RECLAMATION

*Managing Water in the West*


# Embryogenesis and Ammocoete Morphological Development of the Pacific Lamprey (*Entosphenus tridentatus* Gairdner, 1836) from the American River, California

## Tracy Technical Bulletin 2008-3

U.S. Department of the Interior
Bureau of Reclamation
Mid-Pacific Region
Denver Technical Service Center

November 2008

| **1. REPORT DATE** *(DD-MM-YYYY)* | **2. REPORT TYPE** | **3. DATES COVERED** *(From - To)* |
|---|---|---|
| November 2008 | Final | |

**4. TITLE AND SUBTITLE**
Embryogenesis and Ammocoete Morphological Development of the Pacific Lamprