≥8 mm long. The dorsalmost and middle two spines continue to increase in size relative to the other spines, becoming nearly three times as long. The ventralmost two or three spines also increase in size becoming

1.5 to 2 times as long as the other spines. The number of preopercular spines decreases in tranforming larvae >13 mm long. The smaller spines (4-6, 8-10, and 13-15) begin to regress first. Newly settled juveniles possess one large dorsal preopercular spine. The lower spines are visible only as serration or bumps on the preopercular margin. The dorsalmost spine continues to increase in size while the lower bumps eventually disappear in juveniles ≈19 mm long.

Clusters of spines also develop in the parietal and supracleithral-posttemporal regions. One or two spines form at the posterior end of the parietal in larvae ∿6 or 7 mm long. A third spine is added in 7 to 8 mm larvae. Larvae >8 mm have four to six spines located in two rows on each side of the head. Usually, three spines occur in the anterior row while two or three spines are present in a second row posterior to and parallel to the first row. These spines begin to regress in size in transforming larvae >12 to 13 mm long. The anterior spines curve posteriorly, eventually fusing with spines from the posterior row forming a hollow arch and canal. This canal develops into part of the cranial lateral line system in juveniles ∿14 to 15 mm long.

Two small spines develop on the ventral portion of the posttemporal in larvae 6 to 7 mm long. A third spine is added on the posttemporal in larvae >8 mm long. Concurrently, another spine develops on the dorsal tip of the supracleithrum. These spines remain prominent in planktonic larvae ≤12 mm long, however, in transforming juveniles the spines gradually curve dorsally and ventrally and fuse together forming a bony tube or canal. This canal becomes the anteriormost juncture of the lateral line and cephalic lateral line systems in juveniles.

Table 3. Measurements (mm) of young Artedius fenestralis. (Specimens between dashed lines are undergoing notochord flexion.)

Body length	Head length	Snout length	Eye diam	Snout to anus length	Body depth at pectoral	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
L 3.2	0.66	0.10	0.28	1.3	0.62	0.58	-	-	0.34
3.4	0.80	0.10	0.34	1.5	0.76	0.58	-	-	0.34
3.5	0.76	0.08	0.36	1.5	0.72	0.54	-	-	0.34
4.2	0.96	0.18	0.24	1.8	0.90	0.80	-	-	0.34
4.6	1.0	D	0.42	2.3	1.1	1.0	-	-	0.40
4.9	1.1	0.12	0.44	2.1	1.1	1.0	-	-	0.52
5.1	1.3	0.24	0.44	2.6	1.2	1.1	-	-	0.48
5.8	1.2	0.24	0.44	2.6	1.4	1.2	-	-	0.52
5.9	1.3	0.16	0.52	2.7	1.5	1.3	-	-	0.56
6.2	1.4	0.32	0.52	2.7	1.9	1.4	1.7	1.0	0.52
6.6	1.3	0.24	0.60	3.1	1.7	1.8	1.4	1.7	0.60
6.6	1.5	0.28	0.64	3.3	2.0	1.8	1.5	1.8	0.64
6.8	1.5	0.40	0.60	3.0	1.8	1.5	1.7	1.3	0.64
7.0	1.7	0.32	0.64	3.1	2.0	2.0	1.4	1.7	0.72
7.3	1.7	0.36	0.68	3.6	2.0	2.0	1.7	1.9	0.96
7.8	1.6	0.28	0.80	3.7	2.3	2.4	1.8	1.9	1.1
8.0	1.7	0.32	0.72	4.0	2.2	2.3	1.8	2.2	1.4
8.4	2.1	0.40	0.88	3.9	2.4	2.4	1.8	2.1	1.7
8.9	2.1	0.40	1.1	3.9	2.5	2.3	1.9	2.0	1.7
9.5	2.0	0.40	0.80	4.1	2.6	2.5	1.9	2.2	2.0
9.8	2.6	0.74	0.88	4.8	2.9	2.9	2.6	2.2	2.3
9.9	2.8	0.82	0.84	4.7	3.0	2.8	2.6	2.1	2.2
10.5	3.0	0.80	0.92	5.3	3.3	2.9	2.7	2.6	2.9
10.7	3.1	0.82	0.90	5.4	3.4	3.5	2.7	2.7	3.2
10.9	3.0	0.74	0.92	5.2	3.0	3.4	3.0	2.2	3.1
11.2	2.8	0.52	1.1	5.5	3.3	3.4	3.0	2.5	2.9
11.7	2.8	0.60	1.1	6.0	3.2	3.0	3.5	2.5	3.0
11.7	3.3	0.82	0.90	5.7	3.3	3.0	3.4	2.3	3.3
12.2	3.2	0.66	1.1	5.8	3.4	3.4	3.7	2.1	3.6
12.2	3.4	0.82	1.2	5.7	3.3	3.0	3.4	2.3	3.6
13.9	4.0	0.98	1.1	6.6	3.4	2.9	3.6	3.0	3.7
J13.1	4.2	0.83	1.1	6.2	3.5	3.1	3.4	2.6	-
J19.4	6.9	1.6	1.7	9.5	5.0	4.5	6.0	3.9	-
J21.2	7.4	1.7	2.0	10.9	5.1	4.1	7.1	3.8	-

J - Juvenile.
L - Laboratory-reared.
D - Damaged specimens.

Table 4. Meristics and spines of young Artedius fenestralis. (Only specimens with meristic elements formed are included. See Table 3 for complete developmental series included.)

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preopar-cular spines	Parietal spines	Post-temporal spines	Principal caudal rays	Verte-brae	Branchio-stegal rays
5.1	-	-	-	-	-	-	12	-	-	-	-	-
5.8	-	-	-	-	-	-	13	-	-	-	-	-
5.9	-	-	-	-	-	-	9	-	-	-	-	-
6.2	-	-	-	-	-	-	15	-	-	-	-	-
* 6.3	-	-	-	-	-	-	18	2	-	-	33	-
6.6	-	-	-	-	-	-	16	2	-	-	-	-
6.6	-	-	-	-	-	-	14	2	-	-	-	-
6.8	-	-	-	-	-	-	14	1	-	-	-	-
7.0	-	-	-	-	-	-	18	2	-	-	-	-
7.3	-	-	-	-	-	-	21	3	-	-	-	-
* 7.4	-	-	-	-	-	-	22	3	-	-	-	-
7.8	-	-	-	-	-	-	17	5	-	-	-	-
8.0	-	17	13	-	-	-	20	4	-	-	-	-
8.4	-	17	13	-	-	-	23	4	2	-	-	-
* 8.7	-	17	13	14	15	-	21	4	2	-	-	-
8.9	VIII	17	13	-	14	buds	23	5	2	-	-	-
9.5	IX	16	11	15	15	buds	19	4	2	-	-	-
9.8	VIII	17	12	15	15	buds	20	6	2	-	-	-
9.9	IX	16	12	15	15	I,3	22	5	4	-	-	-
* 10.0	VIII	17	12	15	15	I,3	22	4	3	6+6	34	6
10.5	IX	17	12	14	15	I,3	22	5	3	-	-	-
10.7	IX	17	12	15	15	I,3	21	5	2	-	-	-
10.9	IX	17	11	15	15	I,3	19	5	3	-	-	-
* 11.2	IX	17	12	14	15	I,3	23	5	3	-	-	-
11.2	IX	17	12	15	15	I,3	17	6	4	6+6	35	6
11.7	IX	16	12	15	15	I,3	20	5	2	-	-	-
11.7	IX	17	12	15	15	I,3	18	5	2	-	-	-
* 12.0	IX	17	13	15	15	I,3	20	5	4	-	35	6
12.2	IX	16	12	15	15	I,3	15	5	3	-	-	-
* 12.2	IX	17	13	15	15	I,3	19	6	4	6+6	35	6
* 12.7	IX	17	12	15	15	I,3	17	6	5	6+6	34	6
* 13.2	IX	17	13	15	15	I,3	17	5	4	6+6	35	6
* 13.3	IX	16	13	15	15	I,3	18	5	5	6+6	35	6
* 13.6	IX	17	13	15	15	I,3	21	6	5	6+6	35	6
13.9	IX	16	12	15	15	I,3	6	5	-	-	-	-
J13.1	IX	16	12	15	15	I,3	4	-	-	-	-	-
*J13.3	IX	16	13	15	15	I,3	4	0	0	6+6	33	6
J19.4	IX	17	11	15	15	I,3	1	0	0	-	-	-
J21.2	IX	17	12	15	15	I,3	1	1	0	-	-	-

* - Stained with Alizarin Red S.
J - Juvenile.

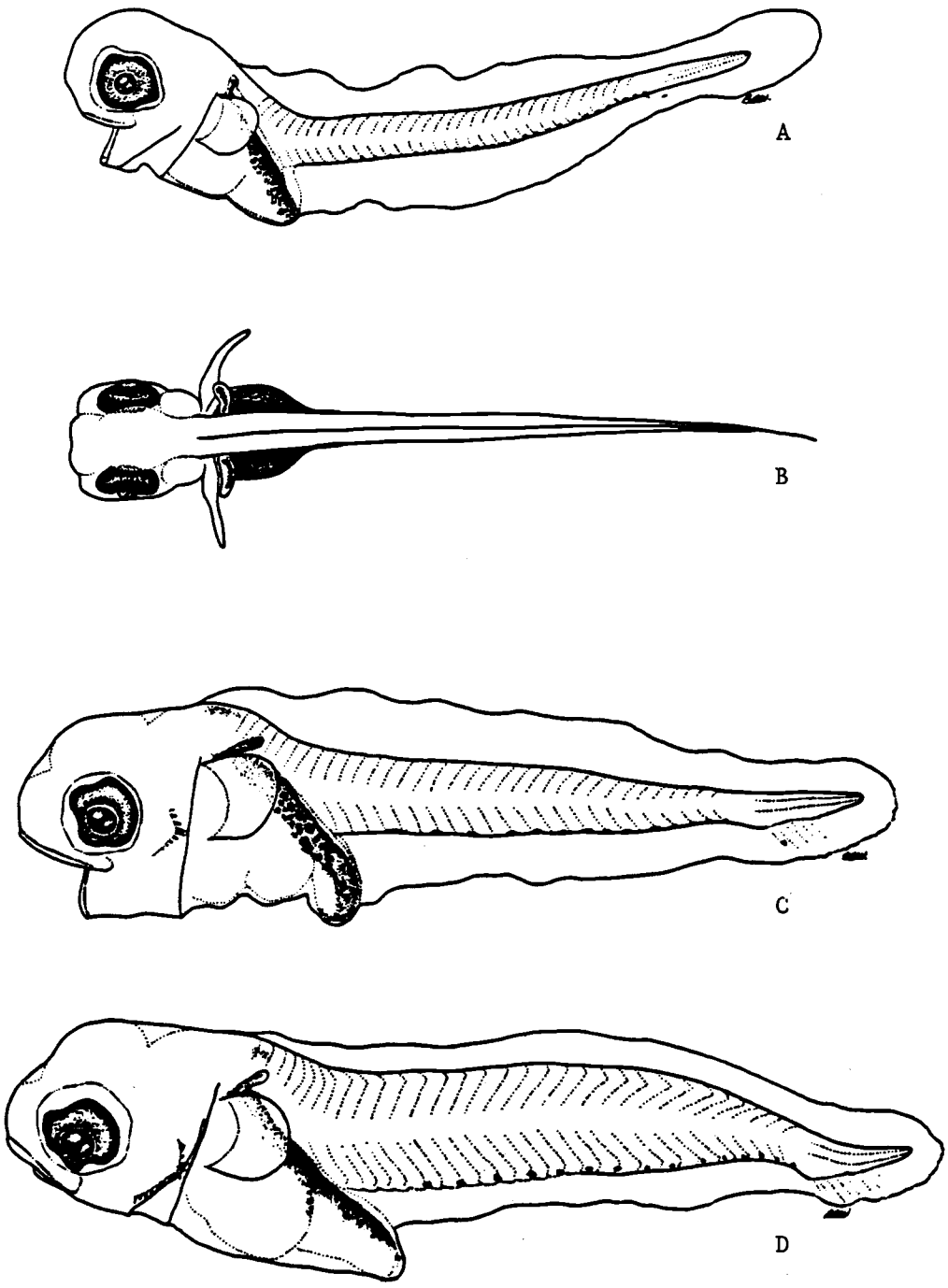

Figure 1. Larvae of Artedius fenestralis: A) 3.0 mm NL, B) 3.0 mm NL, C) 4.7 mm NL, D) 6.0 mm NL (A, B, C, and D from Richardson and Washington 1980).

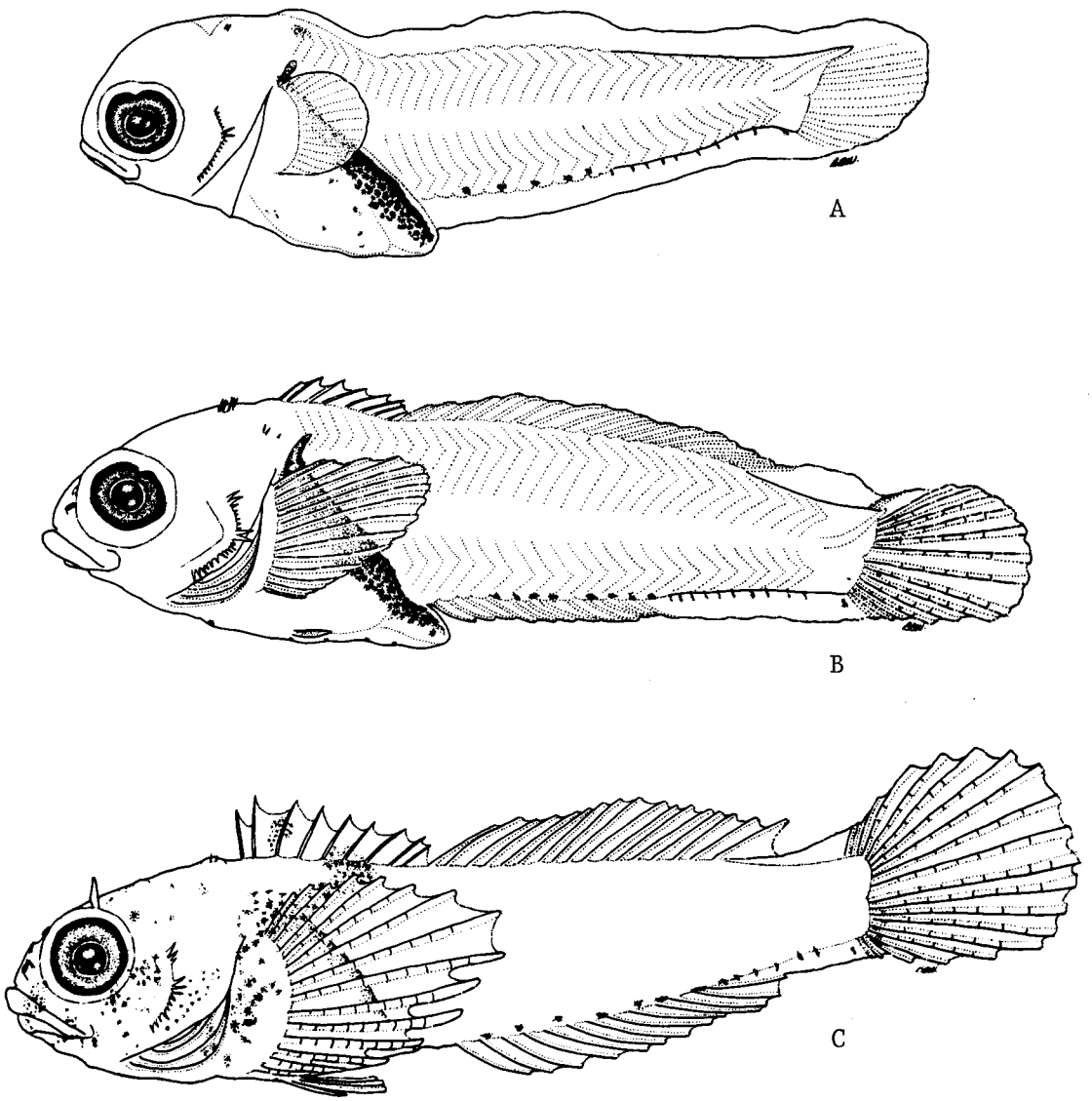

Figure 2. Larvae of Artedius fenestralis: A) 7.2 mm SL, B) 9.9 mm SL, C) 11.8 mm SL (from Richardson and Washington 1980).

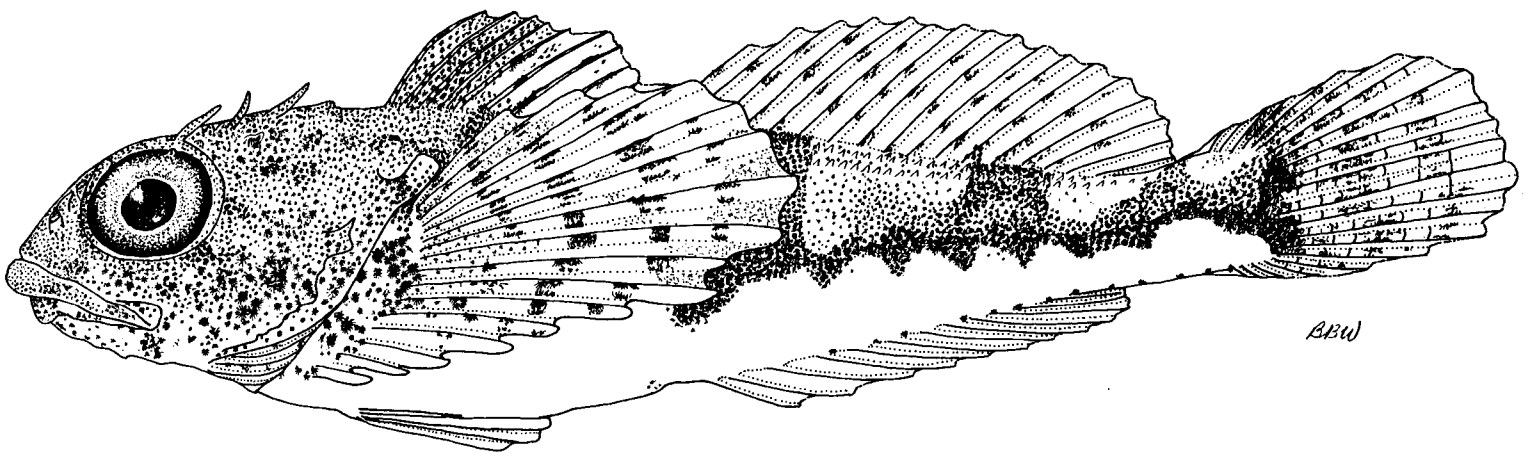

Figure 3. Juvenile of Artedius fenestralis: 19.1 mm SL.

Artedius harringtoni

(Figures 4, 5, 6; Tables 5, 6, 11)

Literature

Blackburn (1973) described a 4.6 mm larva that he called Cottid 6 that is similar to A. harringtoni. Richardson and Washington (1980) illustrated and described 3.0, 4.7, 6.9, 7.3, 9.3, and 13.6 mm specimens.

Identification

Juveniles and adults were identified primarily on the basis of the following characters: high dorsal fin ray counts (16 to 18), low pectoral fin ray counts (usually 14), presence of seven branchiostegals, presence of a preorbital cirrus, scales extending onto the head under only the posterior portion of the orbit, and scales absent on the snout. The developmental series of larvae was linked together by pigmentation, preopercular spination, absence of gut diverticula, body shape, and the possession of seven branchiostegals. Postflexion and transforming larvae were linked with juveniles primarily on the basis of pigmentation, meristics, and presence of a preorbital cirrus.

Distinguishing Features

Characters useful in distinguishing small larval A. harringtoni are a combination of presence of melanistic nape pigment, lack of head pigmentation, a series of 21 to 33 pigment slashes along the ventral midline of the tail, and a humped appearance in the nape region. Absence of dorsal gut diverticula distinguish larval A. harringtoni from similarly pigmented larvae of A. lateralis, A. fenestralis, and A. Type 3.

Postflexion larvae 6.5 mm are distinguished by the presence of 18 to 22 spines along the posterior margin of the preopercle. The dorsalmost and middle preopercular spines are characteristically larger than the other spines. Larvae $^{>}$7 mm have seven branchiostegal rays. Larvae of all other species of Artedius have only six branchiostegal rays.

Juvenile A. harringtoni may be recognized by the dark pigmentation over the head and nape, possession of seven branchiostegals, retention of 18 to 22 ventral midline melanophores, possession of a preorbital cirrus, and dorsal and pectoral fin ray counts.

Pigmentation

Preflexion larvae have no melanistic pigmentation on the head, however, three to five small, external melanophores are concentrated in a dense patch on the nape. The dorsolateral surface of the gut is covered with numerous large, intense melanophores. One to eight tiny melanophores encircle the anus. Posterior to the anus, the only pigmentation consists of a series of 23 to 33 melanophores positioned along the ventral midline. This series originates under the first to third postanal myomere and extends posteriorly toward the tail tip with one or two melanophores positioned under each myomere. An additional one to three melanophores frequently occur on the caudal finfold near the tail tip.

During larval development the head region remains unpigmented. The nape malanophores become embedded in the musculature over the notochord in larvae $^{>}$7 mm. Concurrently, the number of ventral midline melanophores decreases to between 21 to 30 and the posterior half of the series

appear as characteristic pigment slashes that extend onto the ventral finfold.

During transformation, planktonic larvae ≤10 mm begin to develop juvenile pigmentation. Melanophores are added on the tip and base of the lower jaw, on the cheek between the eye and the dorsalmost preopercular spine, on the operculum, and on the isthmus.

Pigmentation increases markedly over the head in newly settled benthic juveniles. Melanophores develop on the snout and upper lip and on the dorsal surface of the head over the brain. Melanophores gradually extend posteriorly from the head and eventually join with the nape pigmentation. Concurrently, melanophores extend posteroventrally from the posttemporal region toward the dorsal gut pigment. Numerous large melanophores form over the base of the pectoral fin, and subsequently extend onto the pectoral fin rays forming four or five distinct pigment bands across the fin. A band of melanophores also extends ventrally from the pectoral fin base and covers the isthmus.

In juveniles ≤13 mm long, the entire head is heavily pigmented. Melanophores extend posteriorly from the head to a vertical line under the seventh dorsal fin spine. A dense patch of melanophores develops at the anterior end of the spinous dorsal fin forming a dark blotch across the fin membrane between the first four dorsal spines. Scattered melanophores are added along the rest of the dorsal fin eventually forming three or four bands of pigment.

Posterior to the head, pigmentation is added in three saddles along the dorsum. The first saddle of pigment forms under the second to fourth dorsal fin rays; the second saddle forms under the seventh to tenth

dorsal fin rays; and the third forms under the 13th to 15th fin rays. Concurrently, an irregular band of faint melanophores develops along the lateral midline. This lateral pigmentation gradually extends posteriorly from the abdominal region to the caudal peduncle. As development proceeds, bands of melanophores extend ventrally from each of the saddles on the dorsum and merge with the lateral midline pigment. As a result, the dorso-lateral surface of the tail is covered by bands of pigmentation which enclose small unpigmented saddles and circles creating a characteristic pattern.

Subsequently, groups of melanophores extend ventrally from the lateral midline pigmentation creating a "scalloped" edge of pigment along the ventro-lateral body surface. Eventually, melanophores from the tips of each scallop extend laterally and join together enclosing four to six distinctive unpigmented circles, characteristic of juvenile A. harringtoni.

In late stages of juvenile pigmentation, the lateral band of melanophores extends posteriorly to the base of the caudal fin. Melanophores are added on the caudal fin rays forming five to seven bands of pigmentation.

Between 18 and 21 ventral midline melanophores remain visible in juveniles $\gtrsim$ 15 mm.

Morphology

The smallest A. harringtoni larva from plankton collections is 3.0 mm NL and still retains remnants of its yolk. The largest planktonic larvae examined is 13.6 mm long and beginning to undergo transformation. The smallest benthic juvenile collected in tidepools is

12.9 mm and is just beginning to develop juvenile pigmentation on the head and pectoral fin base.

Thirty-five selected specimens, 3.0 to 13.7 mm, were examined for morphometrics.

Larvae of A. harringtoni are stubby in shape with a distinctive "humped" appearance in the nape region. Unlike larval A. fenestralis, A. lateralis, and A. Type 3, larval A. harringtoni have no dorsal gut diverticula. The gut is moderately long with snout to anus length ranging from 42% in preflexion larvae to 50% SL in postflexion larvae. Relative snout to anus length decreases slightly in benthic juveniles. The hindgut appears to trail below the rest of the body. Relative body depth at the pectoral fin base increases from 23% in preflexion larvae to 30% in flexion and postflexion larvae, then decreases to 25% SL in juveniles. Relative body depth at the anus also increases from 19% in preflexion larvae to 28% in postflexion larvae, then decreases in juveniles, averaging 21% SL. Distance from the snout to the origin of the pelvic fin base averages 27% SL in postflexion larvae and juveniles while distance from the origin of the pelvic fin base to the anus averages 22% in postflexion larvae and 20% SL in juveniles.

Artedius harringtoni have blunt heads and rounded snouts. Head length increases relative to body length during development, averaging 21% in preflexion larvae, and 34% SL in juveniles. In contrast, eye diameter decreases from 48% HL in preflexion larvae to 34% in postflexion larvae and 31% in juveniles. Snout length increases from 19% to 22% HL during larval development.

Fin Development

A thickening in the hypural region of the developing caudal fin is first visible at 4.7 mm NL, just prior to the onset of notochord flexion which occurs at ∿5.2 mm NL. Caudal fin rays begin to form in larvae ∿6 mm, however, the adult complement of principal caudal rays is not complete until larvae reach ∿7 mm long.

Bases of the dorsal and anal fin rays form in larvae ∿6 to 7 mm long. Dorsal spines begin to form in larvae ∿7 to 8 mm long. The adult complement of dorsal and anal fin rays is complete at 9.3 mm. Pectoral fin rays are first visible between 6 and 7 mm, and the adult complement is countable at ∿7.5 mm. The pelvic fin bud begins to form at ∿7.1 mm, and the adult complement of I,3 is complete by ∿10 mm.

Spination

Eight to ten tiny spines begin to form along the posterior margin of the preopercle in larvae ∿4.5 mm NL. The number of spines increases to 18 to 22 in flexion and postflexion larvae. By the end of flexion, ∿6.7 mm, the middle two spines (7 to 9) begin to increase in size relative to the other preopercular spines. In larvae ≥7.5 mm, the dorsalmost two or three spines also increase in size relative to other spines. As development proceeds, the dorsalmost and middle spines increase in length and diameter creating a characteristic pattern with small, inconspicuous spines situated between the dorsalmost and middle spines, and ventral to the middle spines. In larvae >8.5 mm, the ventralmost four or five spines also become somewhat large relative to the spines directly above them. When larvae reach ∿10 to 11 mm SL, the preopercular spines begin to regress with the small, inconspicuous spines disappearing first.

At the onset of transformation, ∿12 to 13 mm, only four spines remain in the approximate position of the original spines (1-2, 4-9, 12-14, and 18-22). In newly settled juveniles, the dorsalmost preopercular spine becomes quite long and stout while the lower three spines gradually become smaller and visible only as slight bumps on the margin of the preopercle.

Spines never develop in the parietal and posttemporal region of the head. However, in cleared and stained larvae, bony thickenings are visible in the parietal region at the same position as parietal spines found in other cottid larvae.

Table 5. Measurements (mm) of young Artedius harringtoni. (Specimens between dashed lines are undergoing notochord flexion.)

Body length	Head length	Snout length	Eye diam	Snout to anua length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
3.0	0.66	0.16	0.32	1.3	0.72	0.52	-	-	0.12
3.0	0.60	0.06	0.30	1.3	0.66	0.72	-	-	0.24
3.4	0.68	0.10	0.34	1.4	0.70	D	-	-	0.36
4.0	0.88	0.14	0.36	1.6	0.92	0.88	-	-	0.30
4.5	0.96	0.18	0.38	2.0	1.0	0.92	-	-	-
4.7	0.88	0.20	0.39	1.8	1.1	0.98	-	-	0.31
5.0	1.3	0.32	0.52	2.4	1.5	1.4	-	-	0.28
5.2	1.3	0.24	0.56	2.9	1.6	1.8	-	-	0.40
5.3	1.2	0.31	0.36	2.8	1.5	1.4	-	-	0.41
5.9	1.0	0.31	0.47	2.6	1.5	1.4	-	-	0.5
6.4	1.7	0.32	0.64	2.3	1.8	1.8	-	-	0.64
6.7	1.8	0.28	0.72	3.7	2.3	2.2	1.6	2.1	0.92
6.9	1.8	0.39	0.58	3.5	1.6	1.5	-	-	0.72
7.1	2.0	0.40	0.76	3.5	2.1	2.5	1.9	1.6	0.84
7.4	2.0	0.47	0.78	3.4	2.4	2.1	1.9	1.5	0.90
7.5	1.9	0.48	0.68	3.6	2.2	2.0	D	D	1.0
8.8	2.5	0.64	0.84	4.2	3.0	3.0	2.6	1.6	1.7
8.8	2.8	0.57	0.90	4.7	2.9	2.9	2.5	2.2	2.5
9.2	2.7	0.60	0.88	4.5	2.9	3.1	2.5	2.0	2.0
9.3	2.0	0.35	0.94	4.5	3.0	2.8	2.7	1.8	2.0
9.9	3.0	0.57	1.1	5.1	3.0	3.2	2.7	2.4	2.7
10.0	3.1	0.82	0.98	5.4	3.0	3.2	3.0	2.4	3.2
10.2	3.2	0.82	0.98	5.2	3.0	3.1	2.8	2.4	3.0
10.4	3.1	0.66	1.1	5.5	3.2	2.8	3.0	2.5	3.4
10.7	3.0	0.90	1.1	5.6	3.1	3.1	2.8	2.8	3.4
11.1	3.0	0.82	1.0	5.7	2.9	2.7	3.4	2.3	2.6
11.4	3.1	0.90	1.1	5.7	3.3	3.2	3.3	2.4	3.3
11.6	3.4	0.66	1.2	5.7	3.4	3.1	3.4	2.3	3.5
11.9	3.4	0.98	1.1	5.6	3.3	3.3	3.4	2.2	3.8
12.2	3.6	0.90	1.2	5.6	3.4	3.4	3.4	2.2	3.6
12.4	3.9	0.98	1.1	6.0	3.3	3.1	3.7	2.3	4.3
13.4	3.6	1.1	1.1	6.1	3.9	3.4	3.8	2.3	3.8
13.6	4.3	1.1	1.1	6.6	3.8	3.9	3.9	2.7	3.6
J12.9	4.6	1.0	1.4	6.3	3.2	2.7	3.6	2.7	4.5
J13.2	4.0	0.92	1.2	5.7	3.3	2.9	3.2	2.5	4.0
J13.7	4.9	1.2	1.5	6.6	3.4	2.9	4.0	2.6	5.1

J - Juvenile.
D - Damaged.

Table 6. Meristics and spines of young of Artedius harringtoni. (Only specimens with meristic elements formed are included. See Table 5 for complete developmental series examined.)

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preopercular spines	Parietal spines	Post-temporal spines	Principal caudal rays	Vertebrae	Branchiostegal rays
4.5	-	-	-	-	-	-	8	-	-	-	-	-
4.7	-	-	-	-	-	-	12	-	-	-	-	-
5.0	-	-	-	-	-	-	14	-	-	-	-	-
5.2	-	-	-	-	-	-	14	-	-	-	-	-
5.3	-	-	-	-	-	-	13	-	-	-	-	-
5.9	-	-	-	-	-	-	16	-	-	-	-	-
6.4	-	-	-	-	-	-	17	-	-	-	-	-
6.7	-	18	13	-	-	-	20	-	-	-	-	-
6.9	-	-	-	-	-	-	16	-	-	-	-	-
* 7.0	-	-	-	-	-	-	18	-	-	-	-	-
7.1	-	17	12	-	-	-	19	-	-	-	-	-
7.4	-	17	13	14	14	-	18	-	-	-	-	7
* 7.5	-	-	-	14	14	buds	20	-	-	-	33	7
7.5	-	18	12	-	-	buds	22	-	-	-	-	7
* 8.4	IX	16	13	14	14	buds	18	-	-	6+6	34	7
8.8	-	17	12	14	14	buds	21	-	-	-	-	7
8.8	IX	17	12	14	14	3	19	-	-	-	-	7
9.2	IX	17	12	14	14	I,3	21	-	-	-	-	7
9.3	X	16	13	14	14	I,3	21	-	-	-	-	7
* 9.4	IX	17	13	14	14	I,3	21	-	-	6+6	33	7
9.9	IX	17	13	14	14	I,3	19	-	-	-	-	7
10.0	IX	17	11	14	14	I,3	17	-	-	-	-	7
10.2	VIII	17	13	14	14	I,3	21	-	-	-	-	7
* 10.2	IX	18	14	14	14	I,3	20	-	-	6+6	34	7
10.4	IX	17	13	14	14	I,3	20	-	-	-	-	7
* 10.4	IX	16	13	14	14	I,3	20	-	-	6+6	34	7
10.7	IX	17	12	15	14	I,3	20	-	-	-	-	7
* 10.9	IX	17	13	15	14	I,3	17	-	-	6+6	34	7
11.1	IX	17	13	14	14	I,3	19	-	-	-	-	7
* 11.2	IX	17	14	14	14	I,3	21	-	-	6+6	34	7
* 11.4	IX	17	13	14	14	I,3	20	-	-	6+6	-	7
11.4	IX	17	13	14	14	I,3	20	-	-	-	-	7
* 11.5	IX	17	13	14	14	I,3	15	-	-	6+6	34	7
11.6	IX	18	12	14	14	I,3	20	-	-	-	-	7
11.9	IX	17	12	14	14	I,3	13	-	-	-	-	7
12.2	IX	16	13	14	14	I,3	17	-	-	-	-	7
12.4	IX	18	14	14	14	I,3	16	-	-	-	-	7
13.4	IX	18	14	15	15	I,3	18	-	-	-	-	7
* 13.6	IX	17	13	14	14	I,3	11	-	-	6+6	34	7
J 12.9	IX	18	13	14	14	I,3	9	-	-	-	-	7
J 13.2	IX	17	12	14	14	I,3	4	-	-	-	-	7
J 13.7	IX	17	13	14	14	I,3	1	-	-	-	-	7

* - Stained with Alizarin Red S.
J - Juvenile.

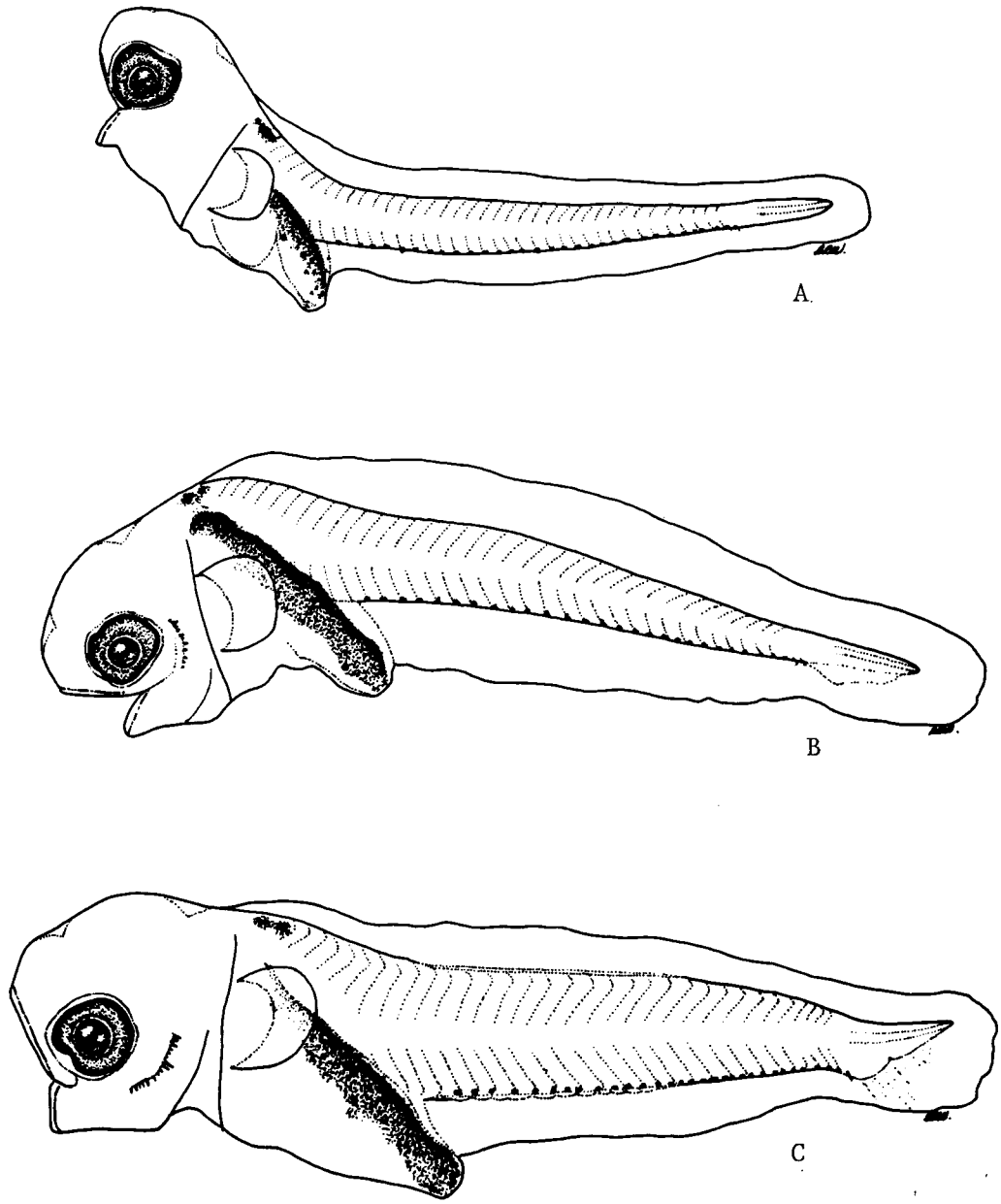

Figure 4. Larvae of Artedius harringtoni: A) 3.0 mm NL, B) 4.7 mm NL, C) 6.9 mm NL (from Richardson and Washington 1980).

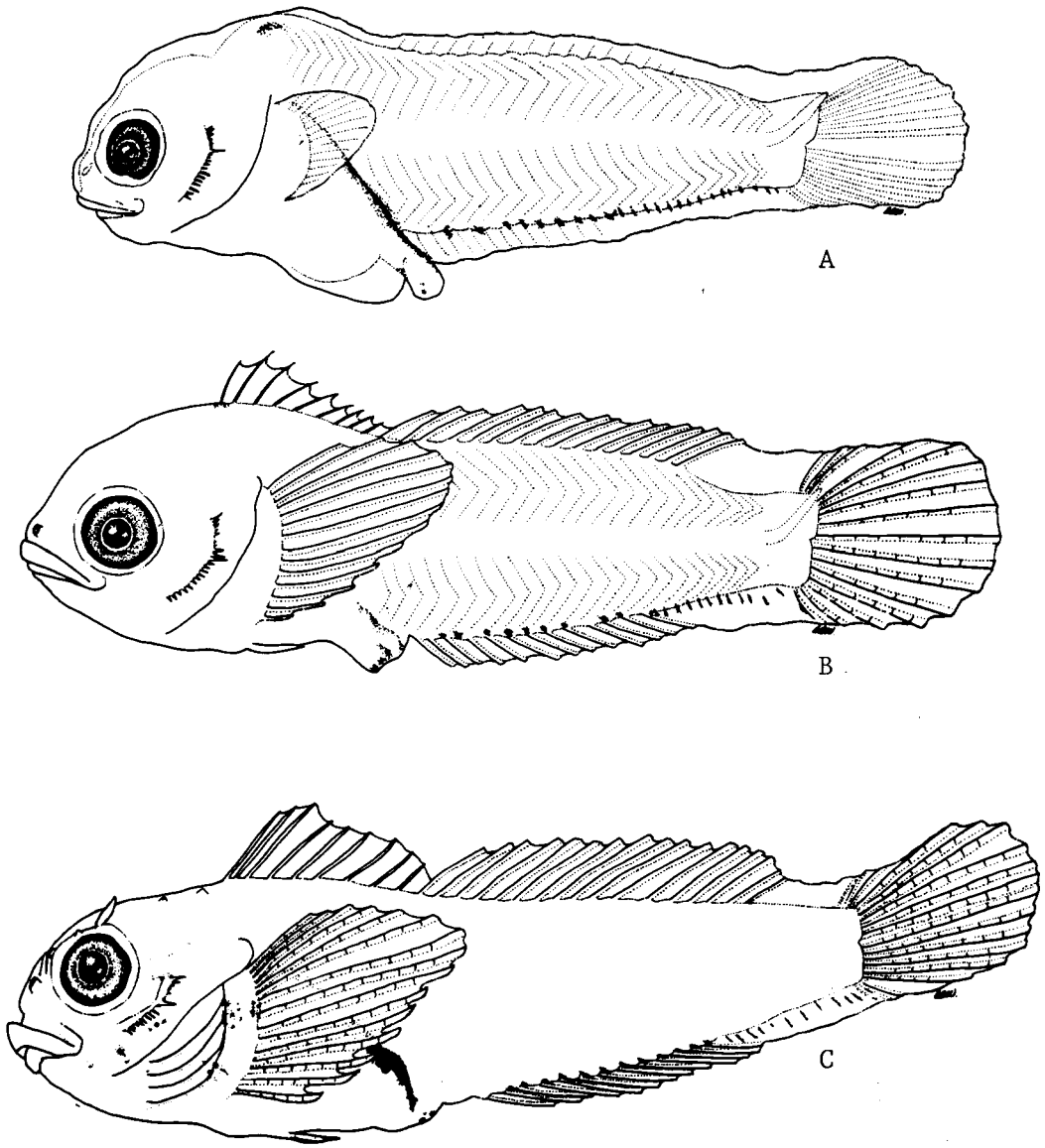

Figure 5. Larvae of Artedius harringtoni: A) 7.3 mm SL, B) 9.3 mm SL, C) 13.6 mm SL (from Richardson and Washington 1980).

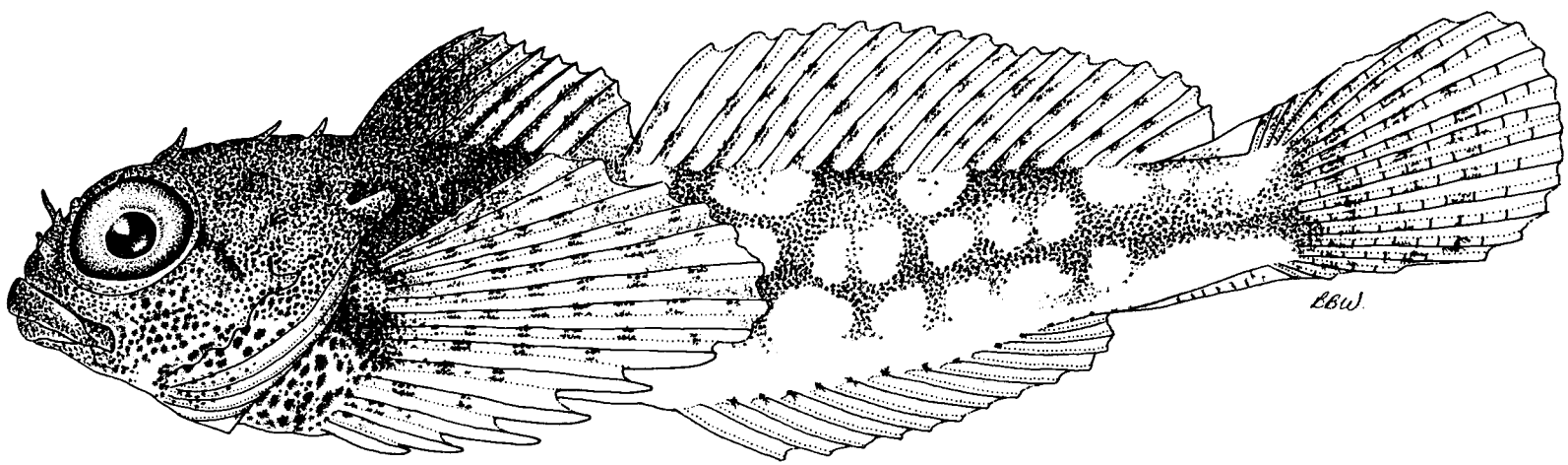

Figure 6. Juvenile of Artedius harringtoni: 13.9 mm SL.

Artedius lateralis

(Figures 7, 8; Tables 7, 8, 11)

Literature

Budd (1940) described and illustrated a newly hatched larva of A. lateralis 4.1 mm TL. Marliave (1975) described larvae of A. lateralis and illustrated 4 mm TL, 8 mm TL, 11 mm TL, and 14 mm TL specimens.

Identification

Small larval A. lateralis were reared from eggs spawned from known adults. Juveniles and adults were identified using the following characters: pigmentation, absence of scales on the head and caudal peduncle, absence of nasal and preorbital cirri, and the presence of 3 to 11 scales in the longest row in the dorsal scale band. The developmental series was linked together primarily on the basis of pigmentation, preopercular spination, presence of gut diverticula, and body shape. Postflexion and transforming larvae were linked to juveniles utilizing pigmentation, cirri patterns, spination, and meristics.

Distinguishing Features

Characters useful in distinguishing preflexion larvae of Artedius lateralis are prominent diverticula which extend dorsolaterally from the dorsal surface of the gut just posterior to the pectoral fin bases, the lack of head and nape pigment in larvae ≤6 mm NL, and a series of from 22 to 32 melanophores which lie along the ventral midline posterior to the anus. The anterior half of the series is characterized by

large melanophores spaced one every myomere while the posterior half of the series are smaller pigment slashes, spaced two to three per myomere.

Postflexion larvae of A. lateralis >6.2 mm, may be distinguished from other Artedius larvae by melanistic pigmentation over the brain.

Juvenile A. lateralis are distinguished by two dark bars of melanophores extending ventrally from the dorsal fins across the lateral surface of the body trunk, the series of 11 to 21 ventral midline melanophores, and meristics.

Pigmentation

Newly hatched larvae of A. lateralis have no melanistic pigmentation on the head or nape. Dense, round melanophores are concentrated over the dorsolateral surface of the gut and extend dorsally onto the gut diverticula. A cluster of from four to six small melanophores surrounds the anus. Posterior to the anus, a series of 22 to 32 melanophores is positioned along the ventral midline of the body. These melanophores originate under the third or fourth postanal myomere and extend posteriorly toward the tail tip where several additional melanophores extend onto the caudal finfold. Melanophores in the anterior half of this series are relatively large and spaced one every myomere. The posteriormost melanophores appear as small pigment slashes which extend onto the ventral finfold and are closely spaced two or three to every myomere.

During larval development, melanophores form on the dorsal surface of the head in larvae >6.3 mm. Two to five melanophores also form at the base of the cleithrum and along the ventral midline of the gut in

larvae ≥5.2 mm. These melanophores are arranged in a characteristic "t"-shape with two melanophores positioned as horizontal slashes at the base of the cleithrum and one to three melanophores extending posteriorly along the ventral midline of the gut.

During transformation, in planktonic larvae ≥8 mm, melanistic pigmentation increases markedly on the dorsal surface of the head with 33 to 44 dark melanophores covering the brain. Melanophores also form just posterior to the lower jaw, on the cheek between the eye and the preopercle, and on the operculum. Ventral midline melanophores remain unchanged in number and spacing.

Pigmentation increases markedly in newly settled juveniles, ≥10 mm long. Dark melanophores form on the dorsolateral surfaces of the head and extend anteriorly onto the snout and upper and lower lips. Several melanophores are added to the gular region beneath the lower jaw. Intense pigment forms on the bases of the pectoral fins and several large melanophores extend onto the pectoral fin rays. Gradually, melanophores from the base of the pectoral fin extend ventrally forming a band of pigment across the isthmus. With development, pigmentation increases on the head so that in larvae ≥12 mm SL, the entire head is darkly pigmented.

Shortly after settling, in larvae between 10 and 11 mm, a patch of melanophores is added to the dorsal fin between the fourth and sixth spines. These melanophores extend ventrally across the dorsum toward the pigmentation on the pectoral fin base. A second band of melanophores forms on the second dorsal fin membrane between the second and fourth fin rays. Gradually this band extends antero-ventrally below

the lateral midline. With development, the two vertical bands of pigment become very dark and intense. Melanophores from these bands extend dorsally across the dorsal fins. Concurrently, three saddles of faint melanophores are added posteriorly along the dorsum. The first saddle of pigment forms under the eighth to tenth dorsal fin rays, the second saddle is added under the 14th to 15th fin rays, and the third saddle forms on the dorsal surface of the caudal peduncle. Gradually, melanophores from these pigmented saddles extend ventrolaterally and join together forming a band along the lateral midline. Lateral pigmentation extends posteriorly and forms a band along the base of the caudal fin. Melanophores extend onto the caudal fin rays, gradually forming two or four distinct bands across the caudal fin. Ventral midline melanophores decrease in number in juveniles numbering from 11 to 21. These melanophores remain visible in juveniles $<$15 mm long.

Morphology

Artedius lateralis larvae are 3.9 to 4.5 mm long at hatching. The largest planktonic specimen observed is 9.2 mm and beginning to develop juvenile pigmentation. A. lateralis settle at a relatively small size, $\sim$9.5 to 10.5 mm. Thirty-three specimens, 4.1 to 12.1 mm, were examined for developmental morphometrics.

Larvae of A. lateralis are rather stubby in shape with a moderately short gut. Pronounced diverticula extends dorsally from each side of the gut just posterior to the pectoral fin base. The diverticula are present in newly hatched larvae and remain prominent throughout larval development. Tiny remnants of the diverticula are present in newly

settled juveniles between 9-10.5 mm long. Body depth at the pectoral fin base averages 23% in preflexion larvae, then increases to 28% SL in postflexion larvae. Relative body depth decreases again in juveniles to 24% SL. Body depth at the anus also increases with development from 20% to 26%, then decreases in juveniles to 20% SL. Snout to anus length averages 40% in preflexion larvae then increases to 48% SL in postflexion larvae and juveniles. Relative distance from snout to the origin of the pelvic fins and from the origin of the pelvic fins to the anus remain constant throughout early development.

Larvae of A. lateralis have a blunt, rounded snout. Snout length decreases from 28% to 24% HL during larval development. Relative eye diameter also decreases from 45% in preflexion larvae to 37% in postflexion larvae and 23% HL in juveniles. In contrast, head length increases from 20% in preflexion larvae to 27% in postflexion larvae and 35% in benthic juveniles.

Fin Development

The notochord begins to flex in larvae ∿5 mm long, and is fully flexed in larvae between 5.7 and 6.3 mm. Caudal rays begin to form during flexion in larvae ∿5.5 mm, however, the adult complement of 6+6 principal caudal rays is not complete until ∿6 mm. Bases of the dorsal and anal fins are first visible in larvae between 6 and 6.5 mm and the adult complement of dorsal and anal rays is complete by about 7.5 to 8 mm.

Pectoral fin rays begin to form between 7 and 8 mm, but the full complement of rays is not formed until larvae are ∿8 mm long. Pelvic

fin buds are first visible in a 7.4 mm larva, however, the fin rays are not countable until 9 mm.

Spination

Eight to nine tiny spines are visible on the posterior margin of the preopercle in preflexion larvae ∿4.5 mm NL. As larvae undergo flexion of the notochord, the number of preopercular spines increases to 9 to 14. By the end of flexion, larval A. lateralis have 14 to 16 preopercular spines. In larvae ≳7 mm, the dorsalmost and middle (the sixth to ninth spine from the top of the preopercle) become slightly longer than the other preopercular spines. These spines never become more than 1.5 times larger than the other preopercluar spines, in contrast to the situation in larvae of A. harringtoni, A. fenestralis, and A. Type 3 in which the dorsalmost and middle preopercular spines may be nearly 2.5 times larger than the other spines. Preopercular spines begin to regress in transforming specimens ≳9 mm. The dorsalmost spine increases in size while the lower spines (number four to six and nine to twelve) decrease in size becoming visible only as small serrations or irregularities on the preopercular margin. Spines seven to eight, and 12 to 13, and 16 to 18 fuse together to form blunt bumps along the preopercular margin. In juveniles ≳13 mm, only the large dorsalmost spine remains. Transforming larvae, reared in the laboratory possess four to five small spines at the posterior margin of the parietals. These spines are not present in planktonic larvae from field collections, nor are they visible in newly settled juveniles from tidepools.

Table 7. Measurements (mm) of young Artedius lateralis. (Specimens between dashed lines are undergoing notochord flexion.)

Body length	Head length	Snout length	Eye diam	Snout to anus length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
L 3.8	0.61	0.21	0.39	1.3	0.68	0.61	-	-	0.32
L 4.1	0.94	0.24	0.44	1.6	1.0	0.90	-	-	0.50
4.5	1.0	0.27	0.41	1.9	1.0	0.96	-	-	0.43
4.6	0.94	0.28	0.44	2.1	1.2	1.0	-	-	0.52
4.8	0.96	0.28	0.42	2.0	1.2	1.0	-	-	0.52
5.0	1.0	0.26	0.46	1.9	1.3	1.3	-	-	0.58
5.4	1.3	0.32	0.56	2.2	1.4	1.4	-	-	0.64
5.5	1.4	0.36	0.52	2.3	1.3	1.3	-	-	0.72
5.6	1.4	0.40	0.56	2.3	1.5	1.4	-	-	0.60
5.7	1.3	0.32	0.50	2.3	1.4	1.4	-	-	0.70
6.2	1.6	0.40	0.64	3.0	1.9	1.9	-	-	D
6.3	1.5	0.34	0.58	3.0	1.8	1.7	-	-	1.0
6.3	1.4	0.32	0.56	2.8	1.6	1.8	-	-	0.84
5.7	1.5	0.38	0.62	2.9	1.8	1.9	-	-	0.96
5.9	1.6	0.36	0.72	2.6	1.7	1.6	-	-	D
6.3	1.7	0.52	0.64	3.0	1.8	1.7	-	-	1.1
6.4	1.7	0.40	0.60	3.2	1.8	1.8	-	-	0.86
6.4	1.6	0.44	0.64	3.2	1.9	1.9	-	-	0.96
7.1	2.0	0.44	0.68	3.6	2.0	1.9	-	-	1.2
7.1	1.9	0.48	0.68	3.4	1.9	1.7	-	-	1.1
7.1	1.8	0.56	0.68	3.4	1.8	1.8	-	-	1.1
7.4	1.8	0.42	0.70	3.4	2.2	1.8	2.4	1.0	1.4
7.5	2.0	0. 2	0.76	3.9	2.4	2.0	1.9	2.0	D
7.6	2.2	0.48	0.80	3.5	2.1	2.0	2.2	1.3	2.1
7.7	1.9	0.48	0.80	3.8	2.1	1.9	2.0	1.8	1.6
8.3	2.3	0.60	0.76	4.1	2.0	2.0	2.8	1.3	1.3
8.4	2.2	0.62	0.81	3.9	2.0	2.0	2.3	1.6	1.4
8.6	2.7	0.52	0.88	4.0	2.4	2.1	2.5	1.5	1.6
8.9	2.4	0.44	0.80	4.4	2.4	2.2	2.2	2.2	2.2
9.1	2.5	0.68	0.88	4.4	2.3	2.3	2.3	1.9	2.2
9.2	2.8	0.72	0.88	4.7	2.6	2.3	2.7	2.0	2.2
J 9.8	2.9	0.72	0.79	4.3	2.2	1.7	2.4	2.0	2.6
J11.1	4.4	1.1	1.0	5.7	2.8	2.6	3.4	2.7	3.8
J12.1	4.3	0.83	0.94	6.2	2.9	2.3	3.2	2.8	3.7

J - Juvenile.
D - Damaged.
L - Laboratory reared.

Table 8. Meristics and spines of young of Artedius lateralis. (Only specimens with meristic elements formed are included. See Table 7 for complete developmental series examined.)

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preopercular spines	Parietal spines	Post-temporal spines	Principal caudal rays	Vertebrae	Branchiostegal rays
4.6	-	-	-	-	-	-	8	-	-	-	-	-
4.8	-	-	-	-	-	-	-	-	-	-	-	-
5.0	-	-	-	-	-	-	9	-	-	-	-	-
5.4	-	-	-	-	-	-	11	-	-	-	-	-
5.5	-	-	-	-	-	-	12	-	-	-	-	-
5.6	-	-	-	-	-	-	14	-	-	-	-	-
5.7	-	-	-	-	-	-	12	-	-	-	-	-
6.2	-	-	-	-	-	-	13	-	-	-	-	6
6.3	-	-	-	-	-	-	11	-	-	-	-	6
6.3	-	-	-	-	-	-	14	-	-	-	-	6
5.7	-	-	-	-	-	-	15	-	-	-	-	6
5.9	-	-	-	-	-	-	17	-	-	-	-	6
6.3	-	-	-	-	-	-	14	-	-	-	-	6
6.4	-	-	-	-	-	-	14	-	-	-	-	6
6.4	-	-	-	-	-	-	15	-	-	-	-	6
7.1	-	-	-	-	-	-	14	-	-	-	-	6
* 7.1	IX	16	13	15	15	buds	16	-	-	6+6	32	6
7.1	-	15	12	15	15	buds	15	-	-	-	-	6
7.4	-	-	12	15	15	buds	15	-	-	-	-	6
7.5	IX	15	13	15	15	buds	15	-	-	-	-	6
7.6	IX	16	12	15	15	buds	15	-	-	-	-	6
7.7	IX	15	13	15	15	buds	16	-	-	-	-	6
8.3	IX	15	12	15	15	buds	16	-	-	-	-	6
* 8.4	IX	16	13	15	15	buds	15	-	-	6+6	33	6
8.6	IX	15	13	15	15	buds	8	-	-	-	-	6
8.9	IX	16	13	15	15	I,3	16	-	-	-	-	6
9.1	IX	16	13	15	15	I,3	15	-	-	-	-	6
* 9.2	IX	16	13	15	15	I,3	16	-	-	6+6	33	6
9.8	IX	16	12	14	14	I,3	14	-	-	-	-	6
*J10.8	IX	16	12	15	15	I,3	16	-	-	6+6	33	6
J11.1	IX	17	13	15	15	I,3	4	-	-	-	-	6
J12.1	IX	16	13	15	16	I,3	1	-	-	-	-	6
*J13.3	IX	16	13	15	15	I,3	2	-	-	6+6	33	6

* - Stained with Alizarin Red S.
J - Juvenile.

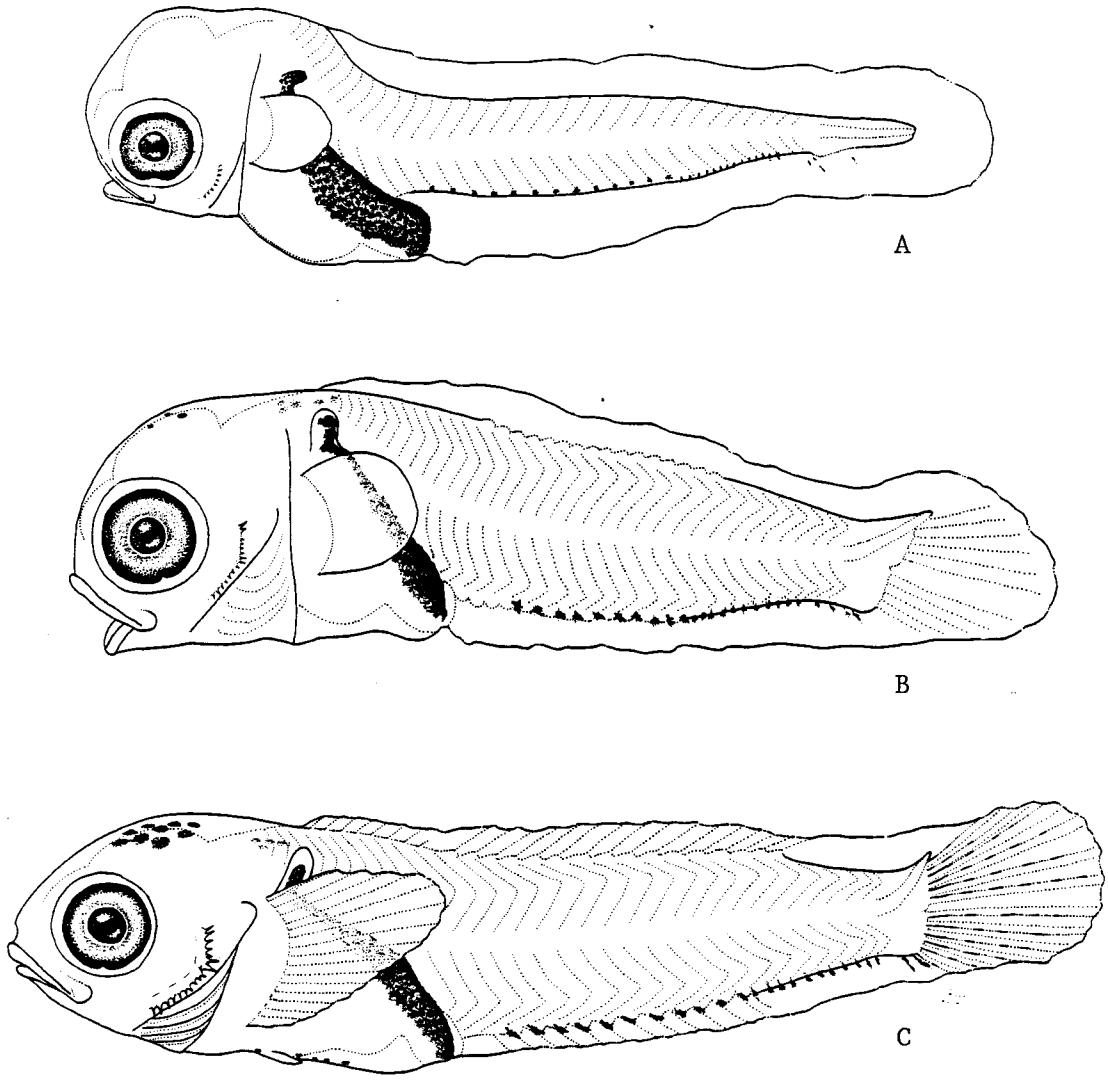

Figure 7. Larvae of Artedius lateralis: A) 4.6 mm NL, B) 6.4 mm SL, 7.1 mm SL.

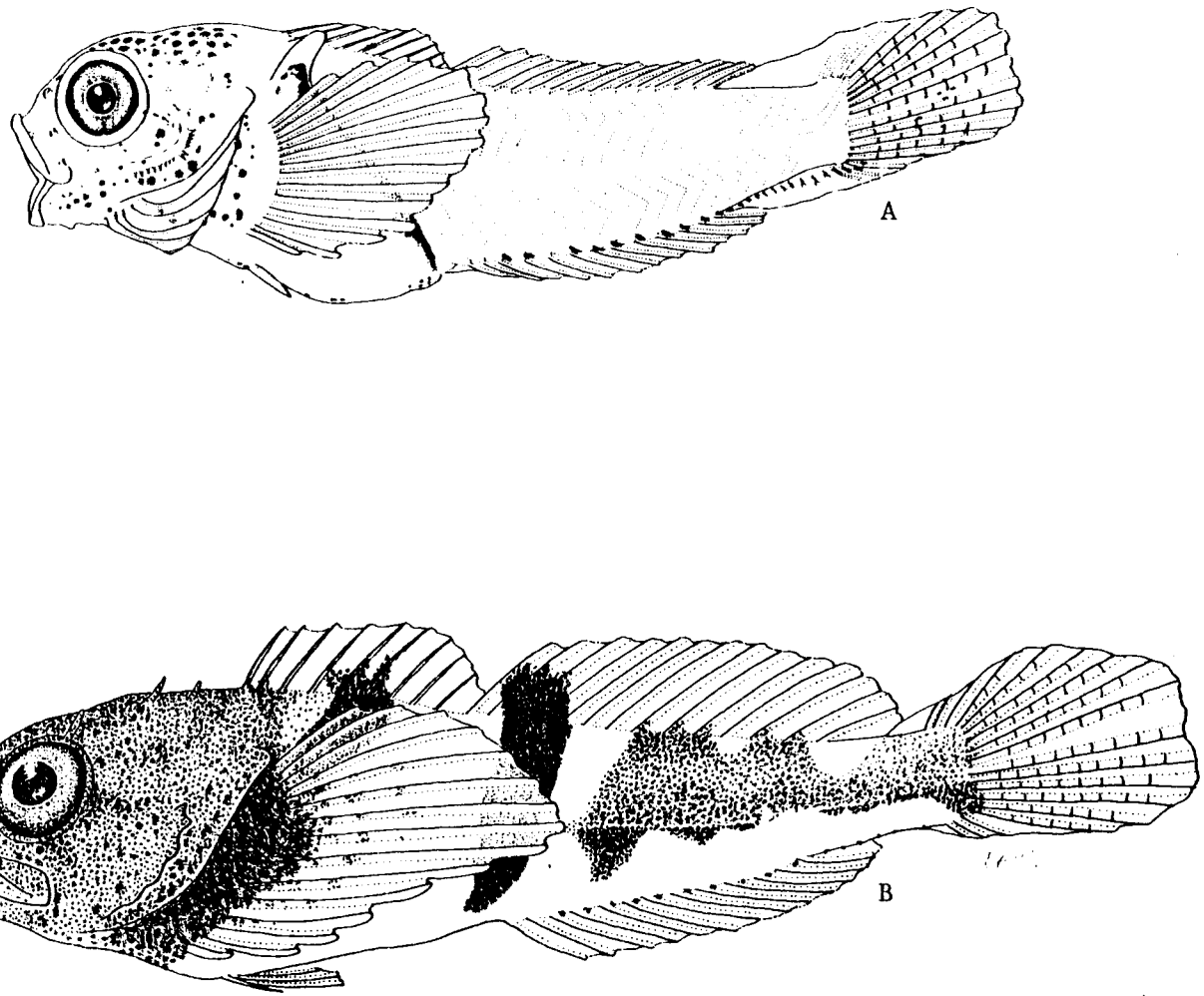

Figure 8. Young of Artedius lateralis: A) 9.1 mm SL, B) 13.3 mm SL.

Artedius Type 3

(Figures 9, 10; Tables 9, 10, 11)

Literature

Larvae of Artedius Type 3 have not been previously described.

Identification

Only a partial size series (2.9 to 7.6 mm) of Artedius Type 3 larvae are available, all from California collections. The presence of prominent gut diverticula and the characteristic "Artedius-type" preopercular spine pattern, with the dorsalmost, mid, and ventralmost spines larger than the others, identify this larval type as an Artedius. Larvae remain unknown for only two species of Artedius, A. corallinus and A. notospilotus. Meristics of the largest larvae of Artedius Type 3 coincide with those recorded for both A. corallinus and A. notospilotus. However, pectoral counts fit those of A. notospilotus most closely. The 7.6 mm larval A. Type 3 possesses 16 pectoral fin rays. Ninety percent of the A. notospilotus examined by Howe and Richardson (1978) possessed 16 pectoral fin rays while only 10% of A. corallinus specimens possessed 16 pectoral fin rays.

Pigmentation along the ventral midline posterior to the anus of A. Type 3 larvae (9 to 13 widely spaced melanophores) coincides most closely with that of juvenile A. corallinus. Several A. corallinus, 13.5 to 14 mm long, possess three to six widely spaced ventral midline melanophores. In contrast, a 16 mm juvenile A. notospilotus possesses 24 ventral midline melanophores spaced every one or two myomeres.

Adult A. corallinus are common in the intertidal areas of the southern California coast where Artedius Type 3 larvae were collected (Miller and Lea 1966). Artedius notospilotus adults are rare in the same area.

Additional larger specimens are needed before larvae of Artedius Type 3 can be specifically identified.

Distinguishing Features

Artedius Type 3 larvae are distinguished as an Artedius by the distinctive diverticula that extend dorsolaterally from the dorsal surface of the gut just posterior to the pectoral fin base. Artedius Type 3 larvae are distinguished from small larvae of A. fenestralis and A. lateralis, which possess similar diverticula, by the low number (9 to 13) of ventral midline melanophores posterior to the anus. Other characters useful in distinguishing small A. Type 3 larvae are absence of head pigmentation and presence of a cluster of two to four melanophores in the nape region. Preopercular spines begin to form in larvae ≥4.1 mm NL. Preopercular spines do not form in other Artedius larvae with multiple preopercular spines until ~4.5 mm NL. Flexion and postflexion larval Artedius Type 3 possess 21 to 24 preopercular spines, more than other larval Artedius (groups A and D), all of which have ≤21 preopercular spines.

Pigmentation

Small preflexion larvae of Artedius Type 3 possess no melanistic head pigmentation. Two to four small external melanophores are clustered on the surface of the nape. Numerous dark, rounded melanophores

are concentrated over the dorsolateral surface of the gut and extend dorsally onto the gut diverticula. One to four small melanophores are clustered around the anus.

Posterior to the abdominal cavity, the only pigmentation consists of a series of 9 to 13 melanophores located along the ventral midline. This series of melanophores originates under the third to fourth post-anal myomere and extends posteriorly toward the tail tip. Each melanophore is spaced approximately two to three myomeres apart. An additional one to five pigment slashes extend onto the caudal finfold near the tail tip.

Pigmentation changes little during larval development. Melanophores are added in the nape reigon and become embedded in the musculature over the notochord in larvae >5.5 mm. Melanophores are also added in the isthmus region and along the ventral midline of the gut.

Morphology

The smallest larval Artedius Type 3 is 2.9 mm NL and possesses remnants of the yolksac. The largest specimen examined is 7.6 mm long and has recently completed notochord flexion. Size at transformation is unknown. Thirteen larvae, 2.9 to 7.6 mm long, were examined for developmental morphology.

Larvae of Artedius Type 3 are rather stubby in shape with a moderately long gut, the posteriormost portion which trails somewhat below the rest of the body. A prominent diverticulum extends dorsally from each side of the gut just posterior to the base of the pectoral fin. Diverticula are present in the smallest larva examined, 2.9 mm NL, and remain pronounced in the largest specimen.

Snout to anus length averages 45% SL in both preflexion and flexion larvae. Body depth at the pectoral fin base increases during development from 26% in preflexion larvae, to 28% in flexion larvae, and 32% SL in the single postflexion larvae. Relative body depth at the anus also increases with development, from 23 to 30% SL. The distances from the snout to the origin of the pelvic fins and from the origin of the pelvic fins to the anus averages 26 and 22% SL, respectively, in late flexion and early postflexion larvae.

Artedius Type 3 larvae have a rather large head with a blunt, rounded snout. Relative head length increases with development from an average of 22% in preflexion larvae to 25% in larvae undergoing flexion of the notochord, and 29% SL in the postflexion larva. Jaw length averages about 43% HL throughout early larval development. In contrast, eye diameter decreases during development from an average of 47% in preflexion larvae to 37% HL in flexion and early postflexion larvae.

Fin Development

A 4.9 mm NL larva exhibits a slight thickening of the hypural region of the forming caudal fin. By 5.6 mm, the notochord of larval A. Type 3 is strongly flexed and caudal rays are beginning to form. Notochord flexion is nearly complete by ∿7 mm and the adult complement of principal caudal rays is countable.

The dorsal and anal fin bases are first visible in larvae between 6.8 and 6.9 mm long. In the largest specimen examined, 7.6 mm, the adult complement of dorsal spines and rays and anal fin rays is complete. Pectoral fin rays are beginning to form in a 6.8 mm NL larva, and 16 pectoral fin rays are countable in the 7.6 mm larva. Pelvic fin buds

are first visible at about 6.8 mm NL, however, pelvic fin rays are not yet formed in the largest specimen.

Spination

Preopercular spines begin to form in small preflexion larvae of A. Type 3, ∿4.1 mm NL. A series of 15 to 17 tiny, equal-sized spines is visible along the posterior margin of the preopercle in preflexion larvae between 4.1 and 5 mm NL. During development, preopercular spines increase in number ranging from 21 to 24 in flexion and early post-flexion larvae.

In late flexion larvae ∿6.8 mm to 6.9 mm NL, the middle two or three preopercular spines (the eighth to eleventh spine from the dorsal margin of the preopercle) begin to increase in size relative to other preopercular spines. In the 7.6 mm larva, the dorsalmost and ventralmost one or two spines are also larger than other preopercular spines. This forms the characteristic preopercular spine pattern found in Artedius larvae with multiple preopercular spines, where the dorsalmost, mid, and ventralmost spines are markedly larger than the other preopercular spines.

No other spines develop on the head in larvae ≤7.6 mm. Head spination in larger larvae remains unknown.

Table 9. Measurements (mm) of young Artedius Type 3. (Specimens between dashed lines are undergoing notochord flexion.)

Body length	Head length	Snout length	Eye diam	Snout to anus length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
2.9	0.62	0.10	0.32	1.3	0.72	0.56	-	-	0.40
3.0	0.62	0.12	0.36	1.3	0.72	0.67	-	-	0.39
3.2	0.74	0.17	0.34	1.6	0.91	0.74	-	-	0.46
3.6	0.80	0.12	0.40	1.7	0.96	0.82	-	-	0.32
3.7	0.78	0.16	0.38	1.6	0.84	0.82	-	-	0.32
4.1	0.96	0.24	0.38	1.7	1.1	1.1	-	-	-
4.1	0.94	0.14	0.32	1.8	1.1	1.0	-	-	0.30
4.9	1.1	0.24	0.48	2.2	1.3	1.3	-	-	0.36
5.6	1.5	0.41	0.53	2.4	1.7	1.6	-	-	0.56
5.8	1.5	0.28	0.56	2.5	1.4	1.5	-	-	0.40
6.8	1.7	0.37	0.62	3.2	1.9	2.1	1.9	1.3	0.99
6.9	1.6	0.40	0.64	3.3	2.0	2.0	1.5	1.8	0.92
7.6	2.2	0.64	0.84	3.8	2.4	2.3	2.2	1.6	1.6

Table 10. Meristics and spines of young of Artedius Type 3. (Only specimens with meristic elements formed are included. See Table 9 for complete developmental series examined.)

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preoper-cular spines	Parietal spines	Post-temporal spines	Principal caudal rays	Verte-brae	Branchio-stegal rays
6.8	IX	14+	12	-	-	-	21	0	0	-	-	-
6.9	-	13+	12	16	15	-	22	0	0	-	-	-
7.6	IX	15	12	16	16	-	24	0	0	6+5	-	6

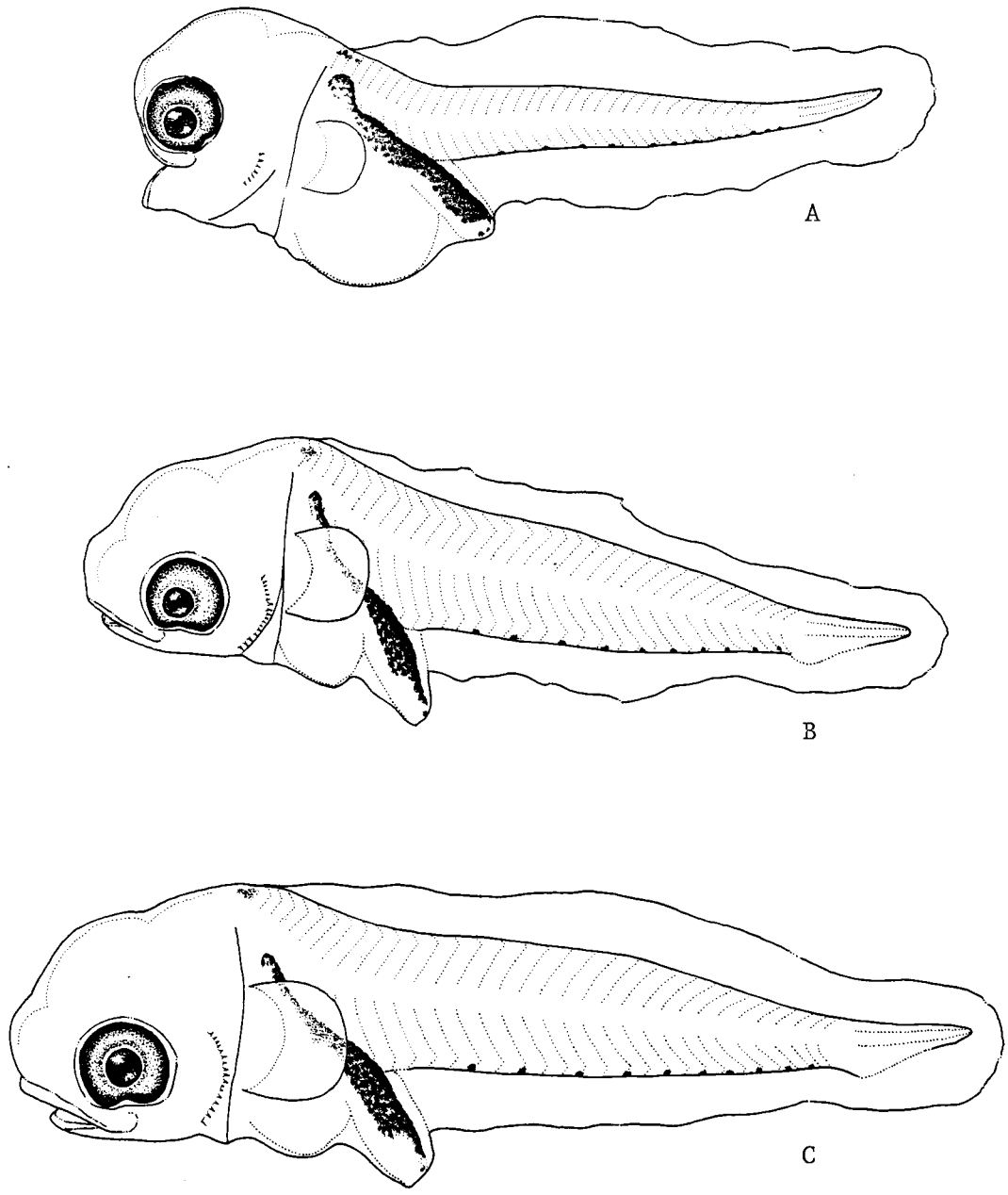

Figure 9. Larvae of Artedius Type 3: 3.2 mm NL, B) 4.1 mm NL, C) 4.9 mm NL.

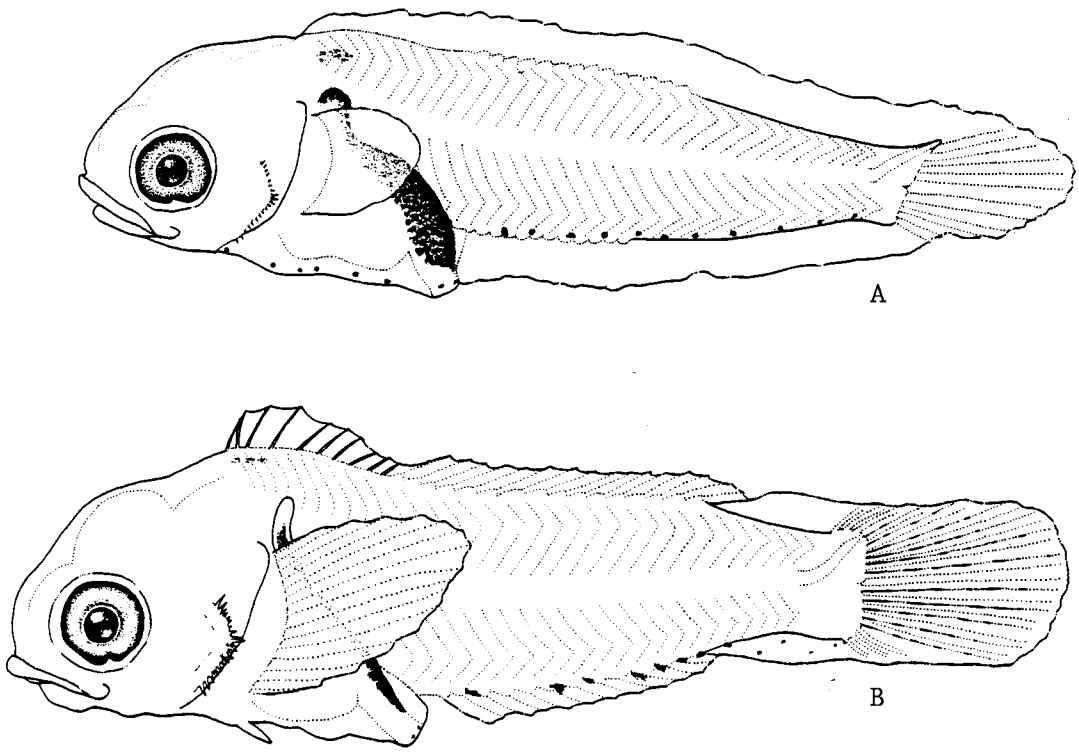

Figure 10. Larvae of Artedius Type 3: A) 6.8 mm SL, B) 7.3 mm SL.

Table 11. Body proportions of larvae and juveniles of Artedius fenestralis, A. harringtoni, A. lateralis, and A. Type 3. Values given are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. (Number of specimens measured may be derived from Tables 3, 5, 7, and 9.)

Item	Artedius fenestralis	Artedius harringtoni	Artedius lateralis	Artedius Type 3
Head length/SL:				
Preflexion	22.2±1.41(21.1-25.0)	20.9±2.30(18.7-22.3)	20.2±2.68(16.4-22.9)	21.8±0.92(20.7-23.2)
Flexion	22.1±1.22(20.3-23.3)	23.1±3.86(24.9-27.0)	23.6±1.92(19.9-26.1)	24.6±1.71(23.3-27.1)
Postflexion	26.1±2.85(20.8-29.4)	29.0±0.50(22.4-34.1)	26.9±1.89(24.3-30.8)	29.0*
Juvenile	33.9±2.08(32.0-34.9)	33.6±3.46(30.4-36.5)	22.7±3.21(19.1-25.3)	-
Snout length/HL:				
Preflexion	15.1±3.77(41.2-50.8)	18.9±5.52(9.9-25.1)	28.0±1.83(25.8-30.1)	19.8±3.85(15.4-24.6)
Flexion	20.4±5.96(44.1-50.3)	23.7±6.14(18.3-19.1)	25.2±1.91(22.9-29.4)	23.2±3.51(19.2-26.7)
Postflexion	21.8±3.57(42.6-50.6)	24.2±4.19(15.8-31.4)	24.7±3.77(19.4-30.6)	29.4*
Juvenile	21.6±2.08(47.2-51.0)	23.1±1.00(22.3-24.3)	23.0±1.73(18.9-24.7)	-
Eye diameter/HL:				
Preflexion	39.7±4.32(33.7-46.9)	44.7±4.57(39.7-50.1)	44.7±2.87(40.8-47.1)	46.7±6.53(39.0-57.6)
Flexion	41.2±3.42(37.4-46.5)	40.4±7.33(38.4-43.2)	40.4±2.88(37.4-45.5)	37.1±2.16(35.3-40.2)
Postflexion	36.9±7.10(27.3-52.1)	32.6±4.09(23.2-39.8)	36.6±4.06(37.9-44.6)	37.9*
Juvenile	29.1±1.00(24.6-27.3)	31.2±5.77(29.8-31.2)	35.3±5.03(22.1-24.8)	-
Snout to anus length/SL:				
Preflexion	45.3±3.59(41.2-50.8)	42.0±3.21(38.2-48.2)	40.4±4.83(33.3-45.6)	44.8±2.76(41.4-49.8)
Flexion	45.9±2.49(44.5-50.1)	47.3±8.30(36.5-55.9)	42.7±3.65(38.2-47.9)	45.1±2.63(43.2-48.1)
Postflexion	48.4±2.26(42.7-51.4)	49.9±2.67(45.9-55.4)	48.4±2.18(44.4-50.9)	50.2*
Juvenile	49.1±2.00(47.0-51.5)	47.4±3.21(43.1-49.2)	48.7±4.04(44.1-51.2)	-
Snout to pelvic fin origin/SL:				
Preflexion	-	-	-	
Flexion	25.6±3.21(20.2-29.8)	-	-	25.3±4.26(21.9-27.6)
Postflexion	26.1±3.21(20.2-29.8)	27.8±1.72(24.5-30.8)	28.1±3.11(24.9-34.1)	29.3*
Juvenile	30.4±3.51(26.5-30.1)	27.4±2.65(24.1-29.4)	27.0±3.61(23.8-31.0)	-
Pelvic fin origin to anus/SL:				
Preflexion	-	-	-	-
Flexion	22.2±5.35(16.1-27.0)	-	-	23.1±6.95(19.1-26.1)
Postflexion	26.1±3.21(20.2-29.8)	27.8±1.72(24.5-30.8)	20.1±4.20(14.4-26.7)	20.9*
Juvenile	18.9±1.15(18.2-20.2)	27.4±2.65(24.1-29.4)	22.3±2.08(20.3-24.1)	-
Body depth at pectoral fin base/SL:				
Preflexion	21.7±1.81(19.0-23.8)	23.7±2.99(20.9-29.7)	23.0±3.16(17.9-26.3)	25.9±1.77(23.4-28.2)
Flexion	28.5±2.70(24.9-30.1)	28.1±2.45(28.0-31.2)	26.6±2.33(24.2-27.1)	28.2±1.76(26.3-30.1)
Postflexion	28.2±1.82(24.2-32.1)	30.5±2.74(23.4-34.1)	28.1±2.29(24.1-32.2)	30.0*
Juvenile	25.8±1.53(24.4-26.8)	22.3±4.15(24.6-25.2)	19.7±3.06(21.9-25.0)	-
Body depth at anus/SL:				
Preflexion	19.0±2.49(4.8-22.2)	27.8±2.45(17.2-27.6)	20.4±2.51(15.8-21.8)	22.9±3.28(18.2-27.2)
Flexion	24.1±2.59(23.6-27.1)	30.4±3.32(28.1-34.7)	26.3±2.29(24.5-31.3)	29.1±2.06(26.1-31.3)
Postflexion	27.9±2.79(21.4-32.8)	20.9±5.77(23.9-34.8)	26.3±2.82(22.4-33.0)	30.3*
Juvenile	21.6±2.65(18.9-24.4)	28.0±1.72(20.8-21.9)	30.3±3.51(17.4-22.8)	-
Pectoral fin length/SL:				
Preflexion	9.1±0.98(8.2-10.9)	7.4±2.34(4.4-11.1)	11.0±1.08(9.6-12.2)	10.4±2.91(7.1-13.8)
Flexion	9.4±0.71(8.4-10.4)	12.1±3.54(9.9-15.4)	12.3±1.98(9.6-15.9)	11.2±3.50(7.4-15.1)
Postflexion	22.6±6.21(9.7-29.7)	24.6±7.59(10.3-34.6)	19.8±4.66(13.3-27.6)	21.0*
Juvenile	26.2±1.53(27.1-28.4)	34.1±3.61(29.9-36.6)	30.3±3.51(26.8-34.2)	-

- = Not present at this stage.
* = Only specimens available in this stage.

Oligocottus maculosus

(Figures 11, 12; Tables 12, 13, 16)

Literature

Stein (1972, 1973) described O. maculosus larvae and illustrated 4.6, 6.0, 6.6, and 9.2 mm TL specimens.

Identification

Larvae in this series were reared from eggs spawned from known adults. Adults and juveniles were identified by the following combination of characters: high vertebral (33-34) and dorsal fin ray (15-18) counts, small size at transformation (8-9 mm), absence of cirri on the nasal spines and along the base of the dorsal fins, and pigmentation. The developmental series was linked together primarily on the basis of pigmentation, preopercular and parietal spination, and body shape. Post-flexion and transforming larvae were linked to juveniles by the serial method utilizing pigmentation, spination, and size at transformation.

Distinguishing Features

Newly hatched larvae of O. maculosus reared in the laboratory are distinguished by the following pigmentation characters: intense melanistic nape pigment; dark dendritic melanophores which extend onto a prominent bubble of skin in the nape region just anterior to the origin of the dorsal finfold; one or two melanophores situated anteriorly on the visceral mass beneath the pectoral fins; and a series of 18 to 36 ventral midline melanophores posterior to the anus. In addition to distinctive pimentation, larvae possess two rounded humps or protrusions

which extend dorsally on either side of the gut just posterior to the pectoral fin bases. These protrusions are similarly positioned and reminiscent of the gut diverticula found in larvae of Artedius, however, they never develop into distinct diverticula and disappear at the completion of yolk absorption about five to ten days after hatching. O. maculosus larvae also possess a distinctive bubble of skin in the nape region just anterior to the origin of the dorsal finfold. This bubble persists in larvae up to 7.5 mm SL.

Flexion and postflexion larvae >6.5 mm, possess a relatively low number of preopercular spines (9 to 13).

Postflexion larvae and juveniles may be distinguished by meristics, especially the high vertebral and dorsal fin ray counts, and the small size at transformation, (8 to 9 mm SL). In addition, juveniles possess a slender postorbital cirrus and two fronto-parietal cirri.

Pigmentation

Newly hatched larvae of O. maculosus possess no melanistic head pigmentation. Fourteen to 16 intense, stellate melanophores are concentrated in the nape region. One to three dendritic melanophores extend anteriorly from the nape pigment patch onto a prominent elevation or bubble of skin located just anterior to the origin of the dorsal finfold. In live larvae, xanthophores cover the bubble of skin and the nape. Three to four dendritic, embedded melanophores are positioned in the otic capsule.

The dorsal surface of the gut is darkly pigmented with 100 to 150 dark melanophores. Two to four pale, dendritic melanophores are located along the antero-ventral margin of the gut, just beneath the pectoral

fins. These melanophores are frequently embedded in the gut musculature and difficult to see. One to five small melanophores are clustered around the anus.

Posterior to the anus, larvae of O. maculosus possess a relatively high number of ventral midline melanophores. However, the actual number of melanophores appears to vary with the geographic location at which the larvae were collected. Stein (1973) recorded between 11 and 20 ventral midline melanophores in his reared larvae, while larvae reared in Oregon possessed between 16 and 20 melanophores along the ventral midline. Marliave found between 26 and 36 ventral midline melanophores in reared larvae from the Straits of Georgia in British Columbia (Pers. Comm.). Regardless of the number of melanophores, this series begins under the third or fourth myomere posterior to the anus and extends toward the tail tip. The first four melanophores in the series are usually spaced one every two to three myomeres, while the remainder of the melanophores are spaced one per myomere. Five or nine additional pigment slashes extend onto the ventral finfold near the tail tip.

During larval development in larvae $\lesssim$6 mm, 15 to 20 melanophores form over the midbrain and interorbital region of the head. Two to five melanophores form on the snout and one to three melanophores form on the cheek just anterior to the dorsalmost preopercular spine in larvae $\lesssim$7 mm. At this size melanophores are also added in the otic capsule, however, they become obscured by the developing musculature and are difficult to see. By $\sim$6 mm, several melanophores are added just ventral to the nape pigment patch. Five to seven of the centrally

positioned melanophores become embedded while the other nape melanophores form a prominent U-shape antero-laterally around the central melanophores.

During transformation, ∿7 and 8 mm, melanistic pigmentation increases markedly over the dorsal surface of the head. Melanophores are added on the snout, on the cheek region anterior to the preopercle, and on the dorsal portion of the operculum. Melanophores also form on the pectoral fin base and gradually extend ventrally onto the isthmus.

Pigmentation over the dorsal surface of the head is intense in benthic juveniles. A band of melanophores forms on either side of the snout, extending from the upper lip to the ventral margin of each eye. The band of melanophores continues posteriorly reaching from the eye to the dorsalmost preopercular spine. Melanophores are also added ventrally along the entire margin of the preoperculum and on the anterior tip of the lower lip. In juveniles, ≯8.5 mm, tiny melanophores cover the entire dorso-lateral surfaces of the head, however, the bands of pigment extending through each eye remain prominent. An irregular band of tiny melanophores forms along the surface of the lateral midline in juveniles ≥9 mm. This band gradually extends posteriorly to the caudal fin base. Two additional bands of pigment form along the dorsum. The third band forms under the eighth to tenth dorsal rays and the fourth band develops under the 14th to 16th dorsal fin rays. These pigment bands eventually extend ventrally and fuse with the lateral midline pigmentation. Tiny melanophores are added over the dorsolateral body surface in juveniles ∿13 mm, however, the intense pigment bands along the dorsum remain distinct. Melanophores extend out onto the dorsal and caudal fin rays, forming three or five bands of pigment.

Morphology

Newly hatched Oligocottus maculosus larvae range in length from 4.2 to 4.5 mm NL. Transformation occurs at a relatively small size ∿7.5 to 8 mm. The smallest benthic juvenile examined was 8 mm long. Eighteen specimens of O. maculosus, 4.3 to 10.8 mm, were examined for developmental morphology.

In newly hatched larvae two prominent bumps or protrusions appear on the dorsal surface of the gut just posterior to the pectoral fin base. These bulges are similar to the dorsal gut diverticula of Artedius larvae, however, they never develop into distinct diverticula. The gut protrusions disappear approximately 5 to 10 days after hatching. O. maculosus larvae also possess a distinctive bubble of skin in the nape region just anterior to the origin of the dorsal finfold. This bubble persists in larvae $\leq$7.5 mm.

Small O. maculosus are slender with a relatively short gut. Snout to anus length averages 39% in preflexion larvae and increases to 44% in postflexion larvae and 45% SL in juveniles. Body depth at both the pectoral fin base and the anus increases during larval development from 19% to 15%, respectively, to 25% SL. Body depth decreases slightly in benthic juveniles averaging 24% SL at the pectoral fin base and 20% SL at the anus. Distance from the snout to the origin of the pelvic fin increases from 24% to 28% SL during larval development, while distance from the origin of the pelvic fin to the anus decreases from 20 to 17% SL.

Relative head length increases markedly during development from 17% in preflexion larvae to 25% in postflexion larvae and 30% SL in

juveniles. Snout length decreases slightly from 30% HL in preflexion larvae to 27% HL in juveniles. Eye diameter decreases from 56% HL to 31% HL.

Fin Development

Larval Oligocottus maculosus begin to undergo notochord flexion at ∿6 to 7 mm. The adult complement of 12 principal caudal rays is complete in larvae ∿6.8 to 7 mm long at about the completion of notochord flexion.

Dorsal and anal fin rays begin to form in larvae ∿6.6 mm long, however, the full complement of fin rays is not complete until larvae are 8 mm long. Dorsal spines also form between 7 and 8 mm. Although pectoral fin rays are visible in larvae by 6.6 mm, the adult complement is not fully formed until larvae reach about 7.6 mm. Pelvic buds are first visible in 7 mm larvae but the fin rays are not formed until ∿8.5 mm.

Spination

Six to seven tiny spines are first visible on the posterior margin of the preopercle in larvae ∿5.8 mm long. Spines increase in number to nine or ten in larvae undergoing notochord flexion. In postflexion larvae, 6.9 to 7.8 mm long, preopercular spines number 10 or 11. Two or three of these spines appear as tiny accessory spines which form just anterior to the bases of the other spines. The dorsalmost spine becomes slightly larger than the lower spines. The third, fourth, and fifth preopercular spines also increase slightly in size relative to the lower spines. In the largest planktonic larvae ∿8 mm long, the preopercular spines begin to decrease in size and number and are covered with skin.

In newly settled benthic juveniles ∿8 to 10 mm long, the dorsalmost spine is quite large and stout with a strong upward curvature. The lower spines persist only as three blunt, bony protrusions on the preopercular margin.

Three tiny spines also form in the parietal region in larvae ∿6 to 7 mm long. Two spines develop anteriorly with a third nuchal spine forming just posterior to them. These parietal spines persist through the larval period, however, they regress in benthic juveniles. During regression, the anterior spines decrease in size and their tips bend posteriorly and fuse with the nuchal spine, forming an arch. This canal and arch become incorporated into the cephalic lateral line system.

Two spines also form on the posttemporal in larvae ∿6 to 7 mm long. By ∿7 to 8 mm, a third spine forms on the posttemporal and a fourth spine forms on the supracleithrum. These supracleithral-posttemporal spines persist through larval development and eventually form the junction of the cephalic and lateral line systems.

Table 12. Measurements (mm) of young Oligocottus maculosus. (Specimens between dashed lines are undergoing notochord flexion.)

	Body length	Head length	Snout length	Eye diam	Snout to anus length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
L	4.3	0.74	0.22	0.43	1.6	0.85	0.67	-	-	0.48
L	4.4	0.79	0.24	0.43	1.7	0.81	0.67	-	-	0.45
L	4.5	0.76	0.22	0.43	1.8	0.86	0.67	-	-	0.45
L	7.2	1.3	0.38	0.72	2.7	1.7	1.8	-	-	1.3
L	7.6	1.6	0.48	0.67	3.2	1.8	1.8	1.8	1.4	1.4
L	6.6	1.6	0.48	0.72	3.2	1.9	1.9	1.9	1.3	1.6
L	6.6	1.5	0.45	0.67	2.7	1.6	1.7	1.5	1.2	1.1
L	6.6	1.7	0.50	0.72	3.2	1.8	1.9	1.7	1.5	0.72
L	6.7	1.8	0.52	0.72	3.2	1.8	1.9	1.7	1.5	0.79
L	6.8	1.5	0.36	0.58	2.7	1.5	1.5	1.5	1.2	1.0
L	6.9	1.5	0.43	0.67	2.8	1.7	1.6	1.6	1.2	1.4
L	6.9	1.8	0.50	0.76	3.2	1.8	1.8	1.8	1.4	1.5
L	6.9	1.8	0.43	0.76	3.2	1.9	1.9	1.6	1.6	1.8
	7.8	2.1	0.69	0.79	3.5	1.9	1.8	2.1	1.4	1.8
	8.0	2.0	0.61	0.73	3.6	1.9	2.1	2.0	1.6	2.0
J	8.5	2.8	0.72	0.88	4.1	2.3	1.9	2.7	1.4	2.7
J	10.4	3.0	0.93	0.88	4.6	2.2	1.9	2.6	2.0	2.8
J	10.8	2.9	0.73	0.97	4.6	2.5	2.3	2.9	1.7	3.0

J - Juvenile.
L - Laboratory-reared.

Table 13. Meristics and spines of young Oligocottus maculosus. (Only specimens with meristic elements formed are included. See Table 12 for complete developmental series examined.)

	Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preoper-cular spines	Parietal spines	Post-temporal spines	Principal caudal rays	Verte-brae	Branchio-stegal rays
*	7.2	VIII	18	13	14	15	-	14	3	2	5+5	35	-
	7.6	-	16	12	14	15	-	14	3	3	5+5	-	-
	6.6	-	-	-	-	-	-	10	3	1	5+5	-	-
	6.6	VIII	17	12	14	-	buds	9	3	3	5+6	-	-
	6.6	VIII	18	12	14	14	buds	11	3	3	6+6	-	-
	6.7	VIII	16	11	14	14	buds	11	3	3	7+7	-	-
*	6.8	-	17	12	14	14	buds	12	3	2	6+6	34	6
	6.9	-	16	12	14	14	buds	10	3	2	6+6	-	-
	6.9	VIII	18	11	14	14	buds	11	3	3	6+6	-	-
	6.9	VIII	16	12	14	14	buds	11	3	3	6+6	-	-
	7.8	IX	17	13	14	14	buds	11	3	3	6+6	-	-
	8.0	VIII	17	12	14	14	3	9	3	3	6+6	-	-
J	8.5	VIII	18	13	14	14	I,3	5	0	2	6+6	-	-
J	10.4	VIII	17	13	14	14	I,3	4	0	0	6+6	-	-
J	10.8	VIII	17	13	14	14	I,3	4	0	0	6+6	-	-
J	8.9	VIII	18	13	14	14	I,3	4	0	0	6+6	34	6

* - Stained with Alizarin Red S.
J - Juvenile.

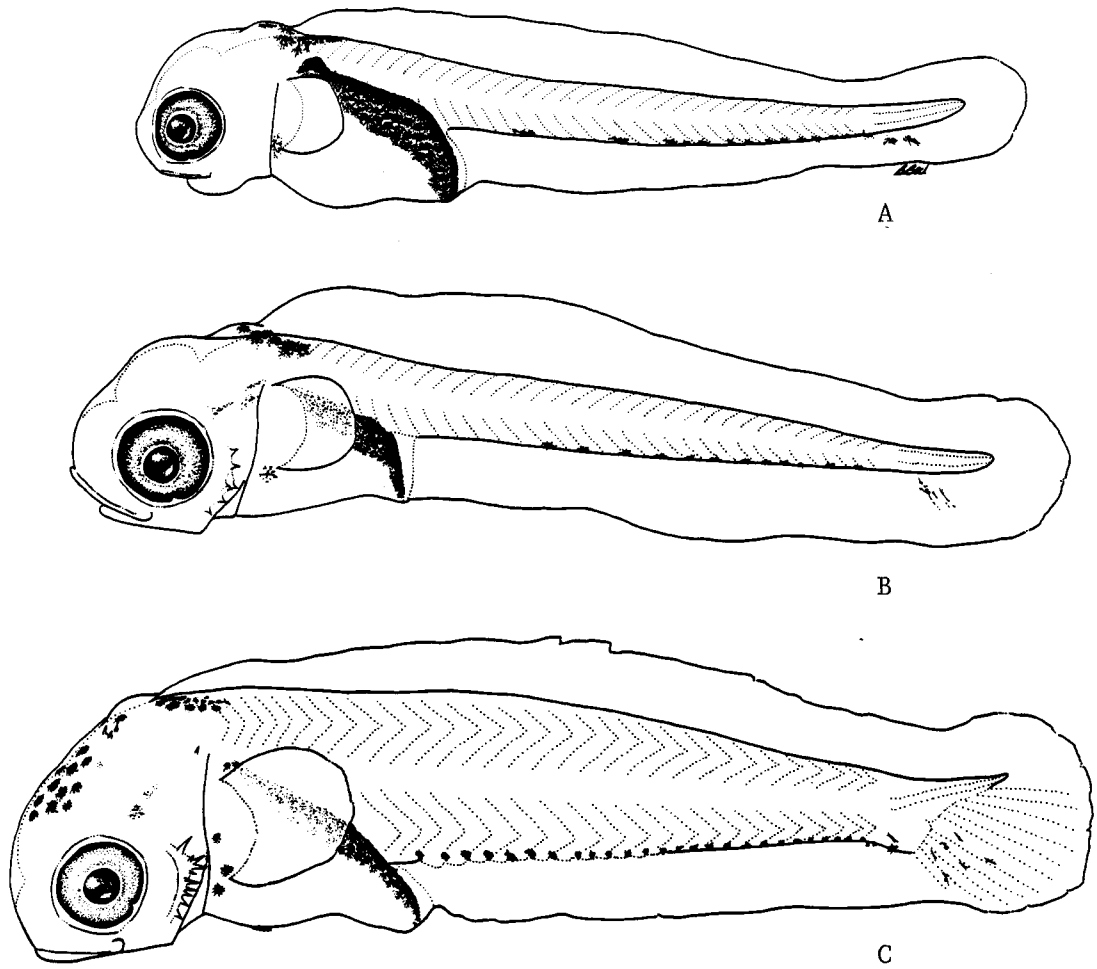

Figure 11. Larvae of Oligocottus maculosus: A) 4.3 mm NL, B) 7.2 mm NL, C) 6.9 mm NL.

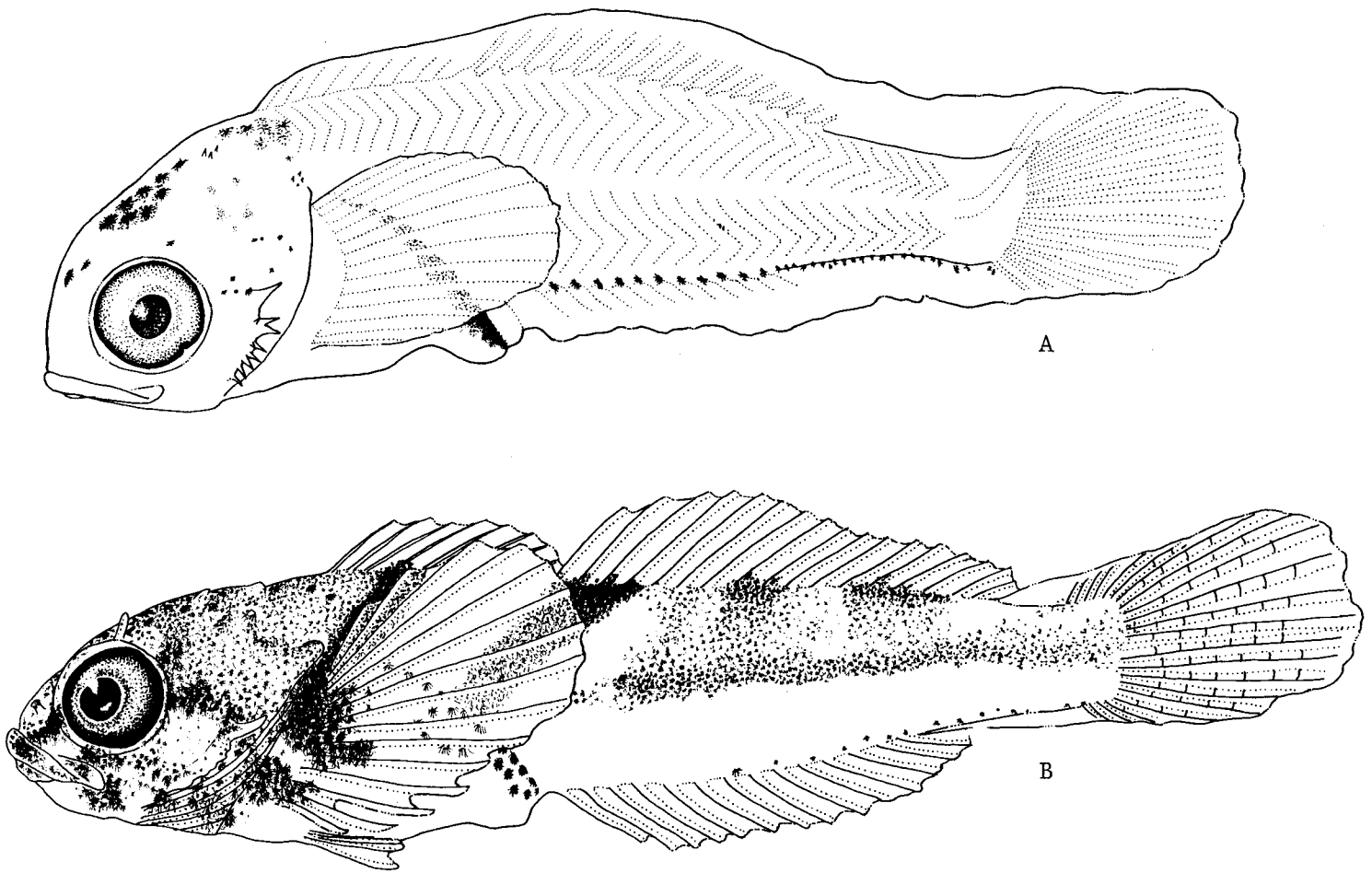

Figure 12. Young of Oligocottus maculosus: A) 7.8 mm SL, B) 10.4 mm SL.

Oligocottus snyderi

(Figures 13, 14; Tables 14, 15, 16)

Literature

Stein (1973) described and illustrated 4.5 and 5.5 mm TL larvae of O. snyderi. Richardson and Washington (1980) called these larvae Cottidae Type 1 and illustrated 4.2, 6.7, and 9 mm specimens.

Identification

Small larvae in this series were reared from eggs spawned from known adults. Adults and juveniles were identified by the following combination of characters: high vertebral (34-37) and dorsal fin ray (17-20) counts, light pigmentation, the presence of cirri on the nasal spines and along the bases of the dorsal fins, and the absence of scales (prickles). The developmental series was linked together primarily on the basis of pigmentation, body shape, and preopercular and parietal spination. Postflexion and transforming larvae were linked to juveniles by pigmentation, meristics, and preopercular and parietal spination.

Distinguishing Features

Distinguishing pigmentation of preflexion larval O. snyderi are melanistic nape pigmentation; relatively light pigmentation over the dorso-lateral surfaces of the gut; and a low number of ventral midline melanophores (5 to 9) situated posterior to the anus. This series of ventral midline melanophores originates beneath the fifth to seventh postanal myomeres and extends posteriorly toward the tail tip. One

melanophore is spaced approximately every four or five myomeres. This characteristic pigmentation changes little during larval development.

In newly hatched larvae, a hump or bubble of skin is present just anterior to the origin of the dorsal finfold. Although diffuse xanthophores are present over this bump in laboratory-reared larvae, no melanophores extend onto this bubble of skin. In contrast, O. maculosus larvae, which also possess this distinctive bubble of skin at the nape, have one to three large dendritic melanophores that extend up onto the bubble of skin from the nape pigment patch.

Larvae of O. snyderi >4.2 mm NL, may be further distinguished from all other known cottid larvae by the presence of a cluster of 10 to 20 minute prickles situated in the parietal region of the head.

Larvae undergoing notochord flexion ≥6 mm long, possess a distinctive pattern of multiple preopercular spination, in which approximately 15 equal-sized spines are positioned along the posterior margin of the preopercle. Ten to 11 small, accessory spines are situated at the anterior bases of the other spines and point anterolaterally.

Postflexion larvae and juveniles may be distinguished by their relatively light pigmentation, the prominent bands of pigment through the eye, and the low number of widely spaced ventral midline melanophores. In addition to pigmentation, juvenile O. snyderi are characterized by high vertebral and dorsal fin ray counts, and by the presence of very long, slender nasal, postorbital, and frontoparietal cirri. In juveniles ≥15 mm, a row of distinctive cirri develop along either side of the bases of the dorsal fins.

Pigmentation

Newly hatched reared larval O. snyderi are lightly pigmented with no melanistic head pigmentation. Several xanthophores are situated over the midbrain in live larvae. Two to eight external melanophores are clustered over the notochord in the nape region. In live specimens several diffuse xanthophores extend dorsally from the nape onto a distinctive bump or bubble of skin just anterior to the origin of the dorsal finfold. However, in contrast to larvae of O. maculosus, melanophores never extend onto this bubble of skin. The dorsolateral surface of the gut is lightly pigmented with 50 to 60 small melanophores forming an elliptical patch over the body cavity. Intense xanthophores also cover the dorsolateral surfaces of the gut. The only pigmentation posterior to the anus consists of a series of five to nine melanophores which originates under the fifth to seventh postanal myomere and extends posteriorly. Each melanophore is positioned approximately every four to six myomeres. Occasionally, one or two melanistic pigment slashes extend onto the caudal finfold just beneath the notochord tip.

During larval development, several melanophores form on the dorsal surface of the head. Size at formation of this melanistic pigmentation appears somewhat variable. One or two melanophores are present over the midbrain in 21-day-old, laboratory-reared larvae, ∿6.5 mm long. Morris[2] reported that four or five melanophores develop in the midbrain region of larvae at four weeks of age (∿8.5 mm). Melanistic pigmentation does not appear over the brain in field-caught larvae until about 10 mm.

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[2]R. W. Morris, 1980. Unpubl. MS, University of Oregon, Eugene, OR.

During transformation, head pigmentation increases markedly in late postflexion larvae, 10 to 14 mm long. Thirteen to 18 large, stellate melanophores form over the midbrain and interorbital regions of the head. Concurrently, several small melanophores form anterior to the orbit and extend anteriorly across the snout onto the upper lip forming a distinct band. Several intense melanophores develop posterior to the orbit forming a dark band extending from the orbit to the dorsalmost preopercular spine. Melanophores are also added at the posterior margin of the lower jaw just ventral to the preopercle, along the dorsal margin of the operculum, and along the pectoral fin rays. A row of intense, embedded melanophores forms just above the spinal cord and extends posteriorly from the nape region two-thirds of the way to the caudal fin. The ventral midline melanophores remain unchanged.

In juveniles between 13 and 15 mm long, numerous tiny melanophores form over the dorsolateral surfaces of the head and extend anteriorly onto the snout between the eyes, ventrally along the preopercle, and along the opercular margin. These diffuse melanophores extend posteriorly to the seventh dorsal spine. Numerous small melanophores also form posterior to the pectoral fin base in an irregular band of pigment along the lateral midline. With development, melanophores are added along the dorsum in an anterior to posterior sequence. Concurrently, melanophores extend dorsally onto the dorsal fins forming four to five distinct bands of pigment. Gradually, the melanophores along the dorsal midline extend ventrally and posteriorly and join the dorsal and lateral areas of pigmentation. This lateral pigmentation extends posteriorly where it forms a dark band at the base of the caudal fin. Melanophores

extend onto the caudal fin rays forming four to five bands of pigment. Juvenile O. snyderi are characterized by uniform diffuse pigmentation over the head and dorsolateral surfaces of the body with a distinct, dark band of pigment extending from the snout, through the orbit, then to the dorsalmost preopercular spine. The characteristic low number of widely spaced ventral midline melanophores remain visible in juveniles up to $\leq$17 to 18 mm.

Morphology

Newly hatched O. snyderi larvae range in size from 4 to 4.5 mm NL. The largest planktonic specimen taken in the field is 10.2 mm and has not yet begun to undergo transformation. The smallest benthic juvenile examined is 12.4 mm. Twenty-four specimens, ranging in length from 4 to 15.1 mm, were examined for development morphology.

Newly hatched O. snyderi larvae are rather stubby in shape with a relatively short gut, the posteriormost portion of which trails well below the body. A small, rounded protrusion extends dorsally from the dorsal surface of the gut just posterior to the pectoral fin base in newly hatched larvae. This protrusion is reminiscent of the gut diverticula found in larvae of several species of Artedius but is much less pronounced and never develops into distinct diverticula. This protrusion decreases in size shortly after hatching and is no longer visible by yolk absorption five days after hatching. In addition, O. snyderi larvae possess a prominent bump or bubble of skin that protrudes dorsally in the nape region just anterior to the origin of the dorsal finfold. This bubble persists in larvae up to $\sim$6.5 to 7 mm.

Snout to anus length averages 42% in preflexion and flexion larvae, then increases slightly to 44% SL in postflexion larvae. Snout to anus length averages 42% SL in benthic juveniles. Relative body depth at the pectoral fin base increases from 23% in preflexion larvae to 25% SL in postflexion larvae. Relative body depth at the anus also increases during larval development, averaging 21% in preflexion larvae and 26% SL in postflexion larvae. Both body depth at the pectoral fin base and at the anus decrease in benthic juveniles, averaging 21% and 22% SL, respectively.

Distance from the snout to the origin of the pelvic fins averages 22% in late flexion and postflexion larvae and increases to 28% SL in benthic juveniles. Distance from the origin of the pelvic fin to the anus also increases from 21% before transformation, to 34% in benthic juveniles.

Relative head length changes little during larval development, averaging 22% SL. Head length increases markedly in benthic juveniles averaging 27% SL. Snout length decreases from 24% in preflexion larvae to 16% HL in postflexion larvae, then increases to 32% HL in benthic juveniles. Eye diameter decreases throughout larval development from 48% to 31% HL.

Fin Development

Larvae of O. snyderi undergo notochord flexion between 6.2 and 8.4 mm. Caudal fin rays first appear at 7.8 mm, however, the full adult complement of principal caudal rays is not complete until larvae reach ∿9 to 10 mm. Rays begin to form in the dorsal and anal fins of larvae between 7.5 and 8 mm long, however, these rays are not fully

formed in larvae ≲9 mm. Dorsal fin spines begin forming in larvae 9 to 10 mm long, and the adult complement of spines is countable in a 10.2 mm specimen. Pectoral fin rays form at 9 mm and are complete by 10 mm. Pelvic buds are first visible in larvae between 8.2 and 9 mm, but the fin rays are not fully formed until larvae reach 10 to 12 mm.

Spination

Five to nine tiny bumps form along the posterior margin of the preopercle in larvae ≲4.2 to 5 mm. By ∿5.1 mm, 10 to 15 tiny equal-sized spines are visible. During notochord flexion the preopercular spines increase in size and number, ranging between 17 and 22. The preopercular spines of O. snyderi larvae are unique in that 10 to 12 spines form along the posterior margin of the preopercle as in other cottids with preopercular spines, yet by ∿7 mm NL, between 8 and 10 small accessory spines form anteriorly at the bases of the original spines. In larvae ≳9 mm, the dorsalmost preopercular spine becomes stouter and longer than the other spines and is separated from the lower spines by a short gap on the preopercular margin. The five to eight spines just ventral to the dorsalmost spine also become slightly larger relative to the lower preopercular spines. Between 12 and 14 preopercular spines are visible in newly settled benthic juveniles. The dorsalmost spine has become much larger relative to the other spines. The smaller, accessory spines have begun to atrophy and are represented only by small bumps or irregularities on the preopercle. By ∿14 mm, only the dorsalmost spine persists.

Distinctive spines also form in the parietal region of the head of young O. snyderi. Larvae as small as 4.2 mm have 7 to 10 small bumps

or prickles visible over the parietals. These prickles increase in number during development, with 10 to 20 prickles present in the parietal region in larvae $\geq$6.2 mm. Eight to 12 tiny prickles remain visible along the posterolateral margin of the parietal bones in 12 to 13 mm cleared and stained benthic juveniles.

A cluster of spines also develops in the supracleithral-posttemporal region in larvae $\leq$8 mm. One spine forms on the supracleithrum and five spines situated in two rows form on the dorsal portion of the posttemporal. These persist throughout larval development but atrophy during transformation until only three bony projections are present in benthic juveniles. These bony projections represent the rudiments of the incipient lateral line system.

Table 14. Measurements (mm) of young Oligocottus snyderi. (Specimens between dashed lines are undergoing notochord flexion.)

Body length	Head length	Snout length	Eye diam	Snout to anus length	Body depth at pectoral fin base	Body depth at anus	Pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
L 3.9	0.80	0.24	0.42	1.7	0.96	0.84	-	-	0.29
L 4.2	0.84	0.20	0.42	1.8	0.98	0.84	-	-	0.20
L 4.5	0.92	0.20	0.46	1.8	1.1	0.94	-	-	0.42
L 5.1	1.0	0.26	0.48	2.1	1.1	1.0	-	-	0.38
5.1	1.1	0.24	0.48	2.2	1.1	0.94	-	-	0.46
5.2	1.2	0.25	0.48	2.2	1.2	1.3	-	-	0.60
6.2	1.2	0.28	0.48	2.4	1.2	1.0	-	-	-
6.2	1.4	0.32	0.60	2.7	1.5	1.4	-	-	0.60
6.4	1.4	0.28	0.64	2.9	1.7	1.7	-	-	0.60
6.5	1.4	0.24	0.60	2.9	1.5	1.6	-	-	0.56
6.7	1.4	0.28	0.62	2.7	1.6	1.6	-	-	0.55
7.5	1.4	0.32	0.62	3.2	1.8	2.1	-	-	1.0
7.5	1.5	0.28	0.64	3.0	1.6	1.7	-	-	0.72
7.8	1.8	0.33	0.68	3.3	1.8	2.1	1.7	1.6	0.96
8.2	1.8	0.40	0.68	3.3	1.9	2.1	1.6	1.7	-
8.4	1.8	0.42	0.64	3.4	1.8	1.9	1.9	1.5	1.1
8.5	1.8	0.36	0.68	3.6	2.1	2.3	1.9	1.7	1.1
9.0	2.1	0.35	0.74	4.2	2.5	3.0	2.0	2.2	1.2
9.4	2.1	0.30	0.76	3.8	2.0	2.2	2.0	1.8	1.3
10.2	2.6	0.34	0.80	4.7	2.6	2.7	2.5	2.2	1.6
J 14.4	3.9	0.85	1.2	5.8	3.0	2.7	3.5	2.3	4.1
J 14.9	3.8	1.2	1.3	6.4	3.5	3.3	3.9	2.5	4.1
J 15.1	4.2	0.91	1.2	6.3	3.6	3.4	3.5	2.8	4.4

J - Juvenile.
L - Laboratory reared.

Table 15. Meristics and spines of young of Oligocottus snyderi. (Only specimens with meristic elements formed are included. See Table 14 for complete developmental series examined.)

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preopercular spines	Parietal spines	Posttemporal spines	Principal caudal rays	Vertebrae	Branchiostegal rays
* 5.2	-	-	-	-	-	-	14	10	-	-	-	-
7.5	18	bases	12b	-	-	-	22	16	-	-	-	6
7.8	-	-	13b	-	-	-	19	18	-	-	-	6
8.2	-	-	12	-	-	buds	20	16	-	-	-	6
8.4	-	19	13	-	-	buds	22	23	-	-	-	6
9.0	IX	18	14	15	15	buds	19	14	-	-	-	6
* 9.4	IX	18	14	14	14	I,3	21	7	6	6+6	36	6
10.2	VIII	19	14	14	14	I,3	19	16	-	-	-	6
*J12.7	VIII	19	15	14	14	I,3	13	8	4	6+6	36	6
*J13.0	VIII	19	14	14	14	I,3	8	0	0	6+6	35	6
*J13.7	VIII	18	14	14	14	I,3	14	0	0	6+6	35	6
J14.4	IX	19	14	14	13	I,3	11	0	0	-	-	6
J14.9	VIII	19	14	14	14	I,3	13	0	0	-	-	6
J15.1	VIII	19	14	14	14	I,3	12	0	0	-	-	6

* - Stained with Alizarin Red S.
J - Juvenile.
b - Bases.

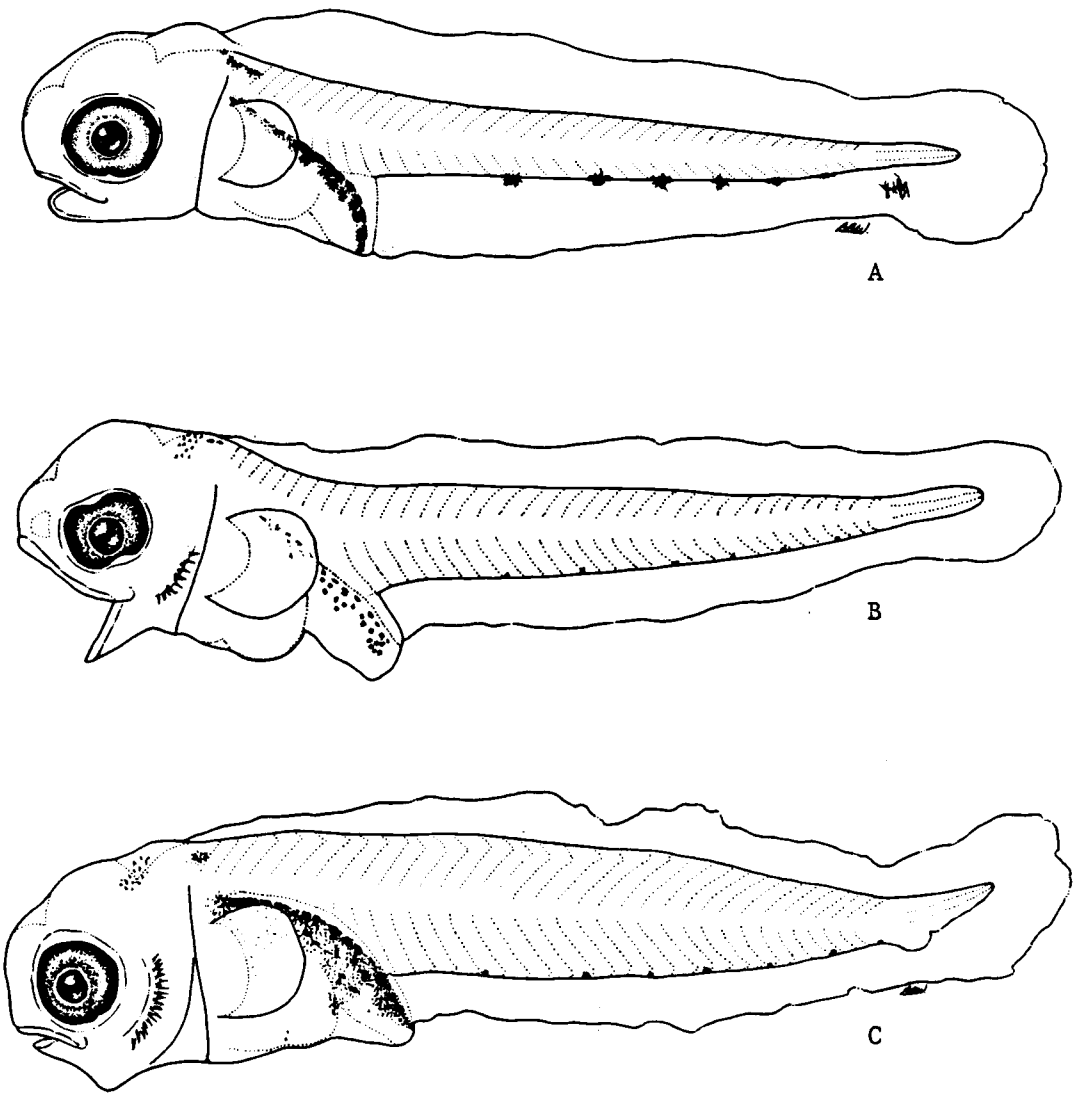

Figure 13. Larvae of Oligocottus snyderi: A) 4.7 mm NL, B) 5.1 mm NL, C) 6.7 mm NL (from Richardson and Washington 1980).

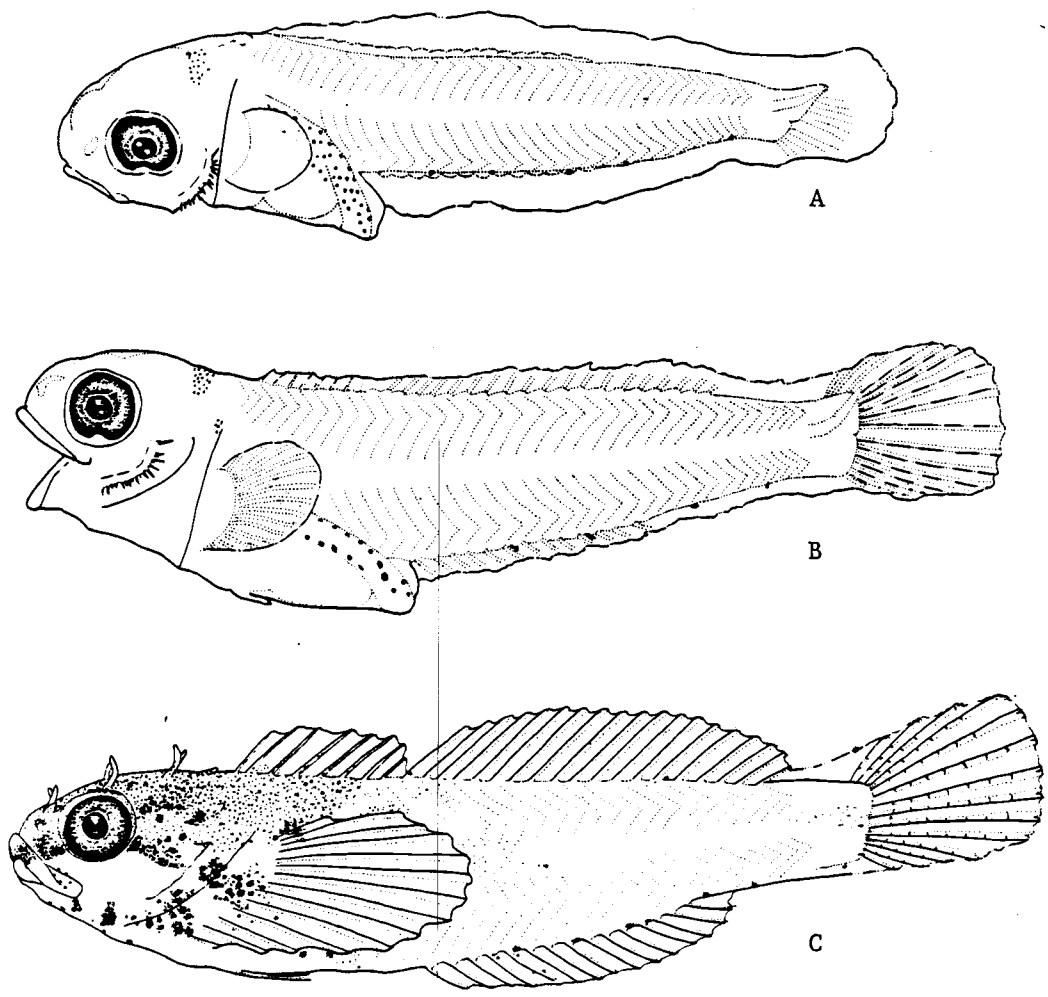

Figure 14. Young of Oligocottus snyderi: A) 8.2 mm SL, B) 10.2 mm SL, C) 14.4 mm SL.

Table 16. Body proportions of larvae and juveniles of Oligocottus maculosus and O. snyderi. Values are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. (Number of specimens may be derived from Tables 12 and 14.)

Item	Oligocottus maculosus	Oligocottus snyderi
Head length/SL:		
Preflexion	17.3±0.61(17.2-18.3)	21.4±1.26(20.1-23.4)
Flexion	24.8±1.89(18.4-21.0)	20.8±1.34(18.9-23.1)
Postflexion	25.3±1.89(22.3-26.6)	23.4±1.71(21.4-28.2)
Juvenile	30.1±3.06(27.1-32.8)	26.9±1.00(26.5-28.0)
Snout length/HL:		
Preflexion	25.7±2.08(24.3-27.9)	23.7±3.37(21.2-25.9)
Flexion	29.5±2.08(26.0-28.1)	21.4±2.43(16.9-23.3)
Postflexion	29.3±2.83(24.4-33.0)	16.1±2.87(13.9-20.4)
Juvenile	27.1±3.22(24.9-31.4)	32.0±0.00(32.0-32.0)
Eye diameter/HL:		
Preflexion	55.6±2.08(53.9-57.2)	47.8±4.80(40.1-52.3)
Flexion	44.9±4.24(42.3-48.2)	42.1±2.95(37.6-46.1)
Postflexion	41.2±4.03(24.4-33.0)	33.3±3.21(31.2-37.9)
Juvenile	31.4±2.01(28.9-34.1)	31.0±2.52(29.0-34.3)
Snout to anus length/SL:		
Preflexion	39.1±1.53(37.2-40.4)	42.1±1.47(40.1-44.4)
Flexion	39.8±2.83(38.1-42.3)	41.8±2.30(39.2-44.9)
Postflexion	43.9±3.39(40.8-48.1)	44.5±1.83(42.1-46.4)
Juvenile	45.0±2.65(42.7-48.5)	42.2±1.53(40.3-43.1)
Snout to pelvic fin origin/SL:		
Preflexion	-	-
Flexion	24.0*	21.0±1.00(20.0-22.0)
Postflexion	24.9±2.15(23.1-26.9)	23.3±1.71(21.0-25.5)
Juvenile	28.1±3.61(25.3-32.1)	24.6±1.53(22.9-26.1)
Pelvic fin origin to anus/SL:		
Preflexion	-	-
Flexion	18.0*	20.0±1.15(19.1-21.1)
Postflexion	20.2±1.89(18.1-22.8)	21.2±1.50(20.1-23.3)
Juvenile	16.9±1.73(16.1-19.4)	18.1±3.21(16.0-22.1)
Body depth at pectoral fin base/SL:		
Preflexion	19.4±1.00(17.8-20.2)	23.2±1.17(21.8-25.5)
Flexion	24.0±0.00(24.0-24.0)	23.4±2.00(20.2-26.6)
Postflexion	25.9±2.17(23.7-29.1)	20.6±1.50(19.4-21.8)
Juvenile	23.9±3.06(20.6-27.2)	21.2±2.00(19.0-23.4)
Body depth at anus/SL:		
Preflexion	15.5±0.61(9.8-11.2)	21.0±2.37(18.1-24.9)
Flexion	18.0±0.00(18.0-18.0)	24.3±2.91(17.9-28.1)
Postflexion	25.9±2.17(23.7-29.1)	26.2±1.50(21.9-27.3)
Juvenile	20.3±2.08(18.1-22.3)	24.1±2.31(19.0-23.0)
Pectoral fin length/SL:		
Preflexion	10.1±0.61(9.8-11.2)	8.2±2.53(6.1-12.1)
Flexion	18.0±0.00(18.0-18.0)	10.1±1.77(9.3-13.4)
Postflexion	21.7±2.96(17.3-26.3)	14.4±1.41(13.1-16.0)
Juvenile	29.1±2.65(26.8-31.9)	24.3±1.53(22.9-26.3)

- = Not present in this stage.
* = Only one specimen available in this stage.

Clinocottus acuticeps

(Figures 15, 16, 17; Tables 17, 18, 25)

Literature

Blackburn (1973) illustrated and described an 8.6 mm specimen which he called Cottid 1 "Biramous anus." Richardson (1977) and Richardson and Pearcy (1977) listed larvae of C. acuticeps as Cottidae sp. 12. Larvae of this species were described by Richardson and Washington (1980). They illustrated 3.7, 3.9, 6.9, 7.6, 10.4, 13.8, and 16.5 mm specimens.

Identification

Small larval C. acuticeps were reared from eggs spawned from known adults. Adults and juveniles were identified by low dorsal fin ray (13-17) and anal fin ray (9-13) counts, the presence of nasal cirri, and a membrane connecting the innermost pelvic fin ray with the abdomen. The developmental series was linked together primarily by pigmentation, body shape, and hindgut diverticula. Postflexion and transforming larvae were linked with juveniles by pigmentation, meristics, and the membrane attaching the pelvic fin rays to the abdomen.

Distinguishing Features

Clinocottus acuticeps larvae are distinguished from all other known cottid larvae by long protrusions (diverticula) which extend posteriorly from the gut on either side of the anus. These diverticula are present in yolk-sac larvae and persist in the largest pelagic specimens (14.5 mm). The gut itself is distinctively long and the posterior portion trails well below the body. Snout to anus length, averaging 62.5% SL, is greater

than in other known larvae of Artedius, Clinocottus or Oligocottus. In addition, these larvae have a flabby appearance with an outer "bubble of skin," which is especially pronounced in the head region.

Other characters useful in distinguishing C. acuticeps larvae are melanistic pigmentation on the snout and head, and relatively few ventral midline melanophores (4 to 10).

Transforming and juvenile C. acuticeps are distinguishable from all other known cottids by the presence of a membrane attaching the inner pelvic fin ray to the belly. Other characters useful in separating juveniles are the relatively light, uniform pigmentation over the body; a band of pigment extending from the snout posteriorly through the orbit toward the preopercle; a dark blotch of pigment at the anterior end of the spinous dorsal; and a low number of ventral midline melanophores.

Pigmentation

Newly hatched larvae reared in the laboratory exhibit four or five dendritic melanophores on the snout and two faint melanophores in each otic capsule. In field-collected larvae ≤3.7 mm NL, the presence of snout pigment is variable, however, all larvae >3.7 mm possess at least two melanophores on the snout. Eight to 15 melanophores are clustered in the nape region of even the smallest larvae. Numerous melanophores are scattered over the dorsolateral surface of the gut extending posterolaterally over the surface of the gut diverticula. These melanophores are much fainter and more irregular in shape than in larvae of other species of Clinocottus.

A series of 4 to 10 inconspicuous ventral midline melanophores originates beneath the 7th to 10th postanal myomeres and extends

posteriorly toward the tail tip. Several additional melanophores appear as streaks of pigment on the ventral finfold near the tail tip.

Pigmentation increases on the head during larval development. Melanophores form first on the head over the midbrain in larvae 5.5 mm NL. Concurrently, several embedded melanophores appear on the nape and extend anteriorly onto the head. Four to five internal melanophores occur in or near the otic capsule. In larvae $\geq$6.5 mm, scattered melanophores extend continuously from the snout to the nape region. Ventral midline melanophores persist in flexion and postflexion larvae, and the posteriormost melanophore, which is located near the notochord tip in small larvae, occurs near the middle of the caudal fin base between the forming hypural plates. The posteriormost melanophores which extended onto the ventral finfold, now occur on the caudal fin. In the largest planktonic larvae, which are beginning to undergo transformation, melanophores are added in a patch just posterior to the orbit. Melanophores also are added along the bases of the pectoral fins and extend onto the pectoral fin rays.

In newly settled benthic juveniles, 13 to 14 mm long, head pigmentation increases markedly. Melanophores extend anteriorly across the dorsal surface of the snout and onto the upper lip. The melanophores at the ventral margin of the snout are especially intense and closely spaced, forming a prominent band that extends from the upper lip to the ventral margin of the orbit. This band continues from the posterior margin of the orbit to the dorsal margin of the preopercle. Additional melanophores are added along the ventral edge of the lower lip, at the base of the preopercle, and on the dorsal portion of the operculum. As

development proceeds, a second band of pigment forms between the ventral margin of the orbit and the preopercle. Melanophores increase on the nape and extend anteriorly onto the head. Four to five internal melanophores occur in or near the otic capsule. In larvae ≥6.5 mm, scattered melanophores extend continuously from the snout to the nape region. Ventral midline melanophores persist throughout larval development, and the posteriormost melanophore which was located near the notochord tip in small larvae occurs near the middle of the caudal fin base between the forming hypural plates by ≥6 to 7 mm SL. The posteriormost melanophores which extended onto the ventral finfold before notochord flexion now occur on the caudal fin.

In the largest planktonic larvae that are beginning to undergo transformation, melanophores are added in a patch just posterior to the orbit. Melanophores are added along the bases of the pectoral fins and extend onto the pectoral fin rays.

In newly settled benthic juveniles, 13 to 14 mm long, head pigmentation increases markedly. Melanophores extend anteriorly across the dorsal surface of the snout and onto the upper lip. The melanophores at the ventral margin of the snout are especially intense and closely spaced forming a prominent band that extends from the upper lip to the ventral margin of the orbit. This band continues from the posterior margin of the orbit to the dorsal margin of the preopercle. Additional melanophores are added along the ventral edge of the lower lip, at the base of the preopercle, and on the dorsal portion of the operculum. As development proceeds, a second band of pigment forms between the ventral margin of the orbit and the melanophores at the base of the preopercle.

Simultaneously, pigmentation increases on the pectoral fin bases while two to three bands of pigment form across each fin.

Between 14 and 15 mm, a dense patch of melanophores forms at the anterior end of the first dorsal fin between the first and third spines. As juvenile pigmentation progresses this patch expands posteriorly to include the fourth dorsal spine, and a second patch of melanophores forms between the seventh and eighth dorsal spines. Melanophores extend ventrally from these two pigment patches forming two distinct bands across the dorsum. Pigmentation proceeds posteriorly along the dorsum. In juveniles between 15 and 16 mm long, a third band (or saddle) of pigment forms under the second to sixth dorsal fin rays; a fourth band forms under the 8th to 11th dorsal fin rays; and a fifth band forms under the last two dorsal fin rays. As these bands of pigment develop along the dorsum, they extend ventrally and eventually unite into a uniform band of pigment above the lateral midline. Concurrently, another band of pigment extends posteriorly along the lateral midline to the caudal fin where melanophores form a dark band at the base of the caudal fin. Melanophores extend onto the caudal fin rays wehre they form four or five bands across the fin. Clusters of melanophores extend first ventrally and then laterally from the lateral midline pigment band and gradually unite enclosing three to five small unpigmented circles below the lateral line. Three to six tiny melanophores remain visible along the ventral midline posterior to the anus in juveniles <17 mm long.

Morphology

Clinocottus acuticeps larvae hatch at the smallest length (3.1 to 3.3 mm NL) of any member of the genus. The largest planktonic specimen collected is 14.5 mm and is beginning to undergo transformation. The smallest benthic juvenile examined is 12.6 mm. Thirty-seven selected specimens of C. acuticeps ranging in length from 3.1 to 16.2 mm, were examined for developmental morphology.

Larvae of C. acuticeps have a distinctive, flabby appearance as if a loose bubble of outer skin surrounds the anterior part of the body.

Larvae are deep-bodied with a long, distinctive gut, the posterior portion of which trails well below the body. Prominent diverticula extend posteroventrally from the hindgut on either side of the anus. These diverticula are well-developed throughout larval development but are not visible in benthic juveniles. Relative body depth at the pectoral fin base and at the anus increase from 24 to 31% and from 21 to 28%, respectively, during development from preflexion larvae to transforming juveniles. Snout to anus length remains relatively constant during larval development, averaging 63% SL. Distance from the snout to the origin of the pelvic fin increases from 31% SL, while distance from the pelvic fin origin to the anus decreases from 37% to 23% SL during larval development.

Head length changes relatively little, increasing slightly from 27 to 29% SL during the flexion stage and then decreasing again to 27% in postflexion larvae. Head length increases markedly in benthic juveniles, averaging 32% SL. Snout length remains about 25% HL throughout larval development, yet increases to 28% HL in benthic juveniles. In contrast,

eye diameter decreases from 42% in preflexion larvae to 32% HL in post-flexion larvae and 28% HL in juveniles.

Fin Development

A 5.6 mm NL larva is just beginning notochord flexion and a concurrent thickening of the hypural region of the forming caudal fin. The adult complement of principal caudal rays is present in a 6.8 mm specimen prior to completion of notochord flexion at ∿7.5 mm. Bases of the forming dorsal and anal fin rays are forming on a 6.9 mm larva. The full adult complement of dorsal and anal fin rays is present by ∿8 mm. However, the adult complement of dorsal fin spines is not present until ∿8.7 mm.

Although pectoral fin rays are visible on a 6.9 mm larva, the full adult complement is not complete until ≤7.6 mm. Pelvic fin buds appear just after completion of notochord flexion in a 7.6 mm larva, however, the fin rays are not fully formed until ∿10 mm.

Spination

Preopercular spines first appear as small bumps at 5.2 mm NL. Nine to 11 small spines are present by the onset of notochord flexion at ∿6 mm. During flexion, spines remain small and evenly spaced with the second and third spines becoming slightly longer than the others. By completion of flexion, at 7.6 mm, 11 to 12 spines are present along the margin of the preopercle. The dorsalmost three spines are beginning to elongate and point dorsally. In a 10 mm cleared and stained specimen, the dorsalmost three spines are nearly four times as long as the ventral spines. In the largest planktonic larvae, 13 to 14 mm long, the

ventralmost spines are beginning to atrophy. The three dorsalmost spines are still prominent in a 15.2 mm juvenile, but the eight ventral spines are miniscule with their tips twisted and bent anteriorly. By ~19 mm, the lower spines have atrophied completely, and only the single large dorsalmost spine persists.

No spines develop in the parietal or supracleithral-posttemporal regions of the head in larvae or juveniles of this species.

Table 17. Measurements (mm) of young Clinocottus acuticeps. (Specimens between dashed lines are undergoing notochord flexion.)

Body length	Head length	Snout length	Eye diam.	Snout to anus length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
L 3.2	0.72	0.16	0.30	1.7	0.56	0.58	-	-	0.34
3.3	0.78	0.26	0.32	2.0	0.84	0.62	-	-	0.30
3.7	0.90	0.14	0.38	2.3	0.90	0.74	-	-	0.26
3.9	0.88	0.16	0.38	2.4	0.86	0.78	-	-	0.40
4.2	1.3	0.30	0.52	3.0	1.2	1.0	-	-	0.48
4.6	1.4	0.28	0.52	3.0	1.1	0.84	-	-	0.56
5.1	1.3	0.32	0.64	2.9	1.3	1.2	-	-	0.60
5.2	1.5	0.32	0.56	3.5	1.3	1.2	-	-	0.56
5.9	1.7	0.44	0.52	3.7	1.4	1.4	-	-	0.68
5.6	1.7	0.52	0.56	3.4	1.6	1.3	-	-	0.60
6.2	1.7	0.44	0.64	3.9	1.5	1.7	-	-	0.60
6.6	2.1	0.48	0.72	4.4	2.0	1.6	-	-	0.60
6.9	2.0	0.56	0.64	4.4	2.0	1.9	-	-	1.0
7.5	2.1	0.52	0.76	4.5	2.0	1.9	-	-	0.84
7.3	2.2	0.68	0.68	4.9	2.4	1.9	2.5	2.4	0.76
7.9	2.4	0.52	0.80	5.5	2.7	2.3	3.0	2.5	1.0
8.2	2.7	0.68	0.80	5.9	2.8	2.3	3.2	2.7	1.5
8.2	2.5	0.68	0.80	5.7	2.9	2.9	2.8	2.9	1.6
8.9	2.6	0.48	0.84	5.6	3.0	3.0	2.6	3.0	1.9
9.7	2.5	0.68	0.84	6.0	3.0	2.6	3.1	2.9	1.7
10.0	2.5	0.41	0.84	6.2	3.5	2.9	3.1	3.1	2.0
10.2	2.7	0.57	0.98	6.2	3.0	3.1	3.1	3.8	3.0
10.9	3.5	0.57	1.1	7.4	3.4	3.0	3.7	3.7	3.1
10.9	3.0	0.92	0.96	6.5	3.3	3.0	3.6	2.9	3.2
11.1	2.9	0.57	1.1	6.7	3.4	2.9	3.9	2.8	3.4
11.9	2.9	0.74	1.1	7.2	3.5	3.4	3.5	3.7	3.4
12.4	2.9	0.66	1.1	7.6	4.1	3.4	4.2	3.4	3.5
12.6	3.4	0.82	1.1	7.4	3.6	3.4	4.3	3.1	3.8
12.8	3.7	0.82	1.1	7.7	3.8	3.4	4.2	3.5	4.0
13.1	3.9	0.95	1.4	7.7	3.8	3.4	4.2	3.5	3.9
13.8	3.5	0.82	1.1	7.8	3.9	3.7	4.3	3.5	4.8
14.1	4.1	0.98	1.2	8.2	4.3	3.8	4.7	3.5	4.5
14.5	4.1	1.1	1.1	8.2	4.3	4.0	4.8	3.4	5.1
J 12.6	4.1	1.1	1.2	6.1	3.5	3.2	4.1	2.0	4.3
J 15.9	5.2	1.4	1.5	8.2	3.8	3.4	5.2	3.0	4.9
J 16.2	5.1	1.5	1.3	8.2	4.3	4.1	5.6	2.6	5.1

J - Juvenile.
L - Laboratory-reared.

Table 18. Meristics and spines of young Clinocottus acuticeps. (Only specimens with meristic elements formed are included. See Table 17 for complete developmental series examined.)

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preoper-cular spines	Parietal spines	Post-temporal spines	Principal caudal rays	Verte-brae	Branchio-stegal rays
5.6	-	-	-	-	-	-	10	-	-	-	-	-
* 6.2	-	-	-	-	-	-	9	-	-	-	-	-
6.6	-	-	-	-	-	-	13	-	-	-	-	-
6.9	-	-	-	-	-	-	13	-	-	-	-	-
7.5	-	15	-	-	-	-	11	-	-	-	-	-
* 7.3	-	16	11	-	-	-	11	-	-	-	-	-
7.8	-	-	-	-	-	-	11	-	-	-	-	-
* 8.1	VIII	15	11	14	14	buds	11	0	0	6+6	32	6
8.2	VIII	16	11	14	14	buds	11	0	0	-	-	-
8.7	IX	17	12	15	14	buds	12	0	0	-	-	-
9.6	IX	15	11	14	15	I,3	12	0	0	-	-	-
* 10.0	VIII	15	12	14	14	I,3	12	0	0	6+6	33	6
* 10.2	IX	16	11	15	15	I,3	11	0	0	6+5	34	6
10.9	IX	15	12	14	14	I,3	12	0	0	-	-	-
10.9	IX	16	12	14	14	I,3	11	0	0	-	-	-
11.1	VIII	15	12	14	14	I,3	12	0	0	-	-	-
* 11.9	IX	16	11	14	14	I,3	13	0	0	6+6	33	6
12.4	VIII	16	11	14	14	I,3	12	0	0	-	-	-
12.6	IX	15	12	14	14	I,3	12	0	0	-	-	-
12.8	IX	15	12	14	14	I,3	11	0	0	-	-	-
13.1	VIII	16	12	14	15	I,3	11	0	0	-	-	-
13.8	IX	15	11	14	14	I,3	10	0	0	-	-	-
* 14.1	VIII	15	12	14	14	I,3	12	0	0	-	31	-
* 14.2	IX	16	13	14	14	I,3	12	0	0	6+5	32	6
14.5	VIII	14	11	14	15	I,3	12	0	0	-	-	-
*J12.6	VIII	15	12	14	14	I,3	7	0	0	6+6	32	6
J15.9	VIII	15	12	14	14	I,3	1	0	0	6+6	-	6
*J16.2	VIII	15	12	14	15	I,3	1	0	0	6+6	33	6

* - Stained with Alizarin Red S.
J - Juvenile.

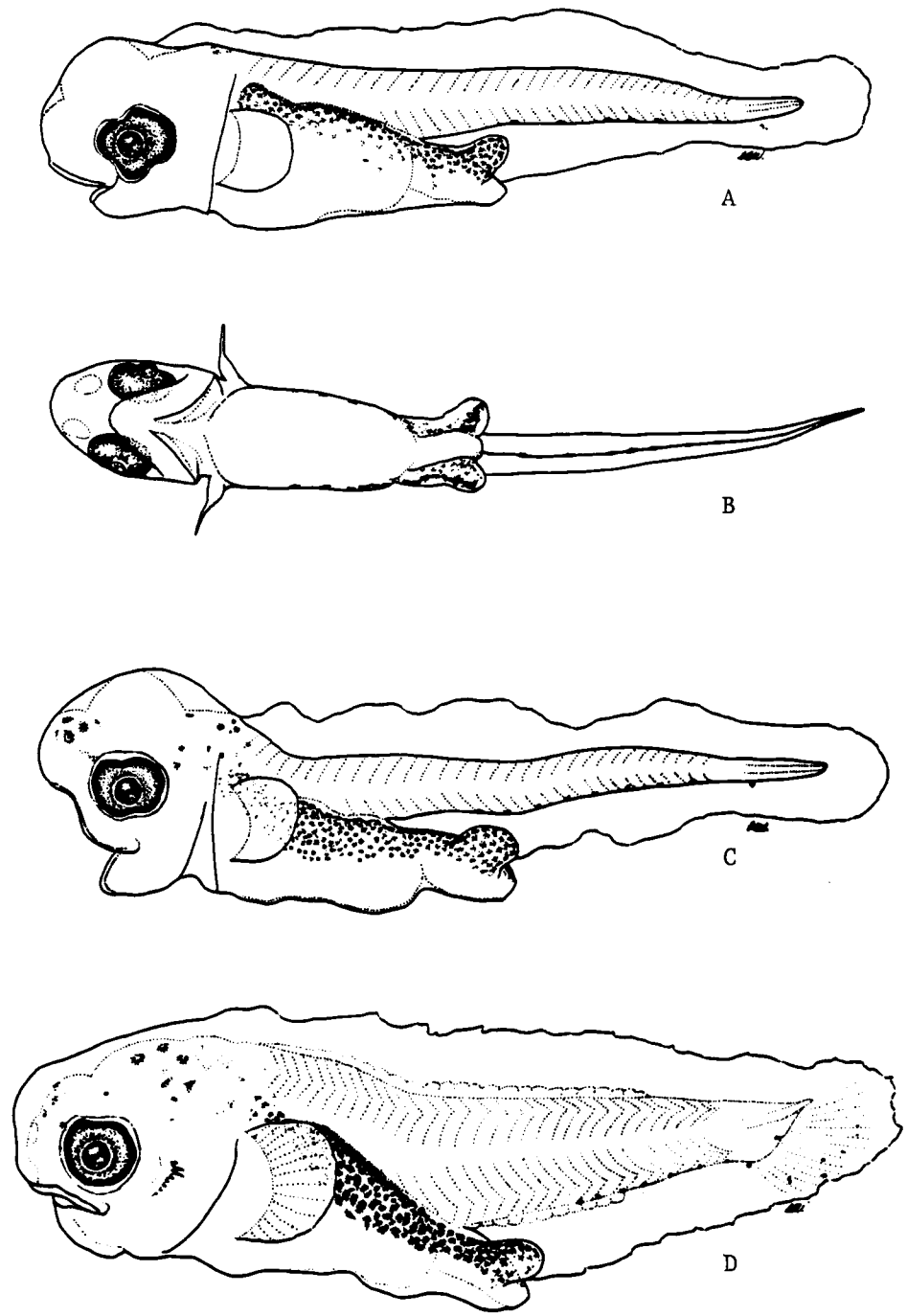

Figure 15. Larvae of Clinocottus acuticeps: A) 3.7 mm SL, B) 3.7 mm SL, C) 3.9 mm SL, D) 6.9 mm SL (from Richardson and Washington 1980).

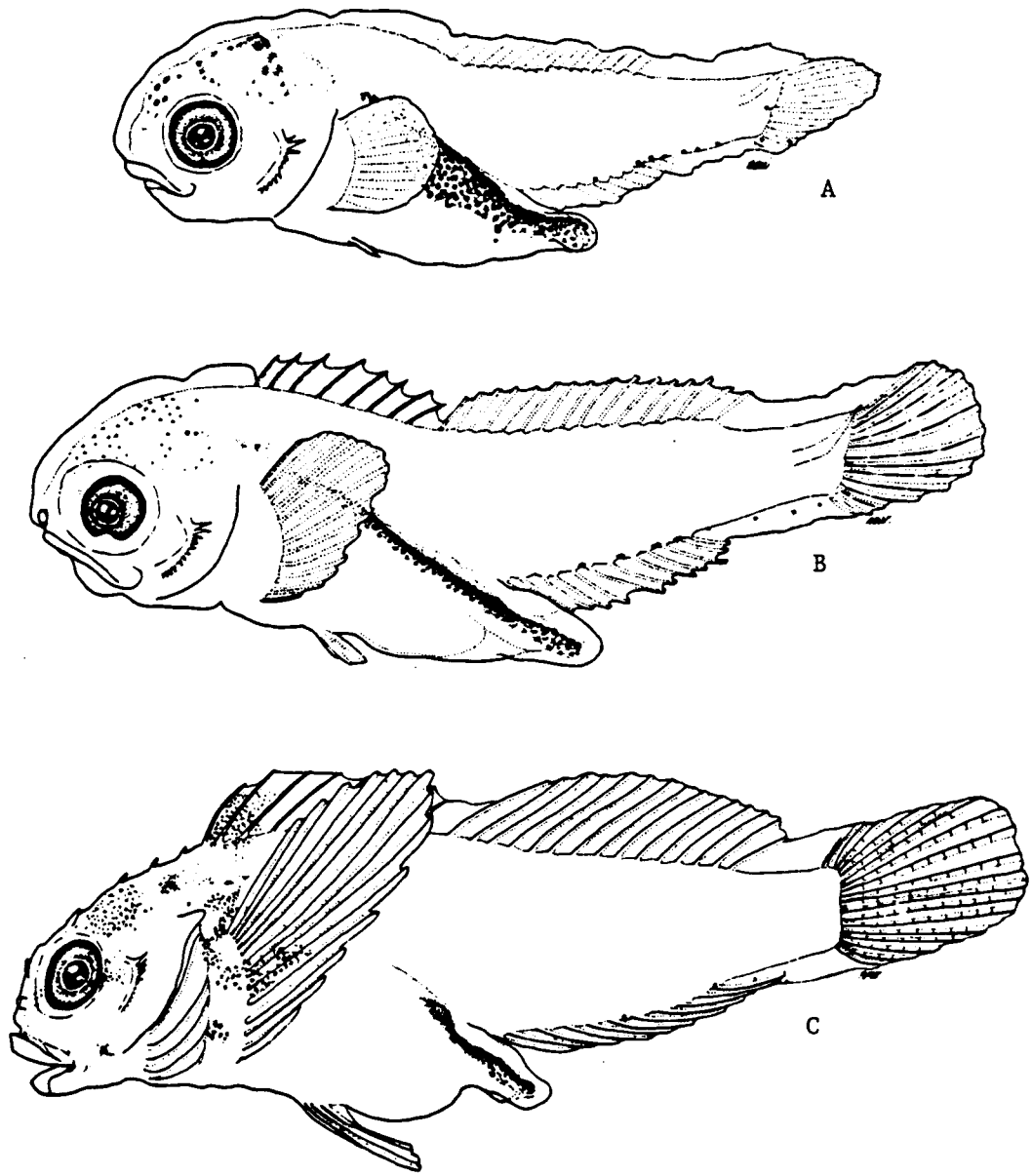

Figure 16. Larvae of Clinocottus acuticeps: A) 7.6 mm SL, B) 10.4 mm SL, C) 13.8 mm SL (A, B, and C from Richardson and Washington 1980).

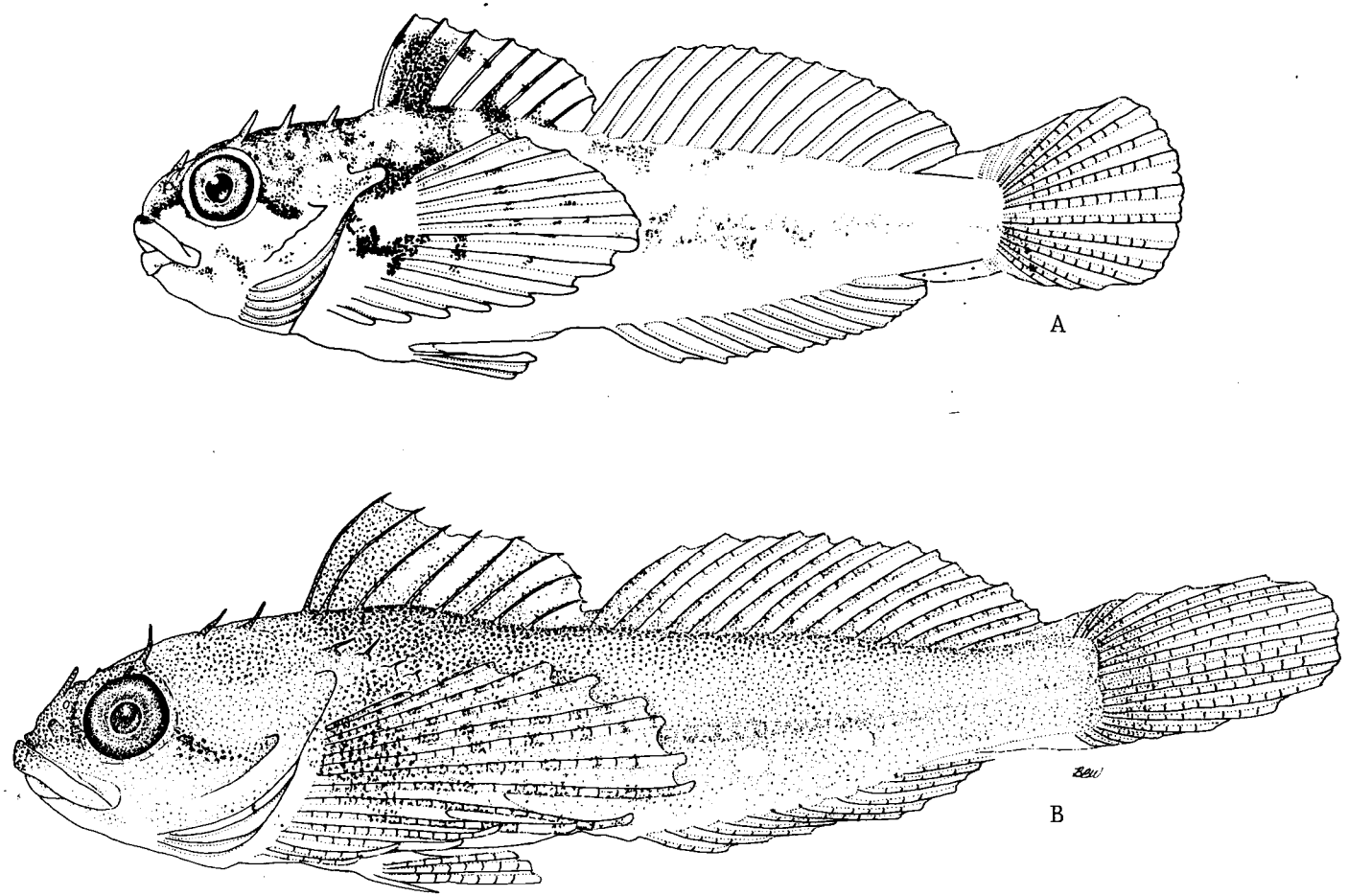

Figure 17. Young of Clinocottus acuticeps: A) 13.8 mm SL, B) 16.5 mm SL (from Richardson and Washington 1980).

Clinocottus embryum

(Figures 18, 19, 20; Tables 19, 20, 25)

Literature

Richardson (1977) and Richardson and Pearcy (1977) listed larvae of this species as Cottidae sp. 20. Richardson and Washington (1980) described these larvae as Cottidae Type 2 and illustrated 4.0, 6.4, and 7.4 mm specimens.

Identification

Juveniles and adults were identified using a combination of the following characters: an advanced anus, light pigmentation, presence of a nasal cirrus, low anal fin ray counts (9-12), and absence of a membrane attaching the pelvic fin rays to the abdomen. The developmental series was linked together primarily on the basis of pigmentation, body shape, and preopercular spination. Postflexion and transforming larvae were linked to juveniles by pigmentation, cirri patterns, meristics, and preopercular spination.

Distinguishing Features

Characters useful in distinguishing preflexion larvae of C. embryum are lack of head pigment, relatively light gut pigmentation, large number of ventral midline melanophores (15 to 21), and relatively long, trailing gut. Head and/or snout pigment is present in larvae of all other species of Clinocottus. Larvae C. embryum are further distinguished from yolk-sac C. acuticeps larvae (in which snout pigment is sometimes absent) by the absence of distinct hindgut diverticula in C. embryum.

In addition to pigmentation characters mentioned above, flexion and postflexion larvae of C. embryum are distinguished by their head spination. Larvae 7.3 mm have 11 to 14 preopercular spines with the dorsalmost spine being largest.

In benthic juveniles of C. embryum, the anus is advanced midway between the origin of the pelvic fins and the anal fin as in other members of the genus. Juvenile C. embryum are distinguished from C. globiceps, C. analis, and C. recalvus by relatively light, mottled body pigmentation and long and slender nasal, postorbital, and frontoparietal cirri. Clinocottus embryum juveniles are distinguished from C. acuticeps by presence of a large number of ventral midline melanophores (15 to 21) and absence of a membrane connecting the inner pelvic fin ray to the abdomen.

Pigmentation

Melanistic pigmentation is absent on the head in preflexion C. embryum larvae. One to five melanophores are scattered over the nape region. The dorsolateral surface of the gut is relatively lightly pigmented and occasionally several faint melanophores are present on the anterolateral surface of the gut below the pectoral fins. Posterior to the anus, a series of 15 to 19 melanophores extends along the ventral midline. This series begins on the fourth or fifth myomere posterior to a vertical line through the anus and melanophores are spaced approximately one per myomere. Several specimens have one or two melanophores on the ventral finfold near the notochord tip.

During larval development, the formation of head pigmentation is variable in larvae between 6 and 9 mm long. Three out of eight larvae

observed possess one to five tiny melanophores over the brain. From one to two melanophores are consistently present beneath the pectoral fin on the anterolateral surface of the gut in larvae ≤6.5 mm. Otherwise, pigmentation remains unchanged.

In transforming larvae ≤9.6 mm long, numerous melanophores appear over the brain. Several melanophores appear on the cheek region between the orbit and the preopercle. Melanophores are also added on the pectoral fin base.

Melanistic pigmentation increases over the head in newly settled juveniles. Large melanophores cover the surfaces of the head over the midbrain and interorbital regions. Several large, intense melanophores are embedded at the posterior margin of the parietal region. A distinct, dense band of melanophores extends from the orbit anteriorly onto the upper lip and posteriorly from the orbit to the dorsal tip of the preopercle. Several melanophores are also present on the cheek beneath the orbit, forming a dark patch. Melanophores are also added to the dorsal surface of the operculum and to the pectoral fin base with several melanophores extending onto the pectoral fin rays.

As development proceeds, pigmentation increases markedly over the head. In a 16 mm juvenile, the bands of pigment extending through the eye are prominent, but numerous small melanophores cover the entire dorsal surface of the head above these bands of pigment. Pigmentation increases on the operculum and pectoral fin base. Three to four bands of melanophores are added across the pectoral fin rays.

Five bands of pigment develop on the body along the dorsal midline in an anterior to posterior sequence. The first band of pigment forms

under the third to fifth dorsal fin spine, and a second smaller band begins to form under the seventh to ninth dorsal spine in juveniles between 13 and 14 mm long. By ∿15 mm, three additional bands of pigment are present on the dorsum beneath the second dorsal fin. The third band forms under the second to fourth dorsal fin rays; the fourth band forms under the seventh to ninth fin ray; and the fifth band forms under the 12th to 15th ray. At the same time, a series of embedded melanophores develops in a row just above the notochord, extending from the nape region toward the caudal fin. A few diffuse patches of external melanophores also form along the lateral midline posterior to the gut.

As juvenile pigmentation develops, the dorsal bands of pigment extend ventrally where they unite above the lateral line, forming four unpigmented saddles between the bands. The melanophores lying along the lateral midline increase in number and extend posteriorly and ventrally toward the caudal fin. As this lateral pigmentation extends posteriorly, it fuses dorsally with the pigment bands. As pigmentation expands and unites over the lateral surface of the body, numerous, irregular, unpigmented circles remain above and below the lateral line, giving juvenile C. embryum a distinctively mottled appearance. Eighteen to 21 small melanophores remain visible along the ventral midline in juveniles up to ∿19 mm long.

Morphology

The smallest C. embryum examined is 4.0 mm NL and is recently hatched. The largest specimen taken in the plankton is 14.0 mm and is beginning to undergo transformation. The smallest benthic juvenile is

13.7 mm. Eighteen C. embryum, ranging from 4 to 14 mm long, were examined for developmental morphology.

Larval C. embryum have a distinctively shaped gut with the posterior portion trailing well below the body. The walls of the hindgut protrude on either side of the anus, reminiscent of the hindgut diverticula of C. acuticeps, however, these bulges never develop into pronounced diverticula. Body depth at the pectoral fin base and anus changes little during larval development, averaging 26% and 25% SL, respectively. Body depth at the pectoral fin base and body depth at the anus decrease slightly in benthic juveniles, averaging 24% and 23% SL, respectively. Relative snout to anus length also remains constant throughout larval development averaging 50% SL. In benthic juveniles, relative snout to anus length decreases to 47% SL. Distance from snout to origin of the pelvic fin is 28% in a 9.6 mm postflexion larva but increases to 32% SL in late postflexion and transforming juveniles. In contrast, origin of the pelvic to anus length decreases from 26% in a 9.6 mm larva to 17% SL in benthic juveniles. This decrease in length coincides with onset of the anterior movement of the anus.

Head length decreases from 26% in preflexion larvae to 24% SL in flexion larvae. In contrast, relative head length increases markedly in benthic juveniles averaging 32% SL. Snout length increases slightly from 21% to 23.5% HL in flexion and postflexion larvae. Relative snout length continues to increase during transformation, averaging 30% HL in benthic juveniles. Eye diameter decreases from 43% in preflexion larvae to 32% in postflexion larvae and 30% HL in juveniles. Jaw length averages 24% HL in both preflexion and flexion larvae but decreases to 19%

in postflexion larvae. Relative jaw length increases again in benthic juveniles, averaging 32% HL.

Fin Development

The onset of notochord flexion is first apparent in a 6.4 mm larva. Caudal rays are present by ∿7.4 mm but the adult complement of principal caudal rays is not complete until about 8.4 mm. Bases of the forming dorsal and anal fin rays are first visible at ∿7.4 mm, however, the adult complement of dorsal and anal fin rays is not present until ∿8.3 mm. Dorsal spines are beginning to form at ∿8.3 mm but are not fully formed. until 9.6 mm. Pectoral fin rays begin to form at ∿8 mm, and the adult complement of fin rays is present by 9.6 mm. Pelvic fin buds are first apparent at ∿9.6 mm, and the adult pelvic fin complement (I,3) is present in postflexion larvae ≥12.4 mm long.

Spination

Eight to ten tiny, evenly spaced spines first appear along the margin of the preopercle at ∿5.2 mm NL. In larvae undergoing notochord flexion, the number of preopercular spines increases, ranging in number from 11 to 14. During the flexion stage, the dorsalmost preopercular spine increases in size relative to the rest of the preopercular spines so that by the end of flexion, the dorsalmost spine is much longer and stouter than the other spines. In the largest planktonic larvae, 13 to 14 mm long, the upper spine is ≥2.5 times longer than the other spines and is separated from them by a slight gap. In newly settled benthic juveniles, the number and size of the lower preopercular spines are reduced. By ≥15 mm, only a second, tiny spine persists just ventral to

the large dorsal spine. The other spines appear as five to seven small bumps or irregularities along the preopercular margin. In completely transformed juveniles $\geq$16 mm long, only the uppermost spine is visible.

Two spines develop in the parietal region of C. embryum larvae. A single small spine is first present at the posterior margin of each parietal at $\sim$6.7 mm. By 9.6 mm, this parietal spine has increased in size and a second smaller parietal spine is present just behind it. As larvae undergo transformation, between 12 and 14 mm, these spines undergo a reduction in size, and the parietal spine eventually fuses with the second parietal spine, forming a hollow central canal between the spines. This canal is part of the incipient cephalic lateral line system. In newly settled juveniles, only a skin-covered bony protruberance is visible in the parietal region.

Three spines also form in the supracleithral-posttemporal region of the head at $\sim$9.6 mm. These spines persist through transformation and eventually become associated with the lateral line system in juveniles $\geq$15 mm long.

Table 19. Measurements (mm) of young Clinocottus embryum. (Specimens between dashed lines are undergoing notochord flexion.)

Body length	Head length	Snout length	Eye diam	Snout to anus length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
4.0	0.99	0.16	0.42	2.2	0.84	0.72	-	-	0.24
5.2	1.5	0.32	0.64	2.7	1.5	1.3	-	-	0.64
5.4	1.5	0.36	0.56	2.6	1.3	1.4	-	-	0.56
6.4	1.5	0.27	0.55	3.0	1.6	1.5	-	-	0.67
6.7	1.6	0.40	0.56	3.8	1.7	1.6	-	-	0.72
6.8	1.5	0.36	0.60	3.1	1.6	-	-	-	0.76
7.3	1.8	0.40	0.68	3.2	1.8	1.9	-	-	0.64
7.4	1.8	0.55	0.66	3.9	2.0	1.8	-	-	0.66
8.3	2.1	0.44	0.60	4.2	1.9	2.0	-	-	1.0
9.6	2.4	0.56	0.88	5.2	2.6	2.6	2.7	2.5	1.7
12.4	3.0	0.66	1.0	6.6	3.5	-	-	-	3.7
13.9	3.4	0.75	1.0	6.6	3.5	3.7	4.1	2.5	4.2
14.0	3.3	0.75	1.2	7.2	3.7	3.8	4.8	2.4	5.2
14.1	3.7	0.84	1.1	7.4	3.7	3.8	5.1	2.3	5.1
J 13.7	4.4	1.0	1.3	7.2	4.4	2.8	3.4	3.5	4.4
J 14.9	4.8	1.5	1.4	7.0	4.7	2.3	3.8	3.3	5.1
J 16.2	4.9	1.4	1.5	7.7	4.8	2.9	3.8	3.6	5.5

J - Juvenile.

Table 20. Meristics and spines of young of Clinocottus embryum. (Only specimens with meristic elements formed are included. See Table 19 for complete developmental series examined.)

Body length	Dorsal spinea	Fin rays	Anal fin raya	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preoper-cular spines	Parietal spinea	Post-temporal spinea	Principal caudal raya	Verte-brae	Branchio-stegal rays
* 6.8	-	-	-	-	-	0	10	1	0	-	34	-
8.3	-	14+	10	-	-	-	13	1	1	-	-	-
9.6	VIII	15	10	14	14	I,3	12	2	3	-	-	6
* 12.4	IX	14	10	14	14	I,3	12	2	3	6+6	33	6
13.9	IX	14	10	14	14	I,3	11	0	0	-	-	6
14.0	IX	15	10	14	14	I,3	12	1	0	-	-	6
*J13.0	IX	15	10	14	14	I,3	1	2	0	6+6	34	6
J13.7	IX	15	10	14	14	I,3	1	0	0	-	-	6
J14.9	IX	14	10	14	14	I,3	1	0	0	-	-	6
J16.2	IX	15	10	14	14	I,3	1	0	0	-	-	6

* - Stained with Alizarin Red S.
J - Juvenile.

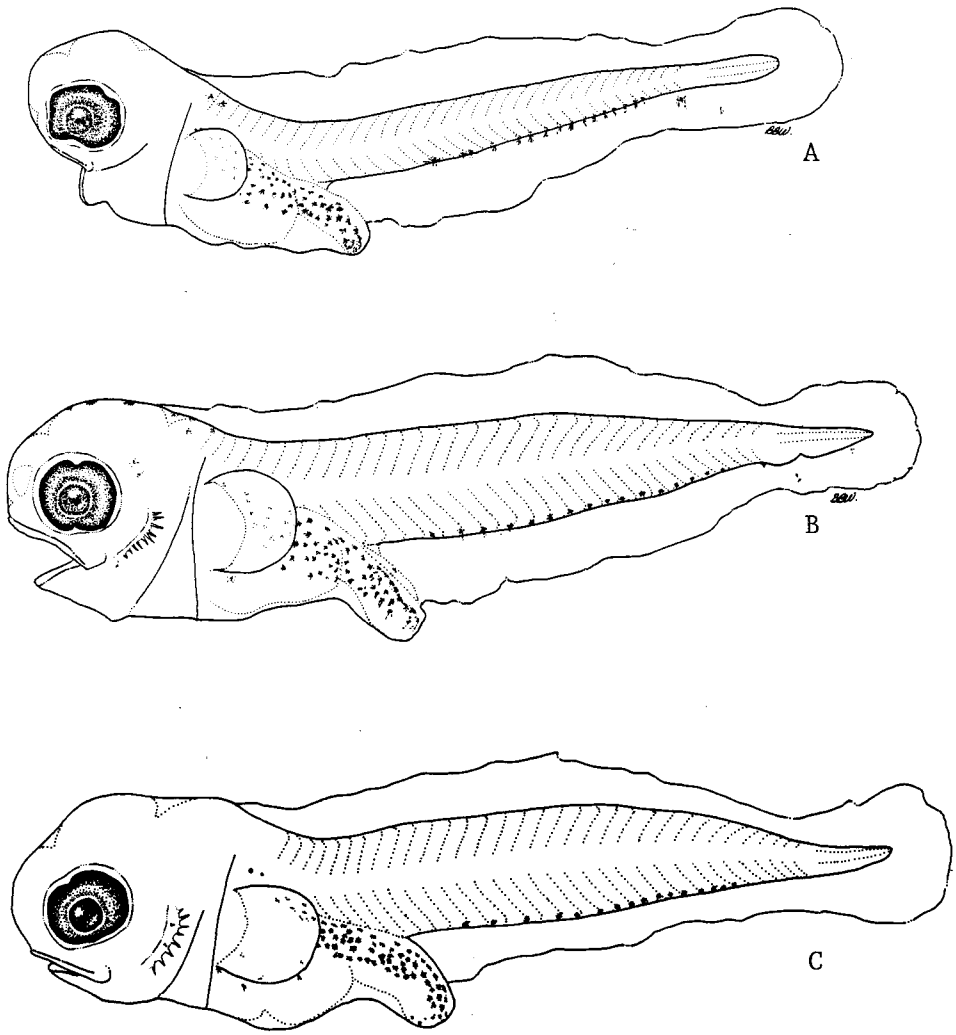

Figure 18. Larvae of Clinocottus embryum: A) 4.0 mm NL (from Richardson and Washington 1980), B) 5.4 mm NL (from Richardson and Washington 1980), C) 6.4 mm NL.

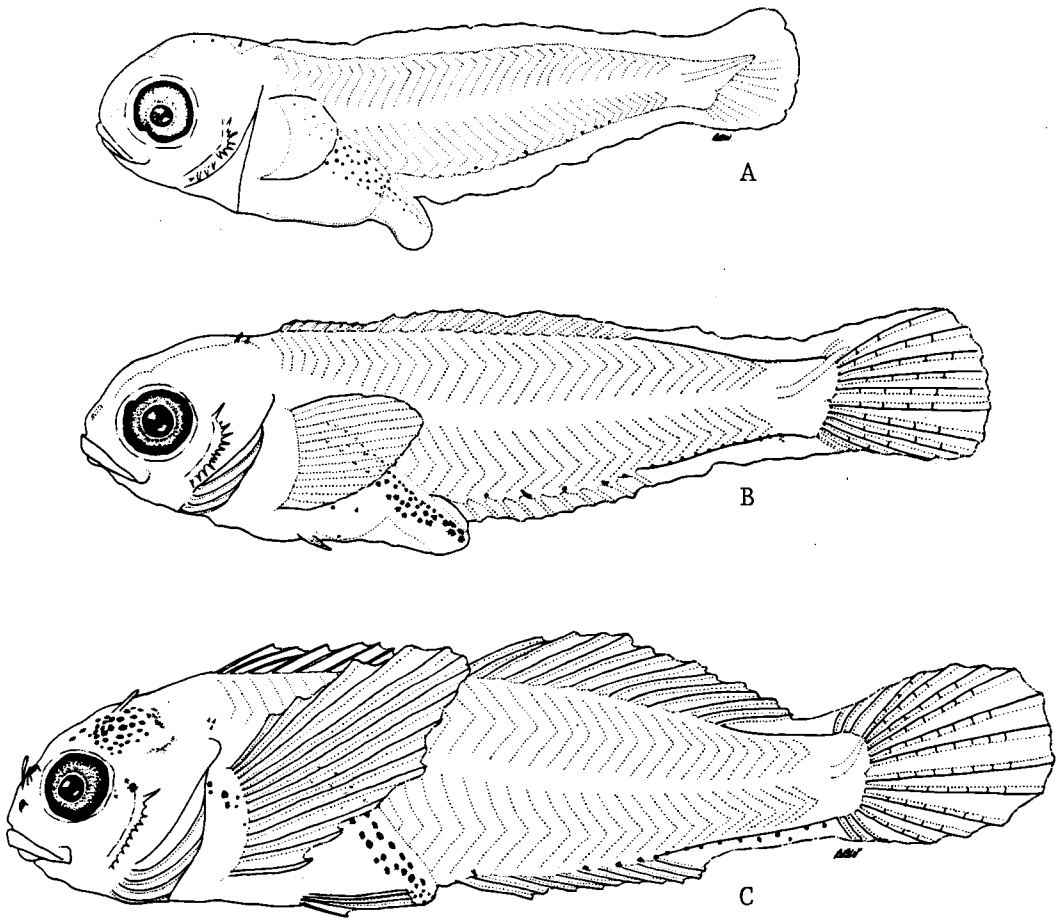

Figure 19. Larvae of Clinocottus embryum: A) 7.4 mm SL (from Richardson and Washington 1980), B) 9.6 mm SL, C) 13.9 mm SL.

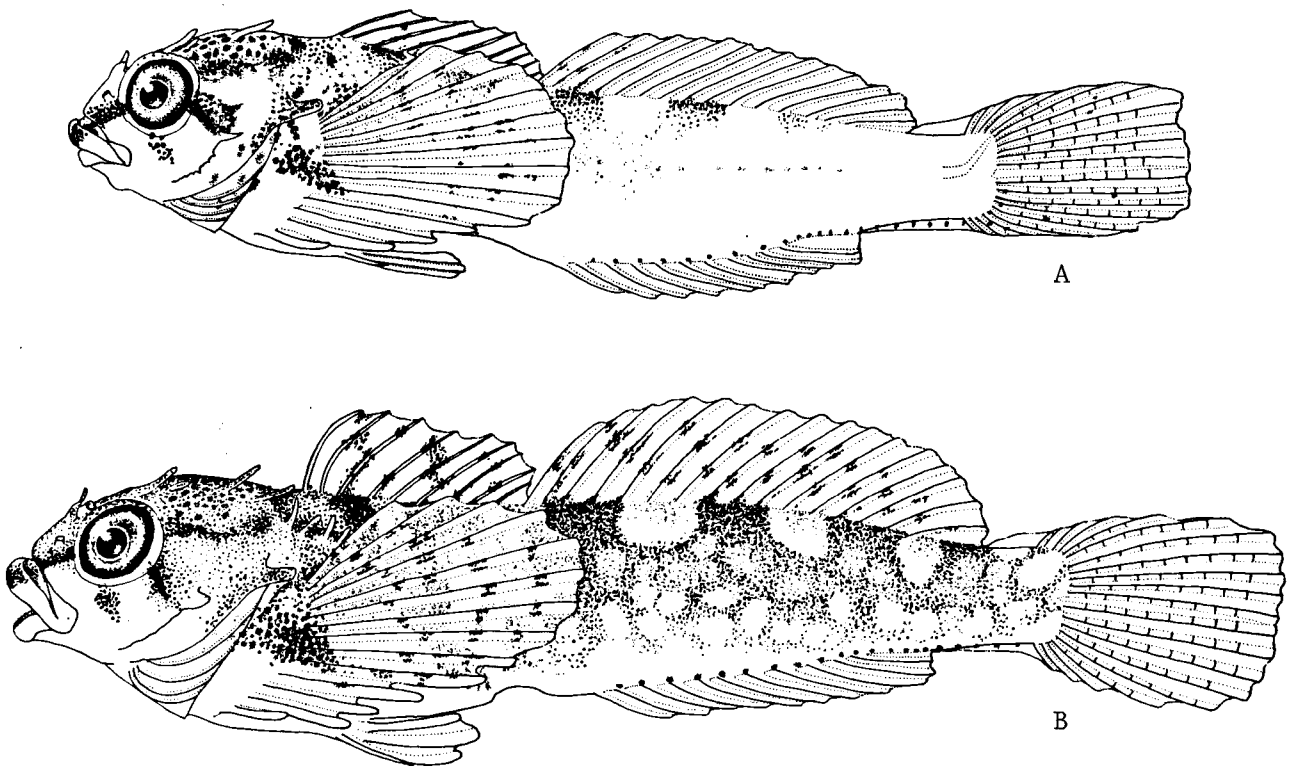

Figure 20. Juveniles of Clinocottus embryum: A) 13.7 mm SL, B) 16.2 mm SL.

Clinocottus globiceps

(Figures 21, 22, 23; Tables 21, 22, 25)

Literature

Larvae of this species were listed by Richardson (1977) and Richardson and Pearcy (1977) as Oligocottus sp. 1. Richardson and Washington (1980) described larvae of this species as Cottidae Type 3. They illustrated 6.3, 7.5, and 12.5 mm specimens.

Identification

Larvae were reared from eggs spawned from known adults. Field-collected larvae were identified through comparison with reared larvae. Identification of larvae and juveniles was further confirmed by the following characters: pigmentation, body shape, an advanced anus, and absence of a nasal cirrus.

Distinguishing Features

Preflexion and flexion larvae of C. globiceps may be distinguished from other cottid larvae, except C. recalvus and C. analis, by the presence of heavy pigmentation on the head, nape and dorsolateral surface of the gut. Larval C. globiceps are distingushed from C. recalvus and C. analis by the number (4-8) and spacing of ventral midline melanophores. Late flexion and postflexion larvae of C. globiceps differ from all other Clinocottus larvae in preopercular and parietal spination.

Transforming and juvenile C. globiceps are distinguished from other cottid larvae by the combination of a blunt, rounded snout and head, heavy pigmentation over the anterior third of the body and two or three

inconspicuous ventral midline melanophores which persist on the caudal peduncle.

Pigmentation

Newly hatched and preflexion larvae of C. globiceps have intense melanistic pigmentation on the head and nape. Eight to 11 large stellate melanophores are present over the midbrain and 21 to 30 melanophores are concentrated in the nape region. These nape melanophores are arranged in a distinctive pattern in which 7 to 10 melanophores are embedded along the dorsal midline of the nape and are surrounded anteriorly and laterally by 14 to 23 dark melanophores lying on the external surface of the nape. Eight to 10 dendritic melanophores occur on both the anterior and posterior walls of the otic capsules. The dorsolateral surface of the but is heavily pigmented with 100 to 150 large round melanophores. The only pigmentation occurring posterior to the anus is a series of four to eight discrete ventral midline melanophores. These are situated under the 10 posteriormost myomeres near the tail tip. Frequently, two to five additional small melanophores extend beyond the tail tip onto the caudal finfold.

Pigmentation changes little during larval development. The midbrain melanophores increase in number ranging from 12 to 16 in larvae >6 mm. By about 8 mm, melanophores are densely concentrated over the nape and extend anteriorly onto the head. Melanophores are added in the midbrain region and several melanophores extend anteriorly over the forebrain onto the snout. As head musculature develops, melanophores in the otic region become obscured so that only five or six melanophores are visible on the posterior wall of the otic capsule.

During transformation, in planktonic larvae 12 to 14 mm long, head pigmentation increases markedly. Several melanophores are added on the upper lip and beneath the orbit. Melanophores are also added in a row along the preopercle and on the dorsal portion of the operculum. Pigmentation over the brain intensifies and expands posteriorly, merging with the nape pigmentation. Concurrently, nape melanophores extend ventrally from the nape forming a continuous band of pigment between the nape and gut. Pigmentation also increases over the body cavity as melanophores extend ventrally over the lateral surfaces of the gut. Several melanophores also are added on the pectoral fin base. Ventral midline melanophores decrease in size and number, until only two to four inconspicuous melanophores persist beneath the caudal peduncle.

Newly settled benthic juveniles of C. globiceps are distinctively pigmented with the anterior third of the body covered with dark melanophores extending posteriorly to about a vertical through the seventh dorsal spine. Only the posterior two-thirds of the pelvic fin rays remain unpigmented. Posterior to the intense head pigment, the two to four small ventral midline melanophores constitute the only pigment. Between 14 and 16 mm SL, juvenile pigmentation is added posteriorly along the dorsum. By about 14 mm, a dark vertical bar of melanophores forms under the second to dourth dorsal fin rays and extends ventrally two-thirds of the way below the lateral midline. Between 15 and 16 mm, three additional saddles of melanophores are added posteriorly along the dorsum. The first saddle forms under the 8th to 10th dorsal fin rays, the second forms under the 14th to 15th fin rays, and the third saddle forms on the dorsal surface of the caudal peduncle. Concurrently,

melanophores are added posteriorly along the lateral midline forming a dark band of pigment at the base of the caudal fin. Several melanophores appear on the pectoral, dorsal, and caudal fin rays.

Morphology

Larval C. globiceps hatch at a relatively large size, 5.1 to 5.4 mm NL. The largest planktonic larva taken in field collections is 12.9 mm and is beginning to undergo transformation. The smallest benthic juvenile is 13.5 mm long. Thirty-eight specimens, 5.1 to 14.6 mm, were examined for developmental morphometrics. Because only 10 larvae were available from field collections, 25 laboratory-reared larvae were included in this morphometric series.

Larval C. globiceps are relatively deep-bodied with the posterior portion of the gut trailing below the rest of the body. When viewed ventrally, the hindgut bulges slightly on either side of the anus similar to, but less pronounced than the bulges in C. embryum.

Relative body depth at the pectoral fin base increases during larval development from 20.7 in preflexion larvae to 28.5% SL in transforming larvae and juveniles. Relative body depth at the anus also increases from 17.2 in preflexion larvae to 27% SL in transforming specimens.

Snout to anus length averages 43.9% SL in preflexion larvae and increases to an average of 49.8% and 52% SL in postflexion and juveniles, respectively. Distance from snout to pelvic fin origin and pelvic fin origin to the anus remain fairly constant in postflexion larvae, averaging 26% SL and 22.5% SL, respectively. However, distance from the snout to the pelvic fin origin increases markedly to 31% in benthic juveniles

while distance from pelvic fin origin to the anus decreases to 20% SL. These changes correspond with anterior movement of the anus in transforming juveniles.

Larval C. globiceps have a notably blunt, rounded head and snout in contrast to the slightly pointed snouts of C. embryum and C. acuticeps. Relative head length increases from 17.0 in preflexion larvae to about 31% SL in transforming juveniles. Snout length also increases from 21% in preflexion to 25% HL in both flexion and postflexion larvae. Eye diameter and jaw length decrease from an average of 50 and 52% to 38 and 30% HL, respectively, during larval development.

Fin Development

The smallest larva beginning to undergo flexion of the notochord is 6.2 mm long. Notochord flexion is complete in larvae between 7.5 and 8.0 mm long. Although caudal rays are present in late flexion stage larvae (7.0-7.5 mm NL), the adult complement of 6+6 principal caudal rays is not countable until the completion of flexion at 7.4 mm.

Dorsal and anal fin bases are just beginning to form at completion of notochord flexion. The full complement of dorsal and anal fin rays is complete at ∿9.5 mm. The dorsal spines are completely formed at ∿10 mm. Development of the pectoral fin corresponds to that of the dorsal and anal fins. Pectoral fin rays are visible on a 7.5 mm larva. The adult complement of rays is fully formed by ∿9 to 9.5 mm. Pelvic fin buds are first visible in larvae between 6.5 and 7 mm long. The adult complement (I,3) is present between 9.5 and 10 mm.

Spination

Preopercular spines first appear as seven to nine small bumps along the posterior margin of the preopercle in 5.5 to 6 mm larvae. Larvae undergoing notochord flexion have 9 to 14 small, evenly spaced spines along the preopercular margin. During postflexion, spines increase in number from 16 to 22 and the dorsalmost spine becomes separated from the rest of the preopercular spines by a short gap. Simultaneously, this dorsalmost spine becomes longer and stouter than the other preopercular spines. In the largest planktonic larvae (12.5 mm SL) this dorsalmost spine is about 2.5 times as long as the other spines. The lower preopercular spines decrease in size and number during transformation. The uppermost spine continues to become longer and stouter in benthic juveniles and is over four times as long as the lower spines in a 14.5 mm specimen. The other preopercular spines are reduced to small bumps or serrations along the lower preopercular margin. In a 17 mm juvenile all remnants of the lower spines have disappeared and only the large dorsal spine persists.

Clusters of spines develop on the head in the parietal region of C. globiceps larvae. One tiny spine is visible on each side of the head in 6 to 7 mm larvae and two spines are present on each side of the head in 7 to 8 mm larvae. By ~9 to 10 mm, five to six spines are present on each side of the head, arranged in a parallel pair of rows with two to three spines in the anterior row and three spines in the posterior row. These spines persist in the largest planktonic specimens examined, 12,9 mm. However, they appear reduced in newly settled benthic juveniles and are present only as bony protruberances situated at the posterior margin of

the parietals. Each protruberance has a hollow canal running through it which eventually forms the incipient cranial lateral line system in the parietal region of the head.

Similar spine clusters also form in the supracleithral-posttemporal region. One or two small spines are first visible in larvae ∿9 mm long. Five or six spines, arranged in two rows of three spines each, are present in both 12 mm specimens. These spines eventually become associated with the lateral line system in benthic juveniles.

Table 21. Measurements (mm) of young Clinocottus globiceps. (specimens between dashed lines are undergoing notochord flexion.)

	Body length	Head length	Snout length	Eye diam	Snout to anua length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic-fin origin	Pelvic fin origin to anua	Pectoral fin length
	5.1	1.1	0.27	0.53	2.7	1.3	1.0	-	-	0.49
L	5.2	1.3	0.32	0.60	2.5	1.3	1.1	-	-	0.64
L	5.3	0.90	0.24	0.56	2.3	1.0	0.96	-	-	0.68
L	5.3	0.96	0.16	0.56	2.1	0.84	0.72	-	-	0.56
L	5.4	1.0	0.20	0.56	2.3	1.1	0.92	-	-	0.64
L	5.5	1.1	0.16	0.60	2.4	1.1	0.92	-	-	0.76
L	5.6	1.1	0.16	0.76	2.4	1.0	0.92	-	-	0.72
L	5.7	1.2	0.24	0.64	2.4	1.2	1.0	-	-	0.64
L	5.8	1.2	0.28	0.68	2.5	1.3	0.84	-	-	0.76
L	5.9	1.2	0.24	0.64	2.5	1.1	1.1	-	-	0.76
L	5.9	1.3	0.32	0.64	2.4	1.2	0.92	-	-	0.68
L	6.5	1.5	0.40	0.68	3.0	1.5	1.4	-	-	0.84
L	6.2	1.4	0.28	0.72	2.8	1.4	1.1	-	-	0.72
	6.2	1.3	0.34	0.53	2.8	1.4	1.1	-	-	0.53
	6.2	1.4	0.38	0.53	3.1	1.4	1.3	-	-	0.64
	6.3	1.4	0.31	0.62	3.0	1.4	-	-	-	0.57
	6.4	1.4	0.38	0.57	3.2	1.5	1.4	-	-	0.65
	6.5	1.4	0.38	0.53	3.3	1.5	1.5	-	-	0.57
L	6.6	1.5	0.32	0.76	3.0	1.5	1.4	1.6	1.4	0.76
L	7.2	1.6	0.44	0.76	3.2	1.8	1.6	1.6	1.6	1.1
L	7.5	1.7	0.48	0.84	3.5	1.8	1.8	2.1	1.4	1.2
	7.5	1.9	0.58	0.74	4.2	2.2	2.0	2.4	1.8	0.96
L	7.6	1.7	0.40	0.84	3.4	1.8	1.6	1.8	1.6	0.84
L	7.7	1.9	0.44	0.88	3.7	1.8	1.6	1.9	1.8	1.1
	8.1	2.2	0.60	0.84	4.0	2.1	1.8	2.2	1.8	1.8
L	8.4	2.0	0.40	0.92	4.0	2.1	2.0	2.2	1.8	1.4
L	8.7	2.0	0.44	0.92	4.1	2.2	2.0	2.1	2.0	1.5
L	9.2	2.2	0.60	0.96	4.6	2.5	2.3	2.5	2.1	1.8
	9.3	2.3	0.58	0.92	4.9	2.6	2.5	2.6	2.3	1.9
L	9.5	2.5	0.56	1.0	4.7	2.4	2.3	2.5	2.3	2.0
L	10.0	3.2	0.64	1.1	5.0	2.5	2.3	2.8	2.2	3.0
L	10.2	2.7	0.60	1.1	4.9	2.6	2.8	2.6	2.3	2.6
L	10.2	3.1	0.76	1.1	5.1	3.1	2.7	2.6	2.5	3.1
	12.3	4.1	1.3	1.0	6.8	3.8	3.8	3.6	3.2	3.2
J	13.7	4.4	1.2	1.2	7.1	3.8	3.7	4.3	2.8	4.0
J	13.8	4.3	1.2	1.2	7.2	3.8	3.7	4.3	2.7	4.1
J	14.6	4.6	1.2	1.2	7.2	3.9	3.4	4.3	2.9	4.1

J - Juvenile.
L - Laboratory reared.

Table 22. Meristics and spines of young Clinocottus globiceps. (Only specimens with meristic elements formed are included. See Table 21 for complete developmental series examined.)

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preoper-cular spines	Parietal spines	Post-temporal spines	Principal caudal rays	Verte-brae	Branchio-stegal rays
* 6.4	-	-	-	-	-	-	-	-	-	-	34	5
6.5	-	-	-	-	-	-	-	-	-	-	-	-
L 6.6	-	-	-	-	-	-	-	-	-	-	-	-
L 7.2	-	-	-	-	-	-	-	-	-	-	-	-
*L 7.5	IX	16	11b	14	14	-	22	22	-	6+6	33	7
7.5	-	-	-	-	-	-	18	18	-	-	-	-
L 7.6	-	-	-	-	-	buds	10	10	-	-	-	-
L 7.7	-	-	-	-	-	buds	16	16	-	-	-	-
8.1	-	15b	10b	14	13?	buds	15	3	-	-	-	-
L 8.4	VIII	14	13	12+	12+	I,3	16	2	-	-	-	-
L 8.7	VIII	16	12	14	13	I,3	15	3	-	-	-	-
L 9.2	IX	16	11?	13+	13+	I,3	19	5	-	-	-	-
*L 9.5	IX	16	13	14	14	I,3	11	-	-	6+6	34	6
L10.0	IX	16	13	14	14	I,3	11	-	-	-	-	-
L10.2	IX	17	13	14	14	I,3	14	-	-	-	-	-
L10.2	IX	16	12	14	13	I,3	13	-	-	-	-	-
* 12.3	IX	16	10	14	14	I,3	12	5	-	-	-	-
12.5	IX	15	12	14	14	I,3	-	5	-	-	-	-
13.7	IX	16	10	15	14	I,3	-	-	-	-	-	-
* 13.8	IX	16	12	14	14	I,3	1	-	-	6+6	33	6
14.6	IX	16	12	14	14	I,3	-	-	-	-	-	-

* - Stained with Alizarin Red S.
L - Laboratory reared.
b - Bases.

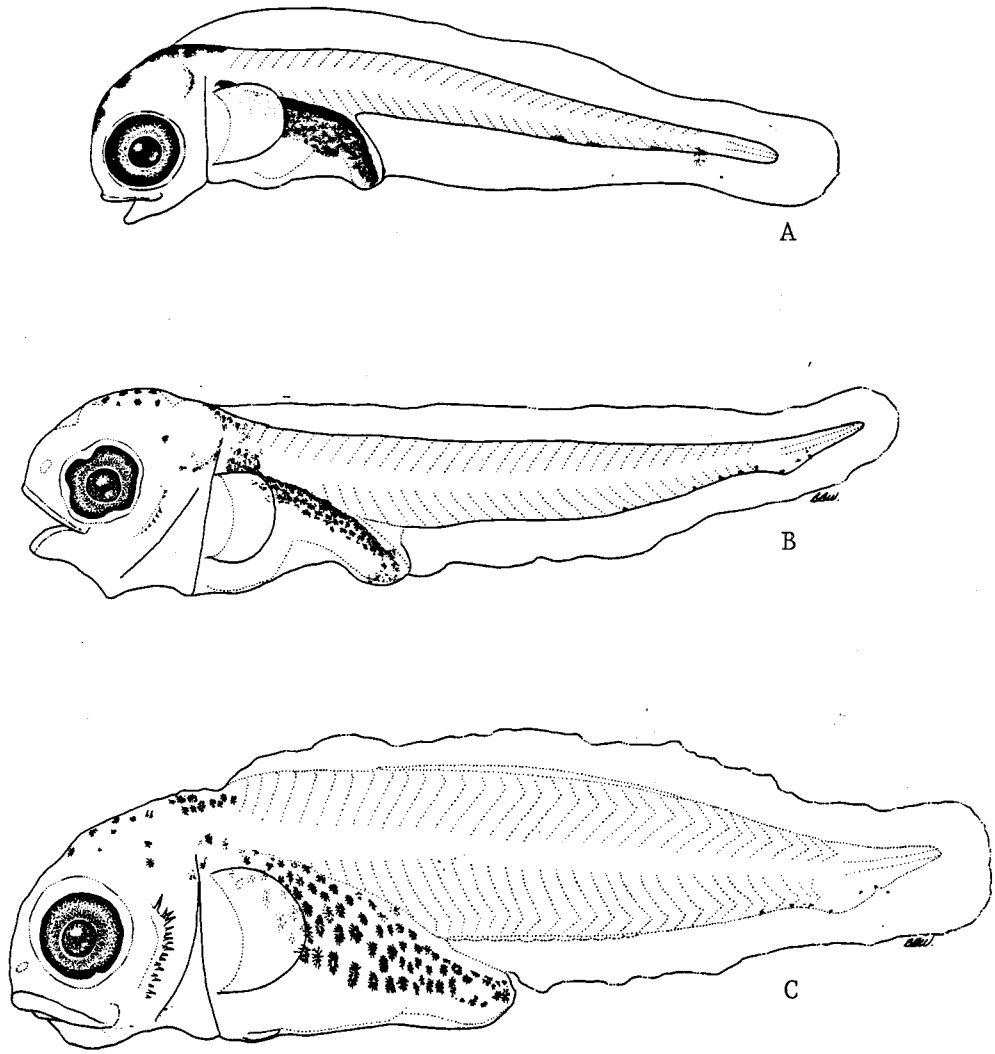

Figure 21. Larvae of Clinocottus globiceps: A) 5.0 mm NL, B) 6.3 mm NL (from Richardson and Washington 1980), C) 7.5 mm NL (from Richardson and Washington 1980).

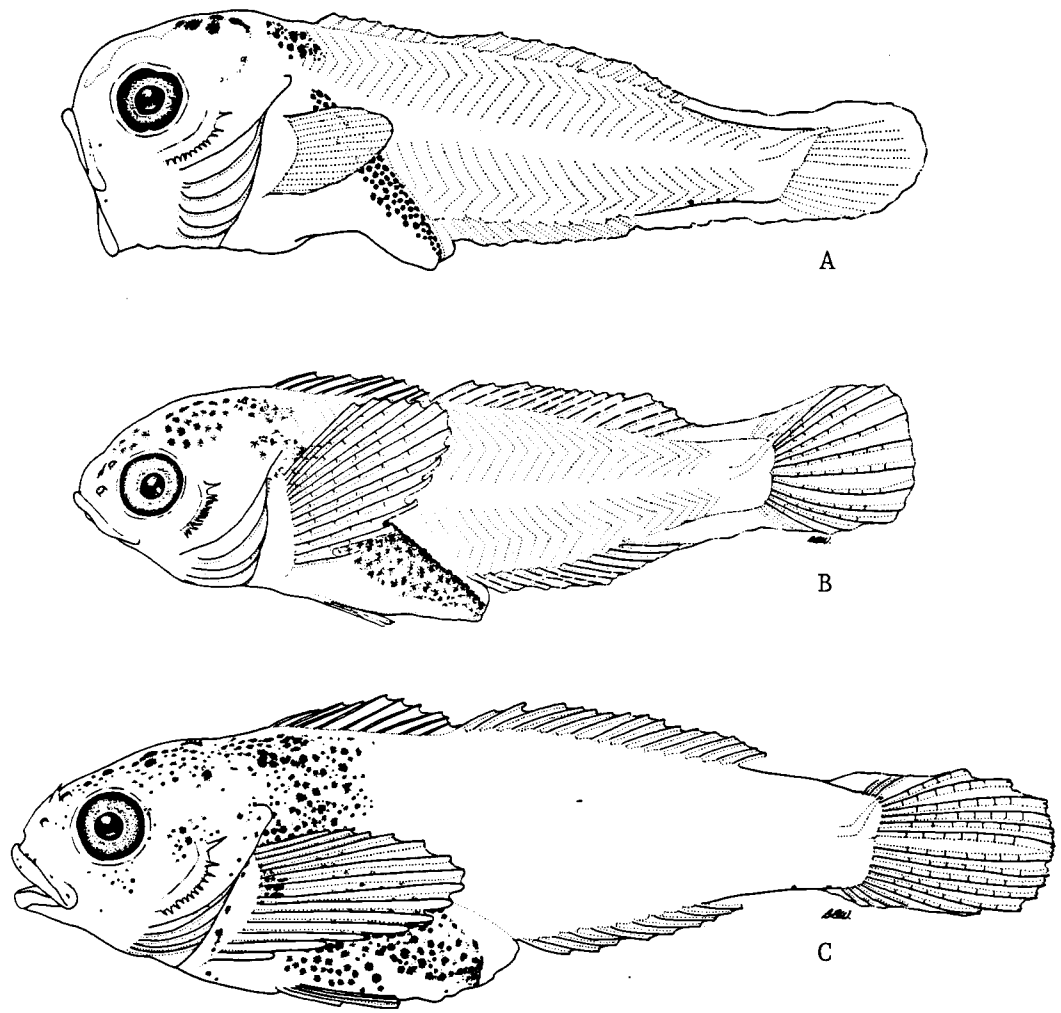

Figure 22. Larvae of Clinocottus globiceps: A) 8.5 mm SL, B) 12.5 mm SL (from Richardson and Washington 1980), C) 12.9 mm SL.

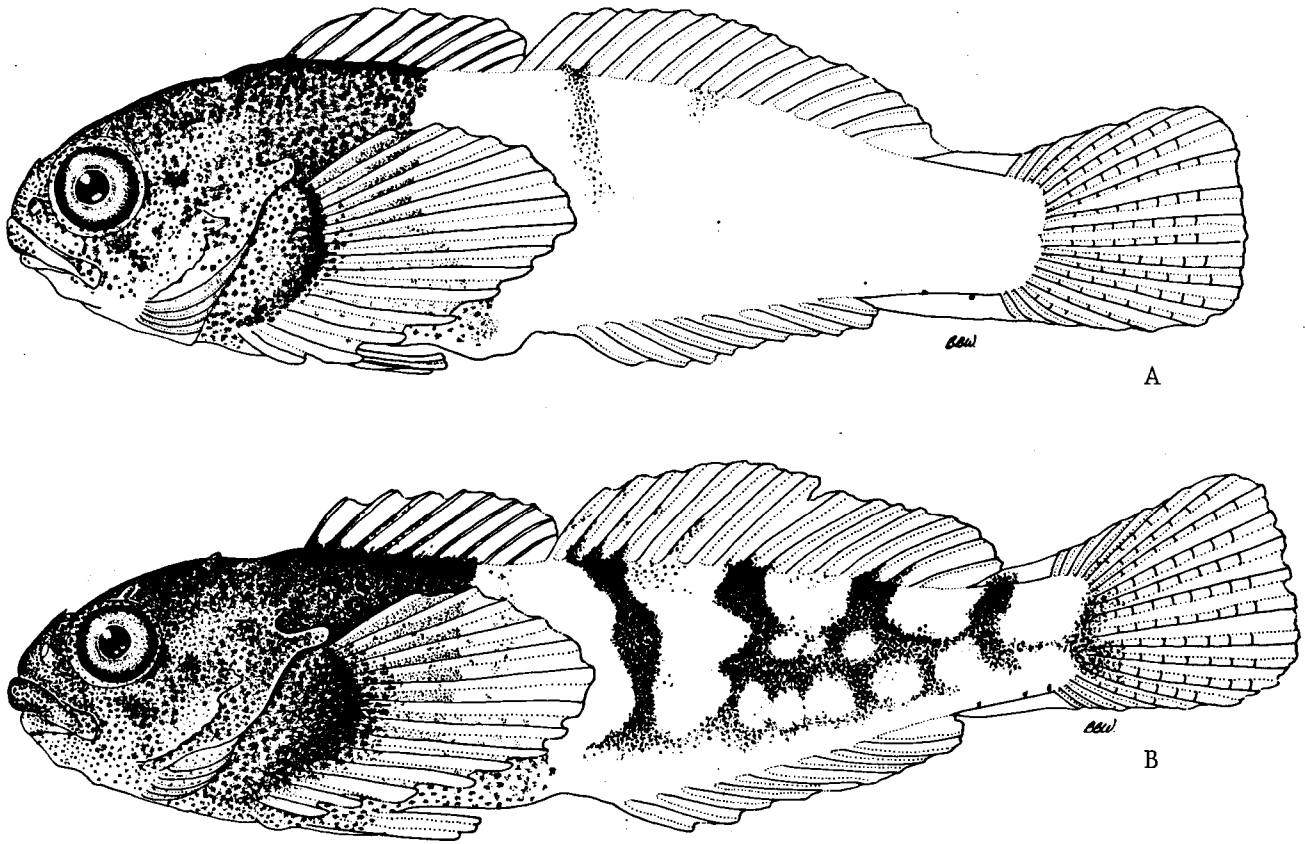

Figure 23. Juveniles of Clinocottus globiceps: A) 13.7 mm SL, B) 14.6 mm SL.

Clinocottus analis

(Figure 24; Tables 23, 24, 25)

Literature

Eigenmann (1892) and Budd (1940) briefly described and illustrated 4 mm specimens of C. analis.

Identification

Juveniles and adults were identified by the following combination of characters: an advanced anus, cirri, head shape, and pigmentation. Pigmentation, preopercular spination, and body shape linked postflexion larvae of C. analis with juveniles and adults.

Distinguishing Features

Late postflexion and transforming specimens of C. analis were identified in collections from southern California. Apart from the two descriptions of newly hatched larvae, intermediate larval stages of C. analis are unknown. A brief diagnosis of postflexion larval C. analis is presented in hope that this information may facilitate the identification of a complete developmental series of C. analis.

Eleven postflexion larval C. analis were examined for developmental morphology, pigmentation, and spination. Clinocottus analis postflexion larvae may be distinguished from all other larvae belonging to the Artedius, Clinocottus, Oligocottus group by the intense band of melanistic pigmentation on the lateral body surface between the bases of the second dorsal and anal fins. Intense melanophores are also present on the dorsolateral surface of the head, the snout, the tips of the lips, and

on the operculum. A patch of melanophores is present on the pectoral fin base and in a band on the dorsum beneath the spinous dorsal fin. Sixteen to 22 small, round melanophores are situated on the ventral midline posterior to the anus.

Postflexion larval C. analis have blunt, rounded snouts and relatively large heads. Snout length and head length are 28% HL and 30% SL, respectively, longer than in other Clinocottus larvae. In addition, C. analis larvae have moderately long, bulging guts. Snout to anus length averages 49% SL in postflexion larvae. Body depth at the pectoral fin base is 28% SL, while body depth at the anus is 26% SL.

Six to 11 spines are present on the posterior margin of the preopercle. The dorsalmost spine is longer and stouter than the other spines. In the smallest specimens, 9.9 to 11.0, the spines are situated in two groups of three to five spines. The ventralmost spines begin to regress in larvae ≥11 mm long, and decrease in size and number and gradually become covered by skin. Two small spines are also present in the parietal region of the head in the 9.9 mm specimen. These spines decrease in size and remain only as bony bumps by ∿11 mm.

Table 23. Measurements (mm) of young *Clinocottus analis*.

Body length	Head length	Snout length	Eye diam	Snout to anus length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
9.9	2.9	0.76	0.92	5.0	2.8	2.6	3.0	2.0	3.0
10.5	3.2	0.88	1.0	5.7	3.0	3.0	3.1	2.6	3.1
10.5	3.1	0.92	1.0	5.1	3.0	3.0	3.3	1.8	3.4
10.5	3.2	0.92	1.0	5.2	2.8	2.6	3.1	2.1	3.1
10.9	3.0	0.92	1.0	5.1	2.9	2.7	3.2	1.9	3.2
11.0	3.3	0.96	1.1	5.7	2.8	2.8	3.4	2.3	3.4
11.0	3.3	0.72	1.0	5.5	3.0	2.9	3.1	2.4	2.8
11.2	3.2	0.92	1.0	5.3	3.2	2.9	3.1	2.2	3.1
11.2	3.5	0.96	1.1	5.3	3.1	3.0	3.2	2.1	3.5
11.4	3.6	1.0	1.1	5.3	3.0	2.8	3.1	2.2	3.4
11.4	3.6	0.92	1.0	5.6	3.3	3.1	3.1	2.4	3.6

Table 24. Meristics and spines of young Clinocottus analis.

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preoper-cular spines	Parietal spines	Post-temporal spines	Principal caudal rays	Verte-brae	Branchio-stegal rays
9.9	IX	16	14	15	16	I,3	11	2	-	6+6	-	6
10.5	IX	15	12	15	15	I,3	10	1	-	6+6	-	6
10.5	IX	16	12	15	14	I,3	8	-	-	6+6	-	6
10.5	IX	15	13	15	15	I,3	6	-	-	6+6	-	6
10.9	IX	15	12	15	15	I,3	10	-	-	6+6	-	6
11.0	IX	16	13	15	15	I,3	9	-	-	6+6	-	6
11.0	VIII	15	12	15	15	I,3	11	-	-	6+6	-	6
11.2	IX	15	11	15	15	I,3	9	-	-	6+6	-	6
*11.2	IX	15	12	15	15	I,3	8	1	-	6+6	34	6
11.4	IX	15	12	15	15	I,3	6	-	-	6+6	-	6
11.4	IX	16	12	15	15	I,3	7	-	-	6+6	-	6

* - Stained with Alizarin Red S.

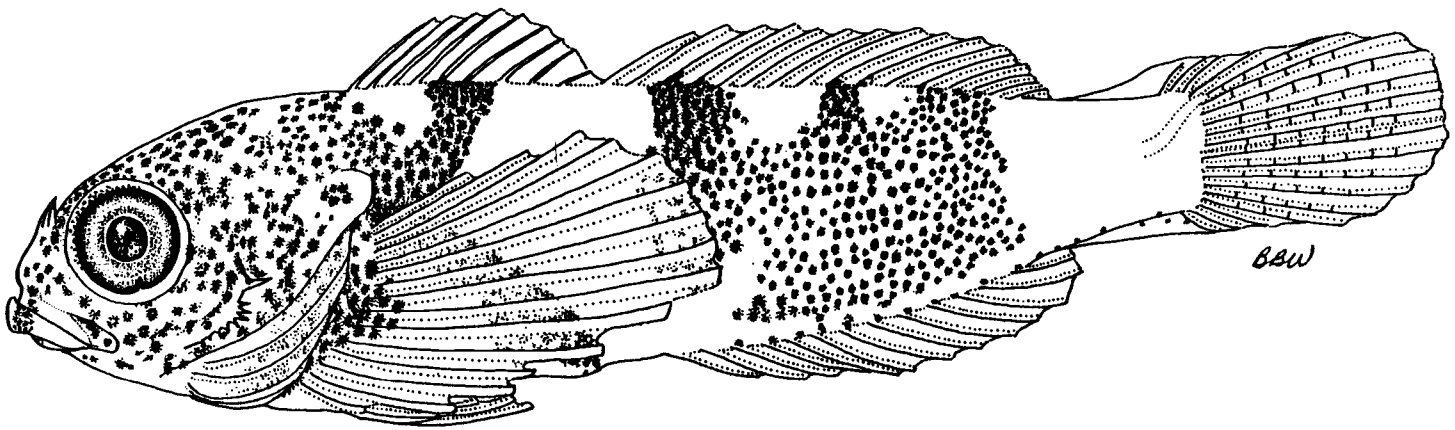

Figure 24. Young of Clinocottus analis: 10.5 mm SL.

Table 25. Body proportions of larvae and juveniles of Clinocottus acuticeps, C. embryum, C. globiceps, and C. analis. Values given are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. (Number of specimens measured may be derived from Tables 17, 19, 21, and 23.)

Item	Clinocottus acuticeps	Clinocottus embryum	Clinocottus globiceps	Clinocottus analis
Head length/SL:				
Preflexion	27.1±3.44(22.3-30.1)	26.1±2.65(26.0-30.1)	20.6±2.21(17.0-25.0)	-
Flexion	29.2±1.92(26.8-32.4)	23.9±1.15(21.8-25.3)	23.0±1.79(21.0-27.2)	-
Postflexion	27.9±2.71(22.9-32.6)	24.0±0.00(24.0-24.0)	27.3±4.09(22.4-33.3)	30.1±1.25(17.8-32.1)
Juvenile	32.2±0.65(31.5-32.7)	31.5±1.13(30.2-32.2)	31.6±0.46(31.2-32.1)	-
Snout length/HL:				
Preflexion	24.6±4.80(21.3-25.9)	21.3±1.53(19.9-23.7)	21.3±4.40(14.5-26.7)	-
Flexion	26.4±2.97(22.9-30.6)	24.1±3.83(18.4-30.8)	25.7±3.39(20.0-30.5)	-
Postflexion	23.6±4.38(16.3-30.9)	22.2±0.58(21.8-23.6)	25.3±4.84(20.0-33.0)	28.3±2.70(22.3-32.2)
Juvenile	27.5±4.36(26.8-29.4)	27.5±1.47(22.7-31.2)	27.1±0.92(26.1-27.9)	-
Eye diameter/HL:				
Preflexion	39.7±6.63(31.5-54.2)	39.3±3.06(35.8-42.1)	50.4±9.16(46.2-63.1)	-
Flexion	34.6±2.41(31.9-36.4)	35.7±3.79(34.8-39.5)	43.7±7.39(37.9-51.4)	-
Postflexion	32.7±3.30(27.1-38.2)	32.1±3.06(29.0-35.3)	38.2±8.09(24.4-46.0)	31.3±1.41(27.8-33.0)
Juvenile	27.9±2.06(25.5-29.3)	29.8±0.74(29.2-30.6)	27.1±0.91(26.1-27.9)	-
Snout to anus length/SL:				
Preflexion	60.7±4.64(54.4-67.2)	51.6±3.51(48.2-55.1)	44.0±3.59(39.6-52.9)	-
Flexion	62.8±2.74(60.3-67.1)	49.9±3.87(43.9-54.4)	48.2±3.27(44.4-56.0)	-
Postflexion	62.5±4.61(57.5-70.3)	0.0±3.06(47.3-53.8)	50.0±3.48(44.7-56.8)	48.9±2.40(46.4-54.3)
Juvenile	50.2±1.64(48.4-51.6)	49.0±3.10(47.0-52.6)	-	-
Snout to pelvic fin origin/SL:				
Preflexion	-	-	-	-
Flexion	-	28.0*	24.6±2.94(21.4-28.0)	-
Postflexion	33.4±2.63(29.4-39.5)	32.1±3.54(29.0-34.2)	26.7±2.33(23.4-30.9)	29.3±1.34(27.2-31.4)
Juvenile	33.3±1.16(32.5-34.6)	31.1±1.31(29.6-32.1)	30.7±1.04(20.0-21.2)	-
Pelvic fin origin to anus/SL:				
Preflexion	-	-	-	-
Flexion	-	26.1*	21.5±1.77(18.7-23.4)	-
Postflexion	29.4±4.56(23.1-37.3)	18.2±0.71(17.1-18.4)	22.9±1.42(21.4-25.2)	19.9±2.26(17.3-22.5)
Juvenile	16.9±1.70(15.9-18.9)	17.9±2.50(15.4-20.4)	20.7±0.64(29.5-31.4)	-
Body depth at pectoral fin base/SL:				
Preflexion	24.3±3.25(17.8-29.1)	25.8±4.36(21.2-29.4)	20.8±2.87(15.8-25.5)	-
Flexion	27.6±2.30(24.3-30.2)	26.3±2.29(23.7-30.2)	23.9±2.02(22.2-29.3)	-
Postflexion	31.3±2.29(28.4-35.0)	26.1±1.53(25.0-28.2)	26.8±2.78(22.1-30.9)	28.1±1.36(25.4-29.1)
Juvenile	26.1±1.99(23.9-27.8)	21.6±1.01(23.5-25.5)	27.3±0.53(26.7-27.7)	-
Body depth at anus/SL:				
Preflexion	21.4±2.94(18.0-24.5)	22.8±4.36(18.2-26.5)	17.5±2.46(13.6-21.6)	-
Flexion	25.4±2.07(23.3-28.1)	25.1±1.51(22.9-27.3)	21.2±2.07(17.7-24.0)	-
Postflexion	28.4±2.43(26.4-35.2)	27.0±0.00(27.0-27.0)	25.7±3.04(21.1-30.4)	25.7±1.50(25.0-29.1)
Juvenile	24.0±2.28(21.4-25.4)	23.3±1.93(22.1-25.5)	25.7±2.08(23.3-27.0)	-
Pectoral fin length/SL:				
Preflexion	11.4±1.27(9.6-13.3)	9.9±3.46(6.3-12.1)	12.1±1.19(9.6-13.8)	-
Flexion	11.0±1.87(9.9-14.5)	11.2±2.75(7.1-17.5)	12.3±4.40(7.5-22.0)	-
Postflexion	26.4±5.95(18.2-35.0)	32.0±4.04(30.1-37.0)	22.7±6.00(11.1-30.4)	29.3±2.15(24.8-32.3)
Juvenile	32.1±1.74(30.8-34.1)	33.4±1.16(32.1-34.2)	29.0±0.82(28.1-29.7)	-

- = Not present at this stage.
* = Only specimen available in this stage.

Artedius creaseri

(Figures 25, 26; Tables 26, 27, 30)

Literature

Larval Artedius creaseri have not been previously described.

Identification

Juveniles and adults were identified by the following combination of characters: low dorsal fin ray (12-14) and anal fin ray (9-10) counts. low vertebral counts (30-31), scales extending onto head under the orbit and on the snout, and the presence of a preorbital cirrus. The developmental series was linked together primarily by preopercular and parietal spination, pigmentation, body shape, and meristics. Postflexion and transforming larvae were linked to juveniles by the cirri pattern, pigmentation, body shape, and meristics.

Distinguishing Features

Preflexion larvae of A. creaseri are characterized by a pointed snout, large head, and relatively deep body. Distinguishing pigmentation includes intense large, round melanophores covering the dorsolateral surface of the gut, one to three large melanophores at the anteroventral margin of the gut, and a series of 7 to 11 large, evenly spaced melanophores along the ventral midline posterior to the anus. A large distinctive, blotch-like melanophore is located on the ventral finfold near the taip tip, and another smaller melanophore occurs just beneath the tail tip.

Larvae of A. creaseri ≤7 mm are further distinguished by the presence of four large, evenly spaced preopercular spines and a prominent parietal and nuchal spine. Late postflexion larvae may be recognized by their pointed snout and long jaw, large head, and the characteristic ventral midline pigmentation. In addition, meristics, especially the low dorsal fin, anal fin, and vertebral counts are diagnostic of this species. Small juveniles possess a long, slender nasal cirrus, a broad, ribbon-like postorbital cirrus with a fringed tip, and two pairs of frontoparietal cirri.

Pigmentation

Small preflexion larvae of A. creaseri are relatively lightly pigmented. They possess no melanistic pigmentation on either the head or the nape. Pigmentation over the dorsolateral surface of the gut is heavy and intense. Melanophores are large, round, and closely packed together. One or two melanophores are present on the ventral surface of the gut lying just posterior to the cleithrum. Posterior to the anus, the sole pigmentation consists of a series of 7 to 11 large, rounded melanophores evenly spaced along the ventral midline, positioned approximately one to every three myomeres. This series originates under the third or fourth postanal myomere and extends posteriorly toward the tail tip. The posteriormost one or two melanophores in this series lie on the ventral finfold and are notable large and blotch-like.

Pigmentation increases markedly during larval development. Two melanophores form over the midbrain in larvae ≤5.7 mm. During flexion, melanophores increase in number and extend anteriorly onto the forebrain. By ∿8.0 mm, the dorsal surface of the head is entirely pigmented.

Pigmentation extends dorsally along the anterior wall of the gut so that three or four large melanophores lie just posterior to the cleithrum. Several melanophores form at the posterior margin of the gut in larvae >6 mm, frequently forming a ring around the anus. The number of postanal ventral midline melanophores ranges from 6 to 12, and the fourth or fifth melanophore in the series increases markedly in size and extends below the body wall onto the ventral finfold. The posteriormost two melanophores in the series move up onto the base of the caudal finfold. One is positioned just posterior to the lower hypural plate and the other lies just below the tip of the notochord at the dorsal base of the upper hypural plate.

Transforming larvae, >10 mm, have melanophores extending ventrally along the preopercle and opercle and two to four melanophores on the lower jaw. Pigment is also added on the pectoral fin.

Morphology

The smallest larval A. creaseri examined is 3.5 mm NL and recently hatched. The largest planktonic specimen is 13 mm and beginning to develop juvenile pigmentation. The smallest benthic juvenile is 13.5 mm and still undergoing transformation. Thirty-two specimens ranging from 3.5 to 13.6 mm were measured for developmental morphology.

Artedius creaseri larvae are relatively deep-bodied with a stubby shape. Body depth at the pectoral fin base averages 26% in preflexion larvae and increases to 29% SL in postflexion larvae. Relative body depth at the anus also increases during development from an average of 22% in preflexion larvae to 29% SL in postflexion larvae. Snout to anus length increases markedly from 44.5% in preflexion larvae to

51.3% SL in postflexion larvae. Distance from the snout to the origin of the pelvic fin averages 29.4% and the distance from the origin of the pelvic fins to the anus averages 24.6% SL.

Larvae of A. creaseri have a large head with a distinctive pointed snout and large mouth. Relative head length averages about 25% in preflexion and flexion larvae and increases to 33% SL in postflexion larvae. Snout length remains 30% HL during larval development while jaw length increases from 50.7% in flexion larvae to 55% HL in postflexion larvae. In contrast, eye diameter decreases from 42% in preflexion larvae to 33% HL in postflexion larvae.

Fin Development

Initiation of a thickening in the hypural region of the developing caudal fin is first evident at 5.7 mm, coincident with the onset of notochord flexion. Caudal rays are present at 6.4 mm, but the adult complement of principal caudal rays is not present until larvae reach ∿8.0 mm.

Bases of the second dorsal and anal fins are countable in larvae ∿7 to 8 mm long, and fin rays are formed between 9 and 10 mm. The adult complement of dorsal fin spines is first countable at 9.7 mm. Pectoral fin rays begin forming at ∿7 to 8 mm, and the adult complement is present at 8.6 mm. Pelvic buds begin to form at ≳8 mm, however, the adult complement of rays is not present until larvae are ≳11 mm.

Spination

Artedius creaseri larvae develop prominent head spines. In contrast to Artedius, Clinocottus, and Oligocottus larvae which have multiple

preopercular spines, A. creaseri larvae develop four equal-sized preopercular spines. Two spines develop first on the posterior margin of the preopercle at ≤5.7 mm. Between ∿6.4 and 7 mm, two additional spines develop, one dorsal and one ventral to the original two spines. The middle two spines remain slightly longer than the outer two throughout larval development. These spines persist through transformation and are present in juveniles. In larvae ≤10 mm, small basal spines or projections form on the base of each of the four main preopercular spines. With development, four bony ridges form on the inner shelf of the preopercle parallel to each basal spine. These ridges grow toward the basal spines and gradually fuse with them forming bony arches over the incipient lateral line canal of the preopercle. Prominent spines also form in the parietal region of the head. A single, parietal spine is first visible at 5.7 mm. By ≥9 mm, a second smaller parietal spine forms just posterior to the first. These spines are quite large and distinctive and they are present in the largest planktonic larvae, ≤13 mm long.

When larvae reach ∿8 mm, a spine forms in the supracleithral-posttemporal region. The supracleithral spine points dorsolaterally. A second supracleithral spine forms just ventral to the first and points dorsally. Larvae ≤9.5 mm form one posttemporal spine. These spines persist in the largest planktonic larvae, 13.6 mm, but regress in young juveniles becoming incorporated into the developing lateral line canal system.

Table 26. Measurements (mm) of young Artedius creaseri. (Specimens between dashed lines are undergoing notochord flexion.)

Body length	Head length	Snout length	Eye diam	Snout to anus length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
3.5	0.88	0.22	0.36	1.5	0.82	0.68	-	-	-
3.7	0.98	0.28	0.34	1.6	1.1	0.74	-	-	-
4.1	0.94	0.28	0.42	1.7	1.0	0.88	-	-	0.42
4.6	1.1	0.34	0.52	2.1	1.2	1.0	-	-	0.49
4.6	1.1	0.34	0.88	2.3	1.3	1.2	-	-	0.46
5.0	1.2	0.40	0.48	2.2	1.2	1.1	-	-	0.52
5.7	1.3	0.48	0.48	2.3	1.5	1.1	-	-	0.72
5.7	1.3	0.52	0.56	2.4	1.6	1.4	-	-	0.68
6.3	1.8	0.56	0.64	3.1	1.7	1.6	-	-	0.88
6.4	1.7	0.50	0.62	3.2	-	1.8	-	-	0.61
6.5	1.6	0.48	0.52	2.6	1.6	1.5	-	-	0.68
6.6	1.7	0.60	0.60	2.8	1.5	1.3	-	-	0.84
7.1	2.0	0.54	0.74	3.3	1.9	1.8	-	-	1.1
7.3	2.1	0.56	0.84	3.2	2.0	1.9	-	-	1.1
7.4	2.2	0.66	0.82	3.3	2.1	1.9	-	-	0.80
7.8	1.9	0.64	0.76	3.1	2.1	1.8	-	-	1.0
7.9	2.0	0.68	0.76	3.2	1.9	1.7	-	-	0.96
8.0	2.4	0.79	0.88	4.1	2.7	2.9	-	-	1.5
8.3	2.2	0.73	0.85	3.7	2.1	2.3	-	-	1.3
8.6	2.5	0.86	0.93	4.2	2.6	2.4	2.4	1.8	1.4
9.5	3.1	1.1	1.1	5.1	2.5	2.5	3.1	2.0	2.0
9.7	3.0	0.85	0.97	4.7	2.7	2.6	3.0	1.7	1.4
10.0	2.9	0.85	1.0	5.2	2.7	2.9	2.7	2.5	1.6
10.0	3.5	0.88	1.0	5.2	2.8	2.9	2.9	2.4	2.5
10.4	4.0	1.2	1.1	5.8	3.3	3.3	2.9	2.9	-
11.0	3.6	1.1	1.0	5.8	3.1	2.9	3.0	2.8	2.8
11.2	3.9	1.1	1.3	6.2	3.6	3.6	3.4	3.8	3.7
12.2	4.4	1.2	1.5	6.2	3.1	3.1	3.5	3.7	3.8
13.0	5.0	1.5	1.4	7.1	4.0	3.8	4.3	2.8	3.3
J 14.0	5.4	1.3	1.6	7.5	3.7	3.2	4.3	3.2	4.1
J 15.8	6.7	1.5	2.1	8.8	3.7	3.1	5.3	3.5	4.9

J - Benthic juvenile.

Table 27. Meristics and spines of young Artedius creaseri. (Only specimens with meristic elements formed are included. See Table 26 for complete developmental series examined.)

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preopercular spines	Parietal spines	Posttemporal spines	Principal caudal rays	Vertebrae	Branchiostegal rays
5.7	-	-	-	-	-	-	2	-	-	-	-	-
5.7	-	-	-	-	-	-	2	1	-	-	-	-
* 6.3	-	-	-	-	-	-	3	1	-	-	-	-
6.4	-	-	-	-	-	-	4	1	-	-	-	-
6.5	-	-	-	-	-	-	2	1	-	-	-	-
* 6.6	-	-	-	-	-	-	2	1	-	-	-	-
7.1	-	-	-	-	-	-	4	1	-	-	-	-
7.3	-	-	-	-	-	-	4	1	-	-	-	-
7.4	-	-	-	-	-	-	4	1	-	-	-	-
7.8	-	-	-	-	-	-	4	1	-	-	-	-
7.9	-	13	10	-	-	-	4	1	-	-	-	-
8.0	VIII	13	10	16	16	-	4	1	1	-	-	-
8.3	-	13	10	16	16	buds	-	-	-	-	-	-
* 8.6	-	13	10	16	16	buds	4	1	1	-	-	-
9.5	X	14	-	16	16	buds	4	1	2	-	-	-
9.7	X	13	10	16	16	buds	4	2	2	-	-	-
10.0	X	14	10	16	16	buds	4	2	2	-	-	-
10.0	X	13	10	16	16	buds	4	2	2	-	-	-
* 10.4	X	14	10	16	16	buds	4	2	3	6+6	31	6
11.0	X	13	10	16	16	3	4	2	3	-	-	-
* 11.1	X	13	9	16	16	I,3	4	2	3	6+6	31	6
11.2	X	13	10	16	16	I,3	4	2	3	-	-	-
12.2	X	15	11	16	16	I,3	4	2	3	-	-	-
* 13.0	X	13	10	15	16	I,3	4	2	3	6+6	31	6
J14.0	X	13	10	16	16	I,3	4	2	2	-	-	-
*J15.8	X	14	10	16	16	I,3	4	2	2	6+6	31	6

* - Stained with Alizarin Red S.
J - Juvenile.

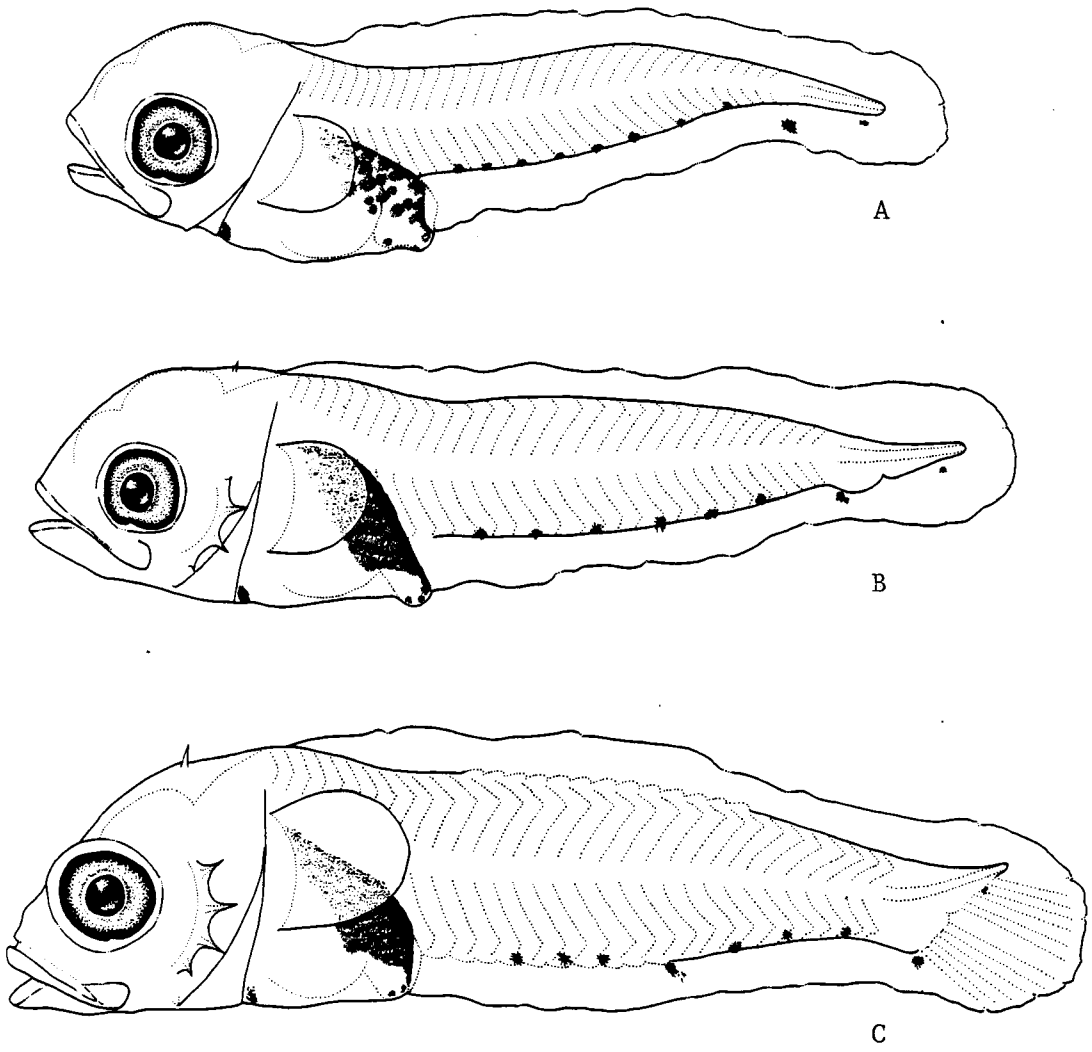

Figure 25. Larvae of Artedius creaseri: A) 5.0 mm NL, B) 6.6 mm NL, C) 7.9 mm SL.

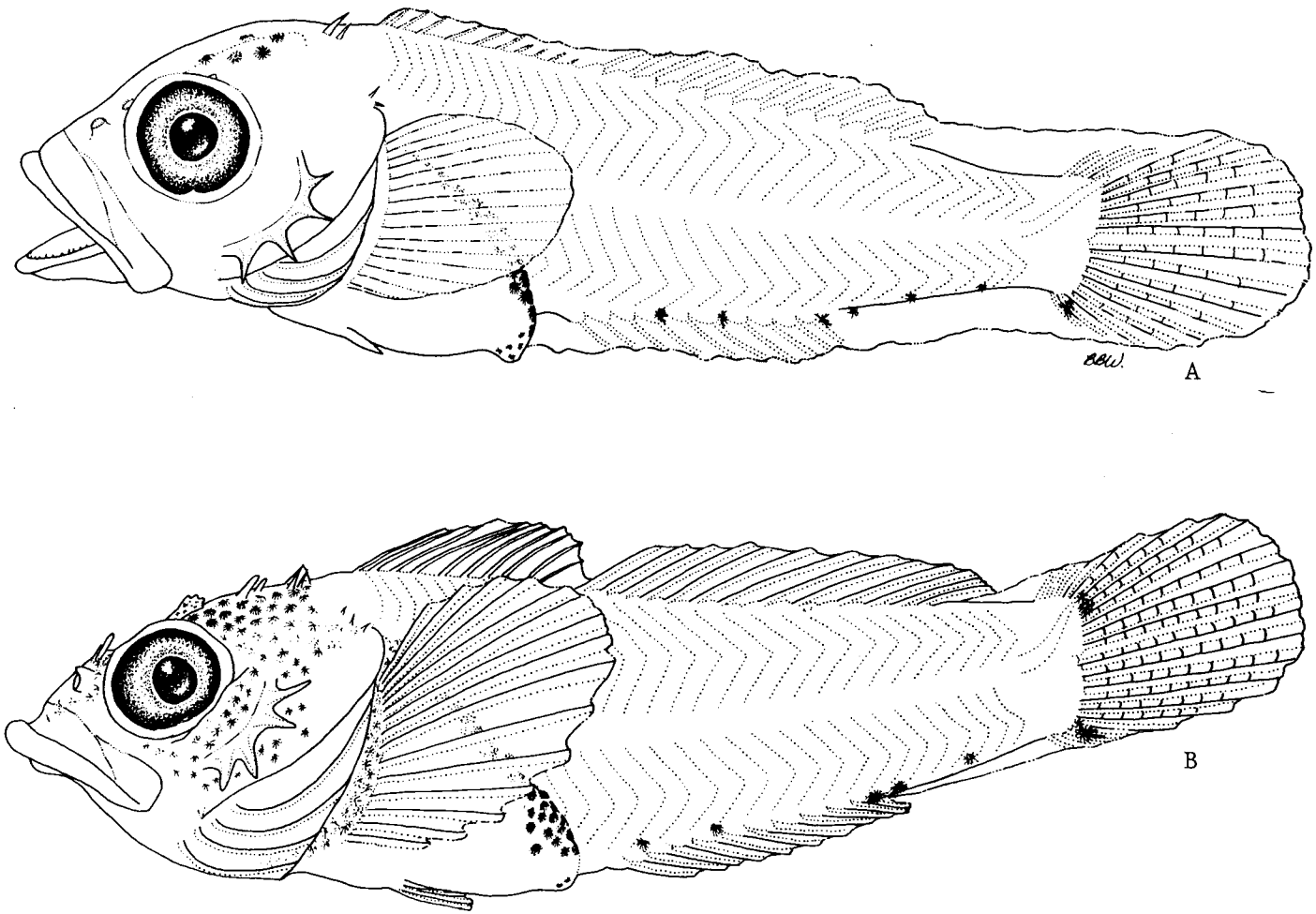

Figure 26. Larvae of Artedius creaseri: A) 9.1 mm SL, B) 13.0 mm SL.

Artedius meanyi

(Figures 27, 28; Tables 28, 29, 30)

Literature

Blackburn (1973) described a 4.3-mm larva resembling A. meanyi, which he called Cottid 3. Richardson (1977) and Richardson and Pearcy (1977) listed these larvae as Icelinus sp. 1. Richardson and Washington (1980) illustrated and described 3.3, 8.6, 10.9, 12.5, 13.5, 15.2, 16.5, and 16.6-mm specimens as Icelinus spp.

Identification

Larval A. meanyi were misidentified as Icelinus spp. on the basis of meristics and the pelvic fin ray count of I,2, which is characteristic of Icelinus. Meristics also match those of A. meanyi, which possess I,3 (rarely I,2) pelvic fin rays (Rosenblatt and Wilkie 1963; Lea 1974). Recently, Howe and Richardson (1978) reexamined Lea's specimens of A. meanyi and reported that "...only one small specimen appeared to have two rays--all others had three rays." Lea's specimens were reexamined in this study. Cleared and stained specimens clearly have I,2 pelvic fin rays. The outermost ray is greatly thickened and branched at the tip in all specimens examined. All of the misidentified "Icelinus" larvae possess this distinctive thickened outer ray.

In addition, during this study, large transforming specimens of A. meanyi were obtained that possess scales on the dorsal surface of the head, the opercle, and in four or five rows on either side of the dorsal fins. Specimens also possessed preorbital cirri and distinctive postocular cirri with three tentacles arising from a single base. The

combination of these morphological and meristic characters conclusively identifies these transforming larvae and juveniles as A. meanyi. The developmental series was linked together primarily on the basis of pigmentation and body shape.

Distinguishing Features

Small preflexion larval A. meanyi are distinguished by their short, compact guts (snout to anus length averages 33% SL) and pointed snouts. Characteristic pigmentation includes a low number of ventral midline melanophores posterior to the anus (<13), several large melanophores situated anteriorly on the visceral mass at the base of the cleithrum, and two distinctive blotches of pigment on both the dorsal and anal finfolds.

Notochord flexion begins at a relatively large size, ∿6.2 mm in A. meanyi larvae, and is complete by ∿9.4 mm. Four large, evenly spaced spines form along the margin of the preopercle in postflexion larvae >9 mm. Two parietal spines develop at the posterior margin of each parietal in larvae >11 mm.

Postflexion and juvenile A. meanyi, 13 to 18 mm long, are distinguished by a low number of blotchy ventral midline melanophores posterior to the anus, a relatively pointed snout and large head (33% SL), a pelvic fin ray count of I,2 with the outermost ray thickened as if two rays are fused together, and other meristics. In addition, juvenile A. meanyi possess a single slender preorbital cirrus, an eyeball cirrus, and a distinctive postorbital cirrus having three tentacles that arise from a single base. The largest specimens (16 to 18 mm) possess rows of

prickle-like scales on the parietal, cheek, and opercular regions of the head and on the dorsal surface of the body and caudal peduncle.

Pigmentation

Small A. meanyi larvae are relatively lightly pigmented. Melanistic pigmentation is absent on the head of preflexion larvae. Two to five round, external melanophores are clustered on the nape. The dorsolateral surface of the gut is lightly pigmented. Two or three large dendritic melanophores are embedded in the anterior musculature of the body cavity just posterior to the cleithrum. Posterior to the anus, a series of 7 to 13 large, blotch-like melanophores is positioned along the ventral midline originating under the second to fourth postanal myomere and extending toward the tail tip. These melanophores vary in size with the third or fourth and the posteriormost melanophores of the series being markedly larger and frequently extending onto the ventral finfold. Two large distinct pigment blotches are present on both the dorsal and ventral finfolds in small larvae. One specimen out of 45 examined possessed three pigment spots on both the dorsal and anal finfolds.

Melanistic pigmentation increases during larval development. Several melanophores are added over the brain in larvae between 7.4 and 8 mm. Melanophores in the nape region become embedded in larvae >6 mm as body musculature develops. Pigmentation increases slightly over the lateral surfaces of the gut. With the onset of notochord flexion and development of the caudal fin, the posteriormost melanophore of the ventral midline series is characteristically positioned at the ventral margin of the forming caudal fin. A second, large melanophore is

frequently added at the dorsal margin of the caudal fin base dorsal to the notochord tip. The blotches of pigment on the dorsal and ventral finfolds disappear in larvae ≳9 mm as fin rays begin to form.

During transformation, between 13 and 19 mm, head pigmentation increases markedly. Melanophores extend anteriorly over the interorbital region and onto the snout. Several melanophores are added just ventral to the orbit, between the eye and preopercle, and along the dorsal margin to the oeprcle. With development, melanophores are also added along the pectoral fin base, in a band across the dorsum, and on the dorsal fin around the first four dorsal spines. Melanophores are also added to the upper and lower lips, across the cheek, along the ventral margin of the opercle, and on the dorsal surface of the head.

Morphology

The smallest larval A. meanyi collected from plankton samples are ∿3 mm long and appear recently hatched. Specimens as large as 18 to 19 mm were collected in plankton and neuston tows. Planktonic larvae ≳15 mm are beginning to undergo transformation indicated by the development of juvenile pigmentation and the formation of scales on the head and dorsum. The smallest benthic juveniles examined were 15 to 16 mm long and were fully transformed. Thirty specimens, ranging in size from 3.3 to 17.9 mm were examined for morphometrics.

Small larval A. meanyi are relatively slender with a characteristic body shape. Body depth is constricted just posterior to the anus; the body bulges slightly in the midtail region and narrows again near the tail tip or caudal peduncle. This distinctive body shape remains apparent throughout larval development. The gut of A. meanyi is short and

tightly coiled. Snout to anus length averages 33% SL in preflexion larvae. With development, snout to anus length increases markedly averaging 40% in flexion and 48% in postflexion larvae. Prior to flexion of the notochord, body depth averages 18% at the pectoral fin base and 15% SL at the anus. However, body depth increases to 25% SL at both the pectoral fin base and the anus in postflexion larvae and juveniles.

Artedius meanyi larvae have small heads with a distinctively pointed snout. Head length averages 19% in preflexion larvae then increases dramatically to 33% SL in late postflexion larvae and juveniles. Snout length remains relatively constant throughout larval development, ranging from 28 to 30% HL. In contrast, eye diameter decreases relative to head length, from 44% in preflexion larvae to 29% HL in juveniles. Jaw length increases in proportion to head length from 43% to 55% HL during larval development and decreases again at transformation, averaging 50% HL in juveniles.

Fin Development

The fins develop relatively late in A. meanyi. Initiation of notochord flexion begins at ∿6.2 mm NL. Although caudal rays are first visible in larvae ≥7 mm long, principal caudal ray number is not complete until after notochord flexion at ∿11 mm. Dorsal and anal soft rays begin to form in larvae 9.5 to 10 mm long. The full complement of fin rays is visible in larvae ∿12 mm. Dorsal spines begin to form at ∿11 mm and are all present by 12 to 13 mm. Pelvic fin buds form in larvae ≥9.5 mm, however, the adult complement of pelvic fin rays is not complete until larvae reach ∿12 to 13 mm.

Spination

Preopercular spines develop relatively late in the development of A. meanyi larvae. Two tiny spines are first visible along the central portion of the preopercle in larvae >6.2 mm with a third spine forming dorsal to these spines between 8 and 8.5 mm. By 9.4 mm, a fourth spine is added at the ventral margin of the preopercle. These four spines remain prominent and approximately equal-sized throughout larval development. In larvae >13 mm, small basal spines or projections form on the base of each of the four main preopercular spines. With development, four bony ridges form on the inner preopercular shelf parallel to each basal spine. These ridges grow toward the basal spines and gradually fuse with them forming bony arches over the incipient lateral line canal of the preopercle. During transformation, between 15 and 17 mm, the dorsalmost preopercular spine becomes longer and stouter than the other spines, however, all four preopercular spines remain clearly visible on the largest pelagic juveniles examined, ∿19 mm long.

Spines also develop in the parietal and supracleithral-posttemporal regions of the head. A single tiny spine first forms at the posterior margin of the parietal in larvae >7 mm long. This spine gradually becomes longer, and in larvae between 12 and 13 mm a second, smaller parietal spine forms immediately posterior to it.

A small spine forms on the dorsal margin of the posttemporal bone between 9 and 10 mm. A second, similarly sized spine is added ventrally on the posttemporal in larvae ∿11 mm. At about the same time, a third spine forms posteroventally to the two posttemporal spines on the dorsal

portion of the supracleithrum. These three spines increase in size during transformation and eventually become associated with the junction of the cephalic and lateral line systems.

Table 28. Measurements (mm) of young Artedius meanyi. (Specimens between dashed lines are undergoing notochord flexion.)

Body length	Head length	Snout length	Eye diam	Snout to anus length	Body depth at pectoral fin base	Body depth at anus	Snout to pelvic fin origin	Pelvic fin origin to anus	Pectoral fin length
3.3	0.76	0.10	0.32	1.2	0.68	0.52	-	-	0.26
3.6	0.67	0.12	0.31	0.98	0.67	0.43	-	-	0.23
4.6	0.98	0.29	0.38	1.6	D	D	-	-	D
4.8	0.86	0.19	0.41	1.7	0.81	0.91	-	-	0.41
4.9	1.0	0.20	0.35	1.9	1.1	0.88	-	-	0.50
5.1	0.86	0.12	0.39	1.7	1.0	0.92	-	-	0.31
5.1	1.0	0.31	0.43	1.8	0.96	0.84	-	-	0.43
5.5	1.1	0.35	D	1.9	1.1	0.88	-	-	0.50
6.2	1.2	0.26	0.43	2.4	1.1	0.98	-	-	0.53
6.3	1.3	0.29	0.53	2.2	1.2	1.1	-	-	0.41
7.4	1.6	0.53	0.67	3.0	1.4	1.3	-	-	0.49
7.4	1.5	0.48	0.65	2.7	1.5	1.4	-	-	0.57
8.3	2.1	0.66	0.73	3.5	1.8	1.7	-	-	0.73
8.6	2.1	0.67	0.73	3.5	1.8	1.7	-	-	0.61
8.6	1.8	0.50	0.56	3.4	1.7	1.6	-	-	0.69
9.4	2.8	0.97	0.85	4.1	1.9	2.0	2.2	1.9	1.1
9.4	2.7	0.79	0.85	4.4	2.1	2.3	2.6	1.8	1.1
10.0	2.8	0.91	0.82	4.6	2.0	2.2	2.6	2.0	1.3
10.9	2.5	0.80	0.88	4.6	2.2	2.3	2.5	2.1	1.0
11.5	2.9	0.85	0.91	4.4	2.0	2.2	2.5	1.9	1.2
11.9	4.0	1.4	1.2	6.1	3.0	3.2	3.8	2.3	2.7
12.5	4.0	1.0	1.2	6.2	3.0	3.1	3.7	2.5	2.2
13.3	4.3	1.5	1.3	6.9	3.5	3.7	4.2	2.7	D
13.8	4.2	1.0	1.3	6.4	3.6	3.8	3.9	2.5	2.4
14.1	5.1	1.3	1.8	7.1	3.8	3.6	4.0	3.1	3.3
14.1	5.2	1.4	1.4	7.0	4.2	3.9	4.0	3.0	3.0
15.2	5.2	1.2	1.5	7.7	4.0	4.0	4.3	3.4	4.1
16.5	7.2	2.7	1.4	9.0	4.8	4.6	5.3	3.7	3.8
16.6	6.1	1.8	1.4	8.3	4.2	3.9	-	-	3.2
17.9	6.2	2.3	1.6	8.9	4.9	3.9	6.0	2.9	5.0

D - Damaged.

Table 29. Meristics and spines of young Artedius meanyi. (Only specimens with meristic elements formed are included. See Table 28 for complete developmental series examined.)

Body length	Dorsal spines	Fin rays	Anal fin rays	Pectoral fin rays left	Pectoral fin rays right	Pelvic spine & fin rays	Preoper-cular spines	Parietal spines	Post-temporal spines	Principal caudal rays	Verte-brae	Branchio-stegal rays
6.2	-	-	-	-	-	-	2	-	-	-	-	-
7.4	-	-	-	-	-	-	2	1	-	-	-	-
7.4	-	-	-	-	-	-	2	-	-	-	-	6
8.3	-	-	-	-	-	-	3	1	-	-	-	6
8.6	-	-	-	-	-	-	2	1	-	-	-	6
8.6	-	-	-	-	-	-	3	1	-	-	-	6
* 9.4	-	-	-	-	-	-	4	1	1	-	-	6
9.4	-	-	-	-	-	-	4	1	1	-	-	6
10.0	-	-	-	-	-	-	4	1	1	-	-	6
10.9	-	-	12	15	15	-	4	1	1	-	-	6
11.5	-	-	-	-	-	-	4	1	1	-	-	6
* 11.9	X	16	12	15	15	I,2	4	2	3	6,6	34	6
12.5	X	16	12	16	16	I,2	4	2	3	-	-	-
* 13.3	X	15	12	15	15	I,2	4	2	3	6,6	34	6
13.8	X	16	12	16	16	I,2	4	2	3	-	-	-
14.1	X	16	12	16	16	I,2	4	2	3	-	-	-
* 14.4	XI	15	12	15	15	I,2	4	2	3	6,6	34	6
15.2	X	16	12	15	15	I,2	4	2	3	-	-	-
* 15.5	X	16	12	15	15	I,2	4	2	3	6,6	34	6
16.5	X	16	12	16	15	I,2	4	2	2	-	-	-
* 16.6	X	16	13	15	15	I,2	4	2	2	6,6	34	6
* 17.9	X	16	12	15	15	I,2	4	2	2	6,6	34	6
* 18.0	X	16	12	15	15	I,2	4	2	2	6,6	34	6
* 18.2	X	16	12	15	15	I,2	4	2	2	6,6	34	6

* - Stained with Alizarin.Red S.

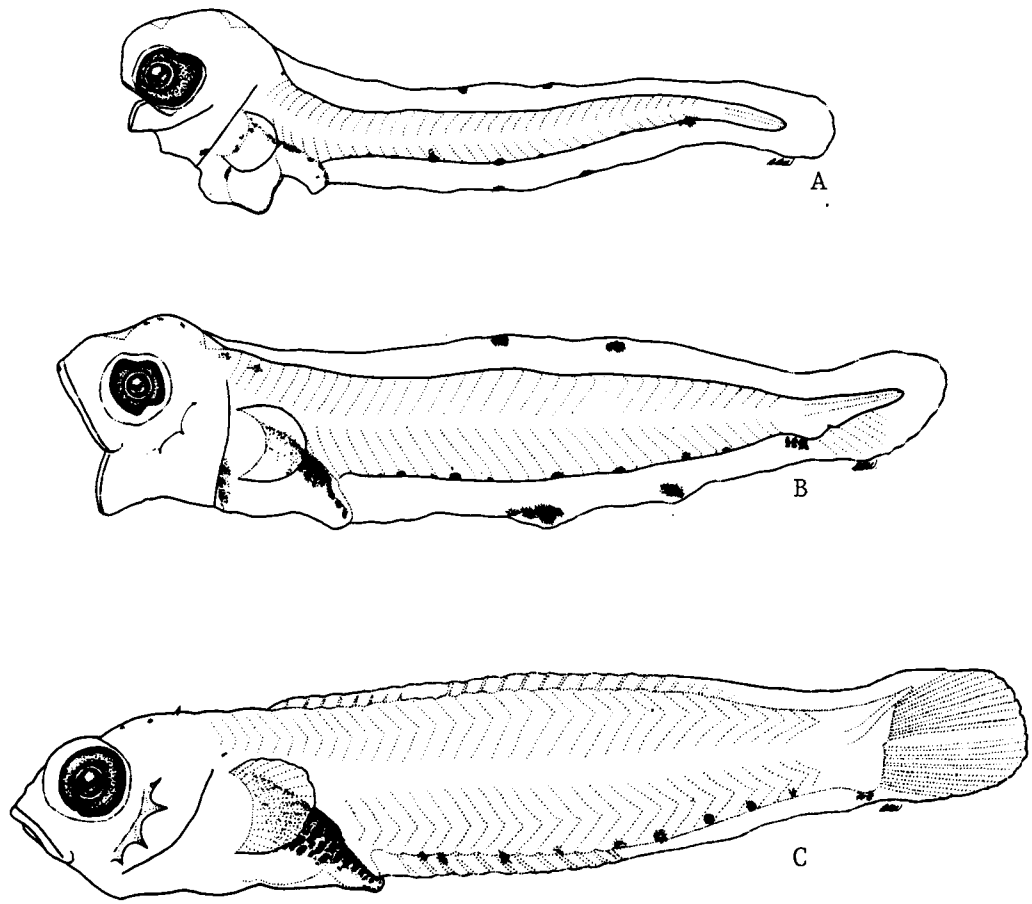

Figure 27. Larvae of Artedius meanyi: A) 3.3 mm SL, B) 8.6 mm SL, C) 10.9 mm SL (from Richardson and Washington 1980).

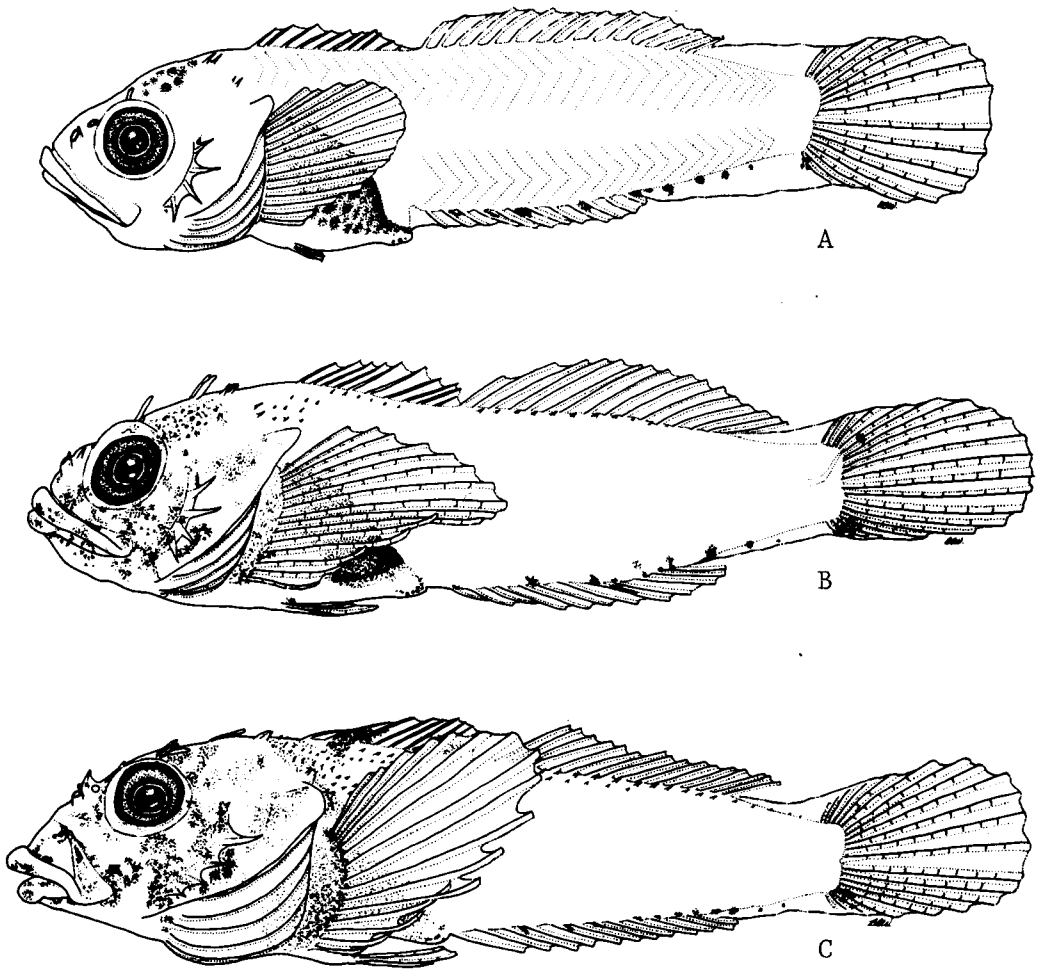

Figure 28. Young of Artedius meanyi: A) 13.8 mm SL, B) 15.2 mm SL, C) 16.5 mm SL (from Richardson and Washington 1980).

Table 30. Body proportions of larvae and juveniles of Artedius creaseri and A. meanyi. Values are standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. (Number of specimens may be derived from Tables 26 and 28.)

Item	Artedius creaseri	Artedius meanyi
Head length/SL:		
Preflexion	24.4±1.25(22.9-26.5)	18.6±1.77(17.9-21.3)
Flexion	26.0±2.46(22.8-28.8)	22.7±3.53(19.4-38.0)
Postflexion	32.6±3.80(26.5-38.5)	32.1±4.68(25.4-38.0)
Juvenile	40.3±2.97(38.2-42.4)	-
Snout length HL:		
Preflexion	29.7±2.74(25.0-33.0)	27.5±7.50(15.1-31.0)
Flexion	31.9±3.58(26.7-36.9)	29.5±5.01(22.3-35.4)
Postflexion	30.4±2.95(25.1-35.5)	29.4±4.34(23.1-37.3)
Juvenile	23.2±1.20(22.4-24.1)	-
Eye diameter		
Preflexion	42.0±4.42(34.7-47.3)	44.0±3.39(35.0-47.7)
Flexion	37.4±3.11(32.5-43.1)	36.6±4.93(30.4-43.1)
Postflexion	33.2±4.01(27.5-38.6)	29.0±3.31(23.2-35.3)
Juvenile	30.4±1.20(29.6-31.3)	-
Snout to anus length/SL:		
Preflexion	44.6±3.01(41.5-50.0)	33.0±2.86(27.2-35.4)
Flexion	43.5±3.83(39.7-50.0)	39.6±2.97(36.1-44.3)
Postflexion	51.5±3.66(44.6-55.8)	48.3±4.43(38.0-55.2)
Juvenile	54.4±1.77(53.2-55.7)	-
Snout to pelvic fin origin/SL:		
Preflexion	-	-
Flexion	-	23.0*
Postflexion	29.5±2.17(27.0-33.1)	29.1±3.16(21.9-33.6)
Juvenile	32.0±2.12(30.5-33.5)	-
Pelvic fin origin to anus/SL:		
Preflexion	-	-
Flexion	-	20.1*
Postflexion	24.6±4.96(17.5-33.9)	19.4±1.60(15.7-22.1)
Juvenile	22.4±0.35(22.2-22.7)	-
Body depth at pectoral fin base/SL:		
Preflexion	26.0±2.54(23.4-29.7)	18.0±1.64(16.2-20.0)
Flexion	26.0±1.78(22.7-28.1)	19.9±1.25(17.7-22.2)
Postflexion	28.8±2.67(25.3-33.8)	24.6±3.65(17.2-30.1)
Juvenile	24.8±1.98(23.4-26.2)	-
Body depth at anus/SL:		
Preflexion	21.8±2.35(19.4-26.0)	15.2±3.11(11.9-19.1)
Flexion	24.0±3.08(19.3-28.1)	18.9±1.55(15.8-21.3)
Postflexion	28.2±3.07(25.4-36.2)	24.6±2.73(19.3-28.4)
Juvenile	21.2±2.19(19.6-22.7)	-
Pectoral fin length/SL:		
Preflexion	-	8.4±1.35(6.4- 9.1)
Flexion	12.2±1.97(99.5-15.1)	9.2±1.77(6.5-12.1)
Postflexion	23.7±6.11(14.5-35.2)	19.0±6.21(10.1-28.3)
Juvenile	30.1±1.34(29.1-31.0)	-

- = Not present at this stage.
* = Only one specimen available at this stage.

SYSTEMATICS

Description of Characters Considered

Preopercular Spination

The number of preopercular spines is a relatively stable, conservative character in larval cottids. Most cottid larvae (21 of 26 known genera) possess four approximately equal-sized spines situated along the posterior margin of the preopercle. Generally the dorsalmost spine increases in size with development while the lower three spines are reduced or lost.

A modification of this basic preopercular pattern is found in larvae of several species of Icelinus and Myoxocephalus. These larvae possess an additional small, auxiliary spine situated on the inner shelf of the preopercle anterior to the bases of the four principal preopercular spines.

A third pattern of preopercular spination is found in larvae of Clinocottus, Oligocottus maculosus, O. snyderi, Artedius fenestralis, A. harringtoni, A. lateralis, and A. Type 3 (Fig. 29). These larvae possess 5 to 24 small spines situated along the posterior margin of the preopercle. Two basic patterns of multiple preopercular spines occur in larvae of this group. In four species of Artedius (Group A), the dorsalmost, middle, and ventralmost spines become enlarged relative to the other preopercular spines. During transformation, the dorsalmost spine continues to increase in size, while the middle spines (7 to 9), midventral spines (11 to 14) and ventralmost spines each fuse together,

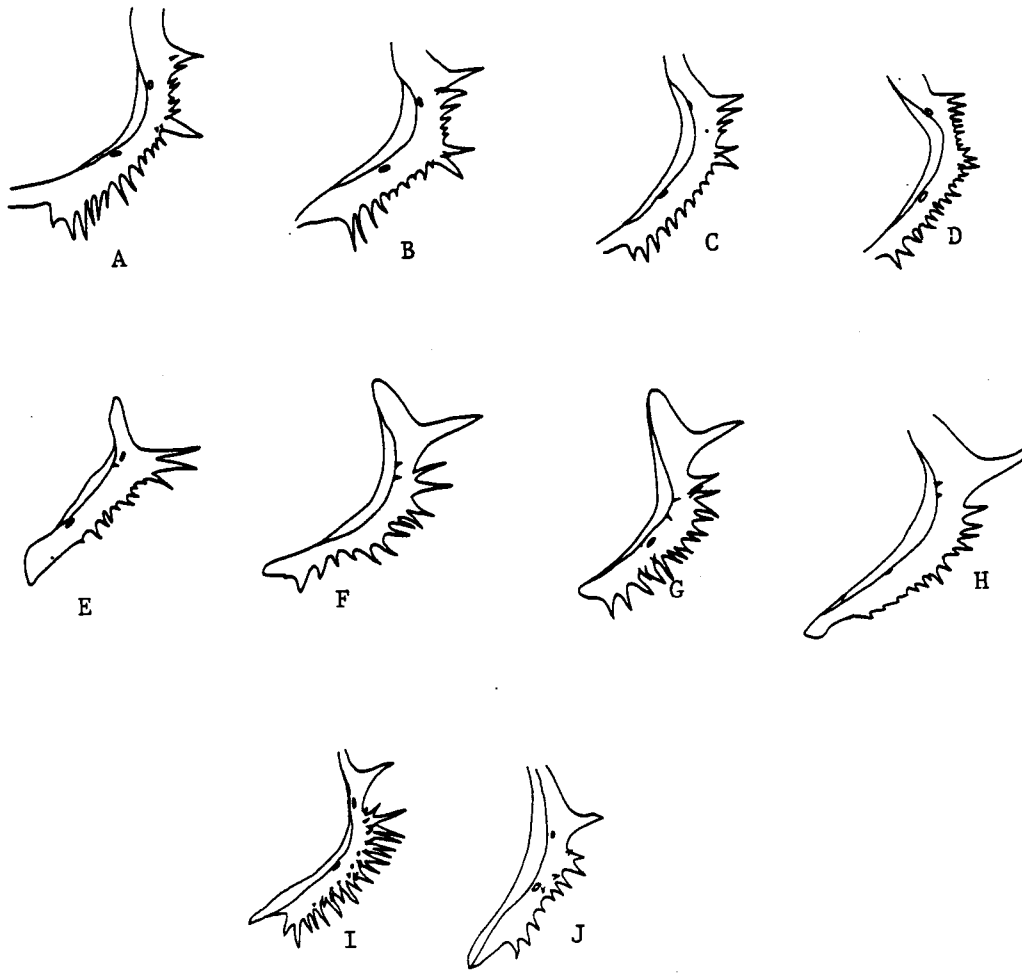

Figure. 29. Multiple preopercular spines in larval Artedius, Clinocottus, and Oligocottus. A = Artedius harringtoni, B = A. fenestralis, C = A. lateralis, D = A. Type 3, E = C. acuticeps, F = C. embryum, G = C. globiceps, H = C. analis, I = O. snyderi, J = O. maculosus.

forming three large bumps on the preopercular margin. The other preopercular spines gradually disappear.

In larvae of Clinocottus and Oligocottus (Groups B and C), the dorsalmost spine increases in size relative to the other preopercular spines. During transformation the lower spines regress and disappear while the dorsalmost spine remains prominent.

Outgroup comparisons with larvae of closely related Scorpaeniformes indicate the presence of five or fewer approximately equal-sized preopercular spines. Sebastes and Stellerina larvae possess five and four spines, respectively; hexagrammid larvae possess four, three or no spines, and cyclopterid larvae have lost all preopercular spines. The cottid taxa that possess four equal-sized preopercular spines also tend to have many other primitive character states. This basic pattern is probably the primitive state for preopercular spines in cottid larvae.

The modified pattern of spines found in larval Icelinus and Myoxocephalus could easily be derived from the basic pattern of four preopercular spines. In fact, larvae of several species of Icelinus and Myoxocephalus possess only four preopercular spines. The presence of an auxiliary spine on the inner shelf of the preopercle probably represents an intermediate character state leading toward multiple preopercular spines.

The multiple preopercular spines of larvae of Artedius (Group A), Clinocottus, and Oligocottus are unique to this group. Multiple preopercular spines are not present in any other known cottid or scorpaeniform larvae. Multiple preopercular spines are derived character states indicative of the monophyletic origin of this group.

Basal Preopercular Spine

Larvae of Artedius meanyi and creaseri and at least two species of Icelinus possess small projections or spines on the base of each of the four main preopercular spines (Fig. 30). These basal spines project out at 90° angles to the axis of the main preopercular spines. The basal spines are most pronounced in early postflexion larvae. With development, four bony ridges form on the inner shelf of the preopercle, parallel to each basal spine. These bony ridges grow toward the basal spines and gradually fuse with them, forming bony arches over the forming lateral line canal of the preopercle. These basal spines are not present in other cottid or scorpaeniform larvae examined and probably are a derived character state.

Inner Shelf Preopercular Spines

Larval Clinocottus possess one or two tiny spines on the inner shelf margin of the preopercle. Clinocottus acuticeps larvae have only one inner shelf spine. All other Clinocottus larvae have two. These spines are transient features which form in postflexion larvae and are lost before transformation. They differ from the inner shelf spines of Icelinus and Myoxocephalus larvae in position and form. They appear to be unique to this group and, as such, to be derived character states.

Nape Bubble

Larvae of Oligocottus maculosus and O. snyderi possess a distinctive bubble of skin in the nape region just anterior to the origin of the dorsal fin (Fig. 31). This bubble is present at hatching and persists

Figure 30. Preopercular spines of larval Artedius meanyi and A. creaseri.

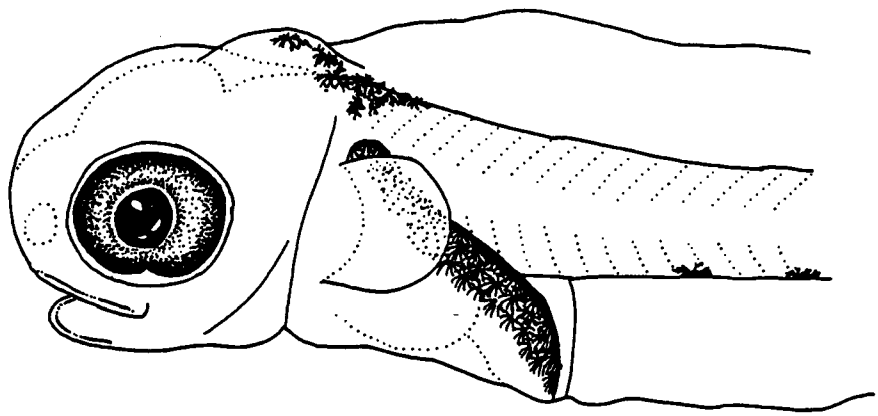

Figure 31. Nape bubble of larval Oligocottus maculosus.

for two or three weeks (to about the beginning of flexion of the notochord). No other known cottid larvae possess a bubble of skin at the nape; accordingly, this bubble is probably a derived character unique to these two species. (Larvae of O. rimensis and O. rubellio are unidentified and it is not known if they also possess this synapomorphy.)

Gut Diverticula

Long, protrusions or diverticula extend dorsolaterally from either side of the abdominal cavity in larvae of Artedius fenestralis, A. lateralis, and A. Type 3 (Fig. 32). These diverticula are present at hatching and persist throughout larval development. Newly hatched larvae of Oligocottus maculosus and O. snyderi possess similar but less pronounced bumps or protrusions on either side of the dorsal surface of the abdominal cavity. These bumps are present at hatching, however, disappear after two to three weeks at about the onset of notochord flexion. The diverticula of Artedius fenestralis, lateralis, and Type 3 and the smaller protrusions of Oligocottus appear to be homologous structures, with the smaller bumps constituting an intermediate form. These diverticula are unique, derived characters not known in other cottid larvae.

Larvae of C. acuticeps also possess long diverticula which extend posteriorly on either side of the anus. Larvae of C. globiceps, C. embryum, and C. analis have bulges on either side of the anus. Although these bulges appear to form an intermediate state in the evolution of hindgut diverticula, histological sections of the guts of larval Clinocottus yielded inconclusive results. Larval C. analis, C. embryum, and C. globiceps possessed an enlarged coelom on either side of the hindgut,

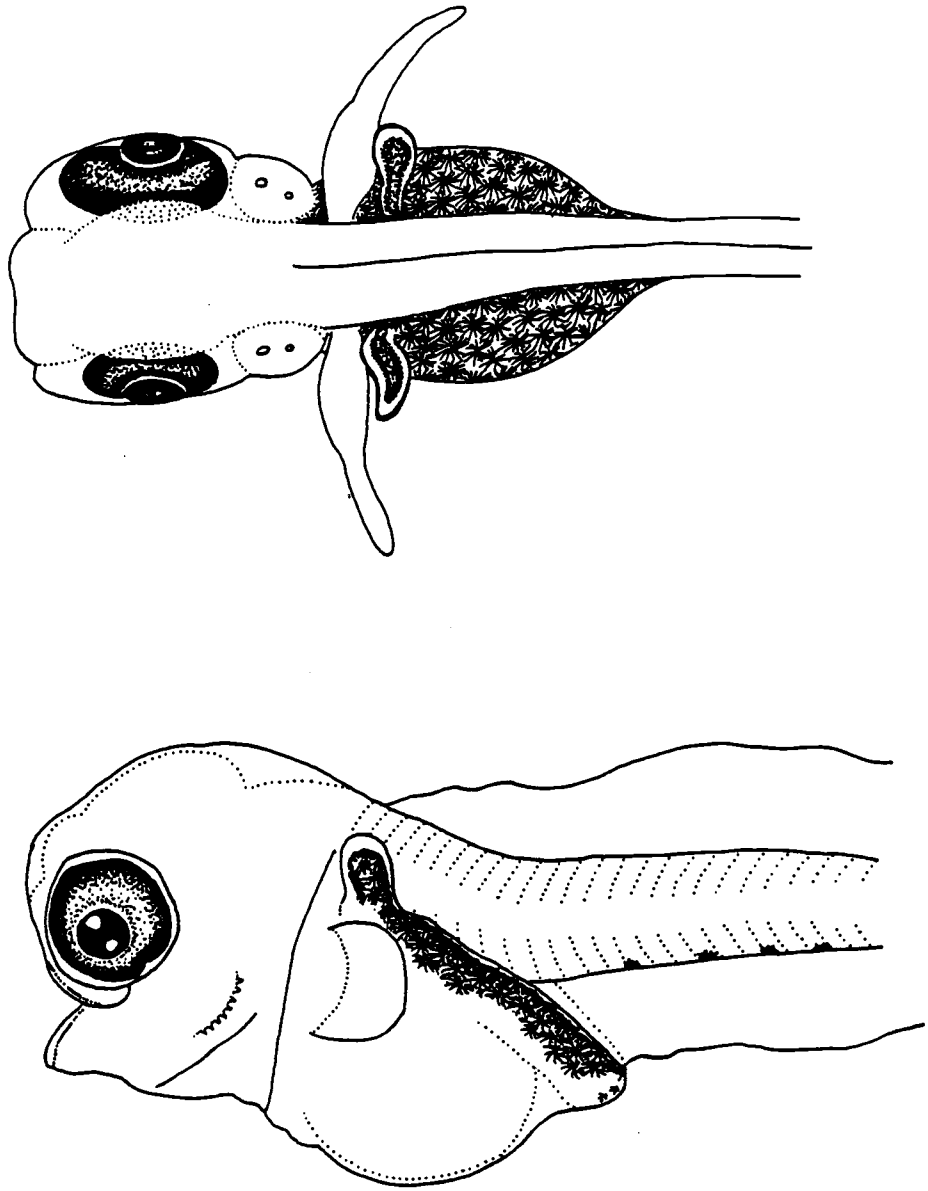

Figure 32. Dorsal gut diverticula in larval Artedius fenestralis.

however distinct diverticula were not observed. Hindgut diverticula appear to be unique to C. acuticeps.

Parietal Spines

Most larval cottids develop two spines, a large anterior parietal, and a smaller posterior parietal spine at the posterior edge of the parietal bones. The anterior parietal spine develops first, followed by a second smaller spine that forms just posterior to it. These spines are generally transient structures that form late in larval development and are reduced or lost during transformation. In many species of cottids, the spines appear to fuse together enclosing a small canal between the bases of the two spines. This canal eventually becomes part of the cranial lateral line system. In other species, the spines decrease in size without fusing together. Concurrently, sheets of bone extend anteriorly and posteriorly from the spines and eventually fuse together, forming an incipient cranial arch.

Similar parietal spines occur in larvae of most other scorpaeniform families and appear to be homologous to those of cottid larvae. The presence of two parietal spines is probably the primitive or ancestral condition in the Cottidae.

Parietal spines have undergone modification and elaboration in larvae of most of the species of Clinocottus, Oligocottus, and Artedius fenestralis, A. harringtoni, A. lateralis, and A. Type 3. Two species (Artedius harringtoni and Clinocottus acuticeps) have lost these spines completely. Three species (Clinocottus analis, C. embryum, and C. recalvus) have retained the primitive condition of possessing two parietal spines. The remaining species (A. fenestralis, A. lateralis,

O. maculosus, O. snyderi, and C. globiceps) have tended toward an elaboration and increase in number of parietal spines. Generally, these larvae develop a cluster of three to six spines that are situated in two transverse rows at the posterior margin of the parietal region. During transformation, these clusters of spines decrease in size and disappear. At the same time, sheets of bone extend anteriorly and posteriorly from the bases of the two rows of spines and eventually fuse together. This bony arch becomes a part of the cranial lateral line system in juveniles.

The absence of parietal spines in A. harringtoni and C. acuticeps is probably a secondary loss and, as such, represents a derived condition. The elaboration of spines into clusters is apparently unique to larvae of Artedius, Clinocottus, and Oligocottus and is also a derived state.

Pigmentation

Melanistic pigmentation varies greatly among cottid larvae ranging from relatively unpigmented forms to heavily pigmented ones. Larvae of Artedius, Clinocottus and Oligocottus are all lightly pigmented. All species possess numerous, intense melanophores over the dorsolateral surface of the gut and in a row posterior to the anus. The shape and number of midline melanophores varies between species. Larvae of all but one species, A. creaseri, possess several melanophores in the nape region. The presence of head pigment and anteroventral gut melanophores is variable among the species of the group.

Although pigment patterns are diagnostic at the specific level, they are difficult to evaluate for use in systematic analysis. Many fish larvae in distantly related families, and even orders, are similarly

pigmented. Several other genera of larval cottids also possess similar pigment patterns. Hence, it is difficult, if not impossible, to determine which pigment patterns are primitive and which are derived.

However, trends in certain areas of pigmentation can be discerned. Among known cottid larvae, a discrete nape pigment patch is found only in members of Artedius, Clinocottus, Oligocottus, Enophrys, Myoxocephalus, and Gymnocanthus. Nape pigment is probably derived in cottid larvae. The number of ventral midline melanophores situated posterior to anus ranges from 2 to 33 in larvae of Artedius, Clinocottus, and Oligocottus. In addition, the shape and spacing of these melanophores varies from small dots to long slashes extending onto the ventral finfold to large pigment blotches. Artedius creaseri and A. meanyi both possess irregular shaped blotches of pigment along the ventral midline. Artedius fenestralis, A. harringtoni, and A. lateralis all possess distinctive pigment slashes. Oligocottus and Clinocottus larvae possess small round melanophores. Although these pigment patterns bind certain species together, it is difficult to determine ancestral versus derived states. Both pigment blotches and distinctive midline slashes are found in larval Icelinus. Pigment, as well as other characters indicate that Icelinus shares close affinities with Artedius, however, directions of the evolution of pigment patterns cannot be determined.

Morphometrics

Cottid larvae exhibit a diversity of body forms. Body shape ranges from short and stubby (Artedius [Group A], Enophrys) to long and slender (Radulinus, Icelus) to globose (Malacocottus). Larval Artedius (Group A),

Clinocottus, and Oligocottus have short, stubby bodies with blunt, rounded snouts. Gut length is moderately long and the posterior portion of the hindgut trails well below the rest of the body.

Morphometric characters are difficult to evaluate for use in systematic analysis. Measurements of body parts frequently overlap in larval Artedius (Group A), Clinocottus, and Oligocottus because of their similarity in body shape. These similarities make it difficult to determine discrete character states or transformation series. In addition, many body parts change markedly during larval development, frequently exhibiting allometry. Because of the extreme diversity of form found in larval cottids, it is difficult to determine primitive and derived character states. Trends can be observed in only a few body parts.

Larvae of Artedius creaseri and A. meanyi have long, pointed snouts. They develop relatively long ascending processes on the premaxillary. The underlying ethmoid cartilage is relatively large causing a pointed, "humped" appearance of the snout. Larval Icelinus also exhibit a pointed snout similar to that of A. meanyi and A. creaseri.

In contrast, all other larval Artedius, Clinocottus, and Oligocottus have blunt, rounded snouts. The ascending processes of their premaxillaries are relatively short and the ethmoid cartilage forms late in development.

Snout length is variable in the outgroup taxa. Sebastes larvae have a somewhat long, pointed snout, however the hexagrammid, cyclopterid, and agonid larvae examined have rounded snouts. Within the cottids, Enophrys, Leptocottus, Hemilepidotus, and Scorpaenichthys

larvae all have blunt, rounded snouts. This condition is probably the primitive condition relative to larvae of Artedius, Clinocottus, and Oligocottus because it is widespread in several divergent genera of cottids and scorpaeniforms. The pointed snout appears to be a derived condition.

Although gut length varies greatly among cottid larvae (Richardson and Washington 1980), larval Artedius (Group A), Clinocottus, and Oligocottus possess distinct guts with the hindgut coiled very loosely and extending posteriorly. The tip of the hindgut extends ventrally well below the rest of the body and posteriorly to the origin of the anal fin. This condition is most pronounced in Clinocottus larvae. A trailing gut is unique to larvae of Artedius, Clinocottus, and Oligocottus, except A. meanyi, and is assumed to be a derived condition.

Pelvic Fin Rays

The number of pelvic fin rays ranges from one spine and five rays to none in cottids.

Pelvic fin rays are generally considered to be undergoing reduction in the cottids. The primitive state is I,5 fin rays as in other Scorpaeniformes. Reduction in number of rays is a derived state.

Larvae of Artedius, Clinocottus, and Oligocottus all possess I,3 pelvic fin rays, except for A. meanyi. Artedius meanyi usually possesses I,2 pelvic fin rays. However, the outermost fin ray is markedly long and thickened with the tips of the ray separated. Icelinus also possesses I,2 pelvic fin rays, however, both rays are relatively short and fine. The thickened outer ray of A. meanyi may well have evolved through a fusion of two fin rays in an ancestral cottid with three pelvic fin

rays. If so, this condition may constitute an intermediate state between three pelvic fin rays of Artedius, Clinocottus, and Oligocottus and the two pelvic fin rays of Icelinus.

Branchiostegal Rays

The scorpaenids, generally atrributed to be the most generalized scorpaeniform (Bolin 1947; Quast 1966), possess seven branchiostegals. However, the hexagrammids and the zaniolepids, which occupy an intermediate position between the scropaenids and cottids, according to Quast (1965), all possess six branchiostegals. Most cottids possess six branchiostegal rays, however, the psychrolutids and some freshwater Cottus species have seven branchiostegals. The psychrolutids are a distinct group which possess many derived characters and apparently have diverged from other cottoids. Similarly, members of Cottus also possess many derived characters that apparently reflect adaptation to a freshwater habitat. Cottids that are generally considered to be primitive because of the retention of many primitive features all possess six branchiostegal rays.

Although the possession of seven branchiostegal rays is probably the primitive condition in the scorpaeniforms, six branchiostegals appear to be the primitive state within the cottids. Cottid genera such as Icelinus and Hemilepidotus, which Bolin (1947) considered to have evolved from the evolutionary line leading to Artedius, Clinocottus, and Oligocottus all possess six branchiostegal rays. Six branchiostegals is probably also the primitive state relative to Artedius, Clinocottus, and Oligocottus. Because cottids generally considered to have evolved from the same evolutionary lineage as Artedius all have six

branchiostegals, it is most parsimonious to conclude that the seven branchiostegals found in Artedius harringtoni and some Clinocottus globiceps are secondarily derived.

Posttemporal-Supracleithral Spines

Larvae of most known scorpaeniforms (including most known cottids) develop three spines in the posttemporal-supracleithral region of the head. Generally, two spines form first on the ventral portion of the posttemporal bone and one spine forms midway along the posterior margin of the supracleithrum. These spines persist during transformation at which time the surrounding portions of the posttemporal and supracleithral bones undergo modification and canals form in these bones between the spines. This entire complex then develops into the junction point of the cephalic lateral line system and the lateral line system. This pattern of spines probably represents the ancestral condition in larval cottids.

In larvae of Artedius, Clinocottus, and Oligocottus the posttemporal-supracleithral spines are frequently modified. The modifications appear to be correlated with those of the parietal spines. Larvae which have lost parietal spines do not develop posttemporal-supracleithral spines and larvae which have evolved complex clusters of parietal spines also develop clusters of posttemporal-supracleithral spines. Neither A. harringtoni nor C. acuticeps larvae develop any spines in the posttemporal-supracleithral region. Larvae of A. creaseri, A. meanyi, C. embryum, and C. recalvus possess two posttemporal and one supracleithral spines. Artedius fenestralis, A. lateralis, O. maculosus, O. snyderi, and C. globiceps all develop more than three posttemporal supracleithral spines.

As described for parietal spines, the posttemporal-supracleithral spines are variable among species of Artedius, Clinocottus, and Oligocottus. This variability among closely related species suggests that these spines may be undergoing rapid modification in this group and loss of spines or possession of clusters of spines may represent convergent or parallel evolution.

As with the parietal spines, the absence of posttemporal-supracleithral spines in A. harringtoni and C. acuticeps is probably a secondary loss and hence a derived state. The trend toward an elaboration of these spines is found only in members of these three genera and is also a derived state.

Characters Selected for Wagner Analysis

A total of 11 characters were selected for use in the Wagner network phylogenetic analysis. Only these were considered to best fit the criteria for character selection listed in the methods. All characters were coded as binary states, 0 or 1 or as additive binary states 00, 01, 11. The primitive state of each character was coded as 0, and the derived state as 1. Characters in which three distinct states were present were coded as additive binary states (characters 2 and 4). Character states were coded as follows:

Character 1: four preopercular spines, state 0; five or more preopercular spines, state 1.

Character 2: preopercular spines approximately equal-sized, state 00; dorsalmost preopercular spine largest, state 01; dorsalmost, middle, and ventralmost preopercular spine largest, state 11.

Character 3: basal spines absent on each preopercular spine, state 0; basal spines present on base of each propercular spine, state 1.

Character 4: auxiliary spines on inner shelf of multiple spine type preopercle absent, state 00; one auxiliary spine on inner shelf of preopercle present, state 01; two auxiliary spines on inner shelf of preopercle present, state 11.

Character 5: bubble of skin at nape absent, state 0; bubble of skin at nape present, state 1.

Character 6: diverticula from dorsal surface of gut absent, state 00; small bumps extending dorsally from gut present, state 01; long diverticula extending dorsally from gut present, state 11.

Character 7: two parietal spines present, state 0; parietal spines modified, state 1.

Character 8: melanophores on nape absent, state 0; melanophores on nape present, state 1.

Character 9: snout rounded, state 0; snout pointed, state 1.

Character 10: hindgut not trailing below body and ending anterior to origin of anal fin, state 00; hindgut trailing slightly below body and to origin of anal fin, state 01; hindgut trailing $>$ eye diameter below body and extending posterior to origin of anal fin, state 11.

Results and Discussion of Phylogenetic Relationships

A hypothesis of evolutionary relationships among species in the cottid genera Artedius, Clinocottus, and Oligocottus resulted from the Wagner analysis (Fig. 33). Two main lineages or sister groups of Artedius, Clinocottus, and Oligocottus larvae are represented in the

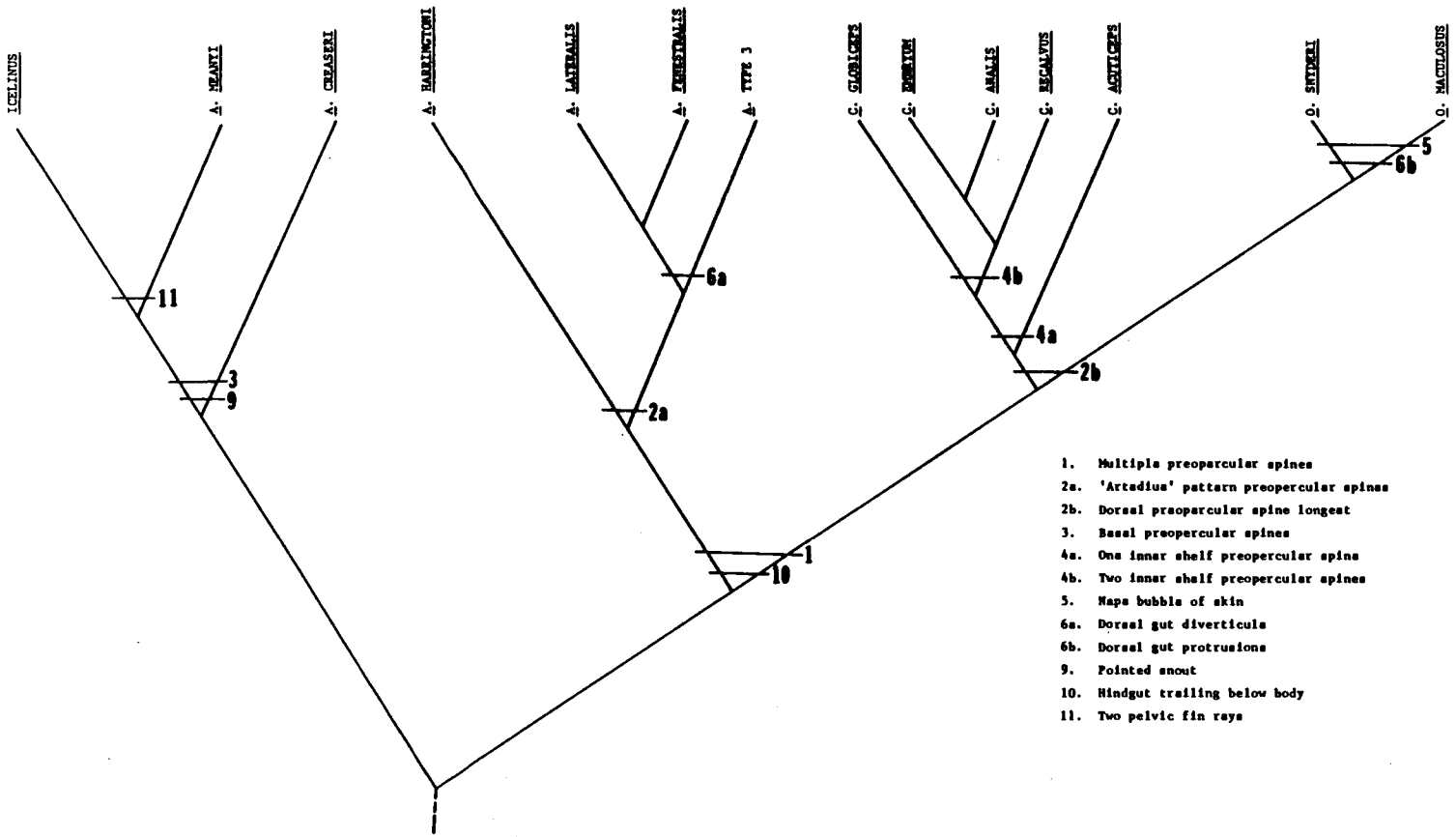

Figure 33. Cladogram based on the unrooted Wagner network showing systematic relationships between Artedius, Clinocottus, and Oligocottus. Characters numbered on cladogram indicate synapomorphies and are more fully explained in the text.

resulting cladogram based on shared derived characters of the larvae. Species with larvae possessing the synapomorphic character, multiple preopercular spines, form one major group. In addition to the possession of shared, derived characters, larvae of this group are extremely similar in pigmentation and body shape. The second major evolutionary line consists of species sharing two derived characters, basal preopercular spines and pointed snouts. This line includes Artedius creaseri, A. meanyi, and Icelinus.

The two main evolutionary lines or groups of Artedius, Clinocottus, Oligocottus, and Icelinus presented in Fig. 33 correspond to Taranets' (1941) classification of these species. Taranets (1941) placed Artedius meanyi and A. creaseri in the subfamily Icelinae, along with members of Icelinus and Chitonotus. He based this decision on the following characters: the upper preopercular spine larger than the lower spines; two rows of bony plates on the body--one along the lateral line and the other at the base of the dorsal fins; and scales usually present on other parts of the body. All of these characters are undergoing reduction and are present in several different genera of cottids. As such, they have low systematic value. Taranets (1941) combined Clinocottus, Oligocottus, and Artedius corallinus, A. fenestralis, A. harringtoni, A. lateralis, and A. notospilotus in the subfamily Oligocottinae. This subfamily was characterized by the absence of spines or ridges projecting through the skin on the head, weakly developed preopercular spines, body naked or with bony plates reduced, and "...other characters." Unfortunately, Taranets did not mention which other characters he examined.

In contrast, other investigators have placed Artedius meanyi and A. creaseri in the genus Artedius along with the five other species of Artedius discussed above. Howe and Richardson (1978) and Bolin (1947) proposed that although Artedius shared close affinities with Icelinus, it was more closely related to Clinocottus and Oligocottus. Jordan (1923), however, stated that Artedius was most closely related to Icelinus because of the common possession of bony plates on either side of the dorsal fins.

The evolutionary lineage (Fig. 33) containing larvae with multiple preopercular spines includes three distinct groups of species. One of these groups includes all the species of the genus Clinocottus. Larvae of this group share one synapomorphic character, inner shelf preopercular spines. This genus has been previously recognized and defined on the basis of adult characters, e.g., loss of scales, an advanced anus, and possession of a heavy, blunt penis (Hubbs 1926; Bolin 1934, 1944, 1947; Taranets 1941; Howe and Richardson 1978). None of these characters is unique only to members of Clinocottus. Several different lineages of cottids exhibit reduction in squamation, advanced anuses, and penises. Larvae of Clinocottus possess one or two auxiliary spines on the inner preopercular shelf. These spines appear to be a derived character unique to members of this genus. This synapomorphy provides strong evidence that the genus is monophyletic.

Synapomorphic characters were not identified in this study which clarified interspecific relationships within Clinocottus. Clinocottus analis, C. embryum, and C. recalvus are grouped together by a

plesiomorphic character. This type of character does not provide strong evidence of close relationship. Clinocottus acuticeps is separated from the other species of Clinocottus on the basis of an autapomorphy, hindgut diverticula. Several pigmentation and morphological characters, for which direction of evolution is unknown, suggest possible intrageneric relationships. Both Clinocottus globiceps and C. recalvus larvae have intense pigmentation over the snout, head, and nape. Both have very blunt, globose heads, large, bulging guts, and a relatively deep body. Juveniles of the two species are nearly inseparable based on external morphology. Clinocottus embryum and C. acuticeps larvae also are similar possessing moderately pointed snouts, a loose bubble of skin in the head region, a long trailing gut with bulges or diverticula, and light pigmentation. Postflexion larvae C. analis differ from all other postflexion larvae in possessing an intense band of melanistic pigmentation over the lateral surface of the body. Unfortunately, the polarity (direction of evolution) of many of the transformation series of morphometric and pigment characters could not be determined, hence, these characters could not be used in the phylogenetic analysis. Pigmentation and morphometric characters have been useful in several systematic studies based on larvae and have been frequently correlated with other derived characters (Johnson 1974; Moser and Ahlstrom 1974; Okiyama 1974; Okiyama and Ueyanagi 1978; Richardson, in press). Clarification of relationships among the species of Clinocottus must await identification of new derived characters or a better understanding of the evolution of pigmentation and body shape within cottid larvae.

The relationships among species of Clinocottus postulated by Bolin (1947) are in close agreement with relationships suggested by larval characters. Bolin placed C. acuticeps in its own subgenus because of its unique possession of a modified penis with a tri-lobed tip and a membrane connecting the innermost pelvic fin ray with the abdomen. Bolin also placed C. analis in its own subgenus because of the retention of minute prickles covering the body. All other members of the genus are scaleless. Clinocottus embryum, C. globiceps, and C. recalvus were placed in the same subgenus because of their large, rounded heads and the retention of a pore behind the last gill. The latter character is plesiomorphic and, hence, of little value for evaluating relationships. Bolin (1947:163) described C. recalvus and C. globiceps as, "two extremely closely related species" because of their hemispherical head shape, an increased number of cirri on the head, and a pair of lateral knobs near the tip of the penis.

Another group of species within the lineage having multiple preopercular spines consists of Oligocottus maculosus and O. snyderi. They share two synapomorphies--a bubble of skin at the nape and dorsal gut bumps. Larval O. rimensis and O. rubellio are not yet identified and, therefore, it is not known if these larvae also possess the synapomorphic characters binding O. snyderi and O. maculosus together.

Bolin (1934, 1947) defined the genus Oligocottus on the basis of the following adult characters: absence of scales, presence of a long, slender, simple penis, and modification of the anterior anal fin rays in males. Only the last character appears to be unique to members of this genus. As mentioned above, evolution of penes and loss of scales

have occurred in several diverse cottid genera. Bolin placed O. maculosus, O. snyderi, and O. rubellio in the same subgenus because of the greatly modified anal fin in males, a permanently external penis, and loss of all but lateral line scales. He further speculated that O. maculosus was the least specialized member of the subgenus and O. rubellio was the most specialized.

Larval O. snyderi possess the derived, autapomorphic characters of multiple prickles covering the parietal and posttemporal regions of the head. In addition, larval O. snyderi possess an accessory spine at the anterior base of most of the main spines on the posterior margin of the preopercle. Both of these conditions are unique specializations of larval O. snyderi. Clarification of relationships of other Oligocottus species must await identification of larval O. rimensis and O. rubellio.

Larval characters indicate that while Oligocottus and Clinocottus are each a monophyletic group, they are closely related. Larvae of both genera are linked together into a higher level monophyletic unit by the possession of a distinctive preopercular spine pattern.

Taranets (1941) also concluded that Oligocottus and Clinocottus are closely related. He placed both genera in the supragenus Oligocottini because of the presence of a penis and the absence of bony plates in both groups.

Artedius fenestralis, A. harringtoni, A. lateralis, and A. Type 3 form the third group of larvae with multiple preopercular spines. These larvae share one synapomorphy, an "Artedius"-type preopercular spine pattern. In addition, larvae of this group possess distinctive pigment slashes on the ventral midline posterior to the anus and a strongly

humped appearance in the nape region. Known larvae of Oligocottus and Clinocottus do not possess either of these characters, however, larvae of several species of Icelinus and Myoxocephalus do possess similar pigment slashes on the ventral midline. Although these characters are not unique to Artedius species, they provide additional support for the cohesiveness of this group.

Within the Artedius group, A. fenestralis, A. lateralis, and A. Type 3 form a distinct subgroup. Larvae of these species share one synapomorphic character, dorsal gut diverticula. Characters identified in this study do not define relationships between these three species. Artedius harringtoni is probably less specialized than the three species possessing gut diverticula. Artedius harringtoni is further distinguished from other Artedius larvae by the possession of seven branchiostegal rays. All other cottid larvae examined in this study possess six branchiostegal rays except several laboratory-reared C. globiceps. Although seven rays is probably a primitive character in scorpaenoids, A. harringtoni appears to have secondarily derived this condition, since none of the outgroup cottids have seven branchiostegals.

This grouping of Artedius larvae with multiple preopercular spines corresponds to Taranets (1941) classification. He placed Artedius corallinus, A. fenestralis, A. harringtoni, A. lateralis, and A. notospilotus together in the supragenus Artediini in the subfamily Oligocottinae.

Other workers have placed all species of Artedius in the same subfamily and genus (Howe and Richardson 1978; Rosenblatt and Wilkie 1963; Bolin 1934, 1947; Hubbs 1926). Bolin (1947:161) included

A. creaseri in Artedius because of the retention of hemilepidotid-like scales "in various degrees of reduction," large head, an unadvanced anus, and "normal structure of the pelvic fins."

A. meanyi was not reported to occur off California at the time of Bolin's work. Hence, he did not include this species in his classification. Rosenblatt and Wilkie (1963) described A. meanyi as being extremely similar to A. creaseri and placed it in Bolin's subgenus Ruscariops along with A. creaseri.

Reduction in squamation and number of pelvic fin rays is found in many different cottid genera and appears to have evolved separately several times. Icelinus, Chitonotus, and Orthonopias also possess hemilepidotid-like scales in various degrees of reduction. Several species of Icelinus, Orthonopias, and Chitonotus possess large heads and unadvanced anuses.

Characters of the larvae indicate that A. creaseri and A. meanyi form a distinct grouping separate from the other species of Artedius. Two synapomorphic characters, a pointed snout and basal preopercular spines provide strong evidence that A. creaseri, A. meanyi, and Icelinus form a monophyletic group. In addition, A. meanyi, A. creaseri, and Icelinus larvae are very similar in other pigmentation, morphometric, and spination characters, giving further support for the cohesiveness of this group. In a phenetic study of larval cottids, Richardson (in press) also placed A. meanyi in a group with Chitonotus, Paricelinus, Triglops, and Icelus. (A. meanyi was misidentified as Icelinus spp. in Richardson's study. See Literature section of A. meanyi description.) Although her study was based on similarities of the larvae and not

synapomorphies, it supports the grouping of A. meanyi and A. creaseri with Icelinus. Larval Chitonotus and Triglops were examined only briefly in the present study, however, they do not appear to possess the synapomorphy, basal preopercular spines, and hence are probably not as closely related to A. meanyi and A. creaseri as Icelinus.

Both phenetic and synapomorphic characters of the larvae provide strong evidence that the genus Artedius (as defined by Bolin 1934, 1947) is not monophyletic and that A. creaseri and A. meanyi should be placed separately. Artedius meanyi and A. creaseri appear to be more closely related to species of Icelinus than to other species of Artedius. Clarification of relationships among A. meanyi and A. creaseri and species of Icelinus must await identification and examination of all species of Icelinus larvae and a reexamination of characters of adult Artedius and Icelinus.

Although larvae of the A. meanyi-creaseri group and the Artedius-Clinocottus-Oligocottus group are distinct from one another, they share certain similarities in comparison to other cottid larvae. Both groups have similar pigment patterns, morphology, and meristics, suggesting that species of these two groups share a common ancestor. Bolin (1947:159) also speculated that Icelinus, Chitonotus, Artedius, Clinocottus, and Oligocottus comprised a single evolutionary line within the Cottidae. He suggested that "certain details of the more primitive members, particularly the scales, indicate that while these forms undoubtedly did not spring from the modern genus Hemilepidotus, they shared a common and not particularly remote ancestor with the fishes of that genus." Although characters of the larvae do not exclude the possibility of a hemilepidotid-

type ancestor, they do indicate that it would be a relatively distant ancestor. Larval Hemilepidotus differ markedly from larvae of Artedius, Clinocottus, Oligocottus, and Icelinus in many characters including meristics, morphometrics, osteology, spination, and pigmentation. It is much more likely that the ancestor of this group possessed characteristics similar to both the Artedius-Icelinus group and the Artedius-Clinocottus-Oligocottus group. Larvae of at least one species of Icelinus and several species of Myoxocephalus possess a fifth or sixth accessory preopercular spine. Larvae of Myoxocephalus also possess two distinct patterns of pigment, one type is lightly pigmented similar to the two Artedius groups, whereas the other has intense bands of lateral pigmentation. An ancestor similar to Icelinus or Myoxocephalus may well have given rise to Artedius, Clinocottus, Oligocottus, and Icelinus. This hypothesis is supported by the presence of one or two accessory preopercular spines in Myoxocephalus larvae. This preopercular spine condition appears to be intermediate between the primitive pattern of four preopercular spines and the derived pattern of multiple preopercular spines. Hence, larvae of the ancestor of Artedius, Clinocottus, and Oligocottus were probably relatively lightly pigmented with melanophores present on the head, nape, dorsal surface of the gut, and along the ventral midline posterior to the anus. In addition, the ancestral larvae probably possessed four large preopercular spines with one accessory spine on the inner preopercular shelf, two parietal spines, and three posttemporal-supracleithral spines.

In summary, the hypotheses of relationships between Artedius, Clinocottus, and Oligocottus based on larvae characters is in general

agreement with previous classifications based on adult characters. Synapomorphic characters of the larvae provide strong evidence that Clinocottus, Oligocottus maculosus, O. snyderi, A. fenestralis, A. harringtoni, A. lateralis, and A. Type 3 form a monophyletic group within the cottids. Within this group, the genera Clinocottus and Oligocottus are very closely related, however, each genus appears to be monophyletic. Artedius fenestralis, A. harringtoni, A. lateralis, and A. Type 3 also form a monophyletic speices group closely related to Clinocottus and Oligocottus. However, synapomorphic characters of the larvae provide strong evidence that A. creaseri and A. meanyi are more closely related to Icelinus than to species of Clinocottus, Oligocottus, and other Artedius. The genus Artedius as defined by Bolin (1934, 1947) does not appear to be monophyletic; A. meanyi and A. creaseri should be placed separately. Clarification of the exact position of these two species in relation to Icelinus and the Artedius-Clinocottus-Oligocottus group must await identification and examination of larvae of all species of Icelinus and reexamination of characters of adult Icelinus and Artedius.

LITERATURE CITED

Ahlstrom, E. H., J. L. Butler, and B. Y. Sumida. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific. Kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci. 26:285-402.

Bailey, R. M., J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robbins, and W. B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada. Amer. Fish. Soc. Spec. Publ. 6. 149 pp.

Berg, L. S. 1940. Classification of fishes, both recent and fossil. Travaux de L'Institut Zoologique de l'Academie des Sciences de l'URSS 5(2):87-517.

Bertelsen, E. 1951. The ceratioid fishes. Ontogeny, taxonomy, distribution, and biology. Dana Rep. 39. 276 pp.

Blackburn, J. E. 1973. A survey of the abundance, distribution, and factors affecting distribution of ichthyoplankton in Skagit Bay. M.S. Thesis, Univ. Washington, Seattle, 136 pp.

Bolin, R. L. 1934. Studies on California Cottidae: an analysis of the principles of systematic ichthyology. Ph.D. Dissertation, Stanford Univ., Stanford. 337 pp.

_____. 1944. A review of the marine cottid fishes of California. Stanford Ichthyol. Bull. 3(1):1-135.

_____. 1947. Evolution of the marine Cottidae of California with a discussion of the genus as a systematic category. Stanford Ichthyol. Bull. 3:153-168.

Breder, C. M., Jr., and D. E. Rosen. 1966. Modes of reproduction in fishes. Natural History Press, Garden City, N. Y. 941 pp.

Budd, P. 1940. Development of the eggs and early larvae of six California fishes. Calif. Fish Game Bull. 56. 53 pp.

Camin, J. H., and R. R. Sokal. 1965. A method for deducing branching sequences in phylogeny. Evolution 19:311-326.

Clemens, W. A., and G. V. Wilby. 1961. Fishes of the Pacific coast of Canada. Fisheries Res. Board (2nd ed.) Canada. 68. 443 pp.

DeLigny, W. 1969. Serological and biochemical studies on fish populations. Oceanogr. Mar. Biol. Annu. Rev. 7:411-513.

Dingerkus, G., and L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52(4):229-232.

Ege, V. 1953. Paralepididae. I. (Paralepis and Lestidium) Taxonomy, ontogeny, phylogeny, and distribution. Dana Rep. 40. 184 pp.

Eigenmann, C. H. 1892. The fishes of San Diego, Calfiornia. Proc. U.S. Natl. Mus. 15:123-178.

Eldridge, M. B. 1970. Larval fish survey of Humboldt Bay. M.S. Thesis. Humboldt State Coll., Arcata, Cal. 52 pp.

Farris, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. 19:83-92.

Farris, J. S., A. G. Kluge, and M. J. Eckhardt. 1970. A numerical approach to phylogenetic systematics. Syst. Zool. 19:172-189.

Fish. M. P., and W. H. Mowbray. 1970. Sounds of North Atlantic fishes. John Hopkins Press, Baltimore. 207 pp.

Gill, T. 1888. On the classification of mailcheeked fishes. Proc. U.S. Natl. Mus. 11:567-592.

Greenwood, P. H., D. E. Rosen. S. H. Weitzman, and C. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living form. Bull. Amer. Mus. Nat. Hist. 131:345-455.

Hennig. W. 1966. Phylogenetic systematics. Univ. Illinois Press. Inc. Urbana. 263 pp.

Howe, K. M., and S. L. Richardson. 1978. Taxonomic review and meristic variation in marine sculpins (Osteichthys:Cottidae) of the northeast Pacific Ocean. Fin. Rep.,NOAA-NMFS Contr. No. 03-78-M02-120. 142 pp.

Hubbs, C. L. 1926. A revision of the subfamily Oligocottinae. Occ. Pap. Mus. Zool. Univ. Michigan 171. 18 pp.

Johnson, R. K. 1974. A revision of the alepisauroid family Scopelarchidae (Pisces:Myctophiformes). Fieldiana (Zool.) 66:1-249.

Jordan, D. S. 1923. A classification of fishes including families and genera as far as known. Stanford Univ. Publ., Univ. Ser., Biol. Sci. 3:77-243.

Jordan, D. S., and B. W. Evermann. 1898. The fishes of North and Middle America. Bull. U.S. Nat. Mus. 47(pt.2):1241-2183.

Kendall, A. W. 1979. Morphological comparisons of North American sea bass larvae (Pisces:Serranidae). U.S. Dep. Comm., NOAA Tech. Rep. NMFS Circ. 428. 50 pp.

Kluge, A. G., and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18:1-32.

Lea, R. N. 1974. First record of Puget Sound sculpin, Artedius meanyi, from California. J. Fish. Res. Board Can. 31:1242-1243.

Marliave, J. B. 1975. The behavioral transformation from the planktonic larval stage of some marine fishes reared in the laboratory. Ph.D. Dissertation, Univ. British Columbia, Vancouver. 231 pp.

Marx, H., and G. B. Rabb. 1970. Character analysis: an empirical approach applied to advanced snakes. J. Zool 161:525-548.

Matsubara, K. 1943. Studies on the scorpaenoid fishes of Japan (anatomy, phylogeny, and taxonomy). Trans. of Sigenkagaku Kenkyusyo. 1:1-486.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill, Inc. New York. 428 pp.

Mickevich, M. F. 1978. Taxonomic congruence. Syst. Zool. 27:143-158.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game Fish Bull. 157. 235 pp.

Morris, R. W. 1951. Early development of the cottid fish Clinocottus recalvus (Greeley). Calif. Fish Game Fish Bull. 37(3):281-300.

_____. 1955. Some aspects of the problem of rearing marine fishes. Bull. Inst. Oceanogr., Monaco (1082):1-61.

Moser, H. G., and E. H. Ahlstrom. 1970. Development of lanternfishes (family Myctophidae) in the California Current. Pt. 1. Species with narrow eyed larvae. Los Angeles Co. Mus. Nat. Hist. Sci. Bull. 7:1-45.

_____. 1972. Development of the lanternfish, Scopelopsis multipunctatus Brauer 1906, with a discussion of its phylogenetic position in the family Myctophidae and its role in a proposed mechanism for evolution of photophore patterns in laternfish. Fish. Bull., U.S. 70(3):541-564.

_____. 1974. Role of larval stages in systematic investigations of marine teleosts: the Myctophidae, a case study. Fish. Bull., U.S. 70(2):391-413.

Nelson, J. S. 1976. Fishes of the world. Wiley-Interscience, New York. 416 pp.

Ohno, S. 1970. The enormous diversity in genome sizes of fish as a reflection of nature's extensive experiments with gene duplication. Trans. Am. Fish. Soc. 99:120-130.

Okiyama, M. 1974. The larval taxonomy of the primitive myctophiform fishes. Pages 609-621 in J. H. S. Blaxter, ed. The early life history of fish. Springer-Verlag, N. Y.

Presch, W. 1980. Evolutionary history of the South American Microteiid lizards (Teiidae:Gymnophthalmus). Copeia 1980(1):36-56.

Quast, J. C. 1965. Osteological characteristics and affinities of the hexagrammid fishes with a synopsis. Proc. Calif. Acad. Sci. 31(21): 563-600.

Regan, C. T. 1913. Osteology and classification of the teleostean fishes of the order Scleroparei. Ann. Mag. Natur. Hist. 8(11): 169-184.

Richardson, S. L. 1977. Larval fishes in ocean waters off Yaquina Bay, Oregon: abundance distribution and seasonality, January 1971-August 1972. OSU Sea Grant Publ. ORESU-T-77-003. 72pp.

_____. In press. Current knowledge of nrothest Pacific sculpin larvae (Family Cottidae) with notes on relationships within the family. Fish. Bull. U.S. 79:(1).

Richardson, S. L., and W. A. Laroche. 1979. Development and occurrence of larvae and juveniles of the rockfishes Sebastes crameri, Sebastes pinniger, and Sebastes helvomaculatus (Family Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:1-46.

Richardson, S. L., and W. G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75(1):125-145.

Richardson, S. L., and B. B. Washington. 1980. Guide to identification of some sculpin (family Cottidae) larvae from marine and brackish waters off Oregon and adjacent areas. NMFS-NOAA 430. 56 pp.

Rosenblatt, R. H., and D. Wilke. 1963. A redescription of the rare cottid fish, Artedius meanyi, new to the fauna of British Columbia. J. Fish. Res. Board Can. 20:1505-1511.

Simpson, G. G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York. 247 pp.

Sneath, P. H. H., and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Company, San Francisco.

Stein, R. 1972. Identification of some larval Pacific cottids. M.S. Thesis, Humboldt State Coll., Arcata, Calif. 41 pp.

_____. 1973. Description of laboratory-reared larvae of Oligocottus maculosus Girard (Pisces:Cottidae) Copeia 1973:373-377.

Taranets, S. Y. 1941. On the classification and origin of the family Cottidae. Isues. Akad. Nauk. SSR, Otd. Biol. 1943(3):427-447. (Trans. from Russian, Univ. British Columbia Mus. Contr. 5:1-28.)

Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596):1-17.

White, W. A. 1977. Taxonomic composition, abundance, distribution and seasonality of fish eggs and larvae in Newport Bay, California. M.S. Thesis, Calif. State Univ., Fullerton. 107 pp.

Zehren, S. J. 1979. The comparative osteology and phylogeny of the Beryciformes (Pisces:Teleostei). Evol. Monogr. 1:1-389.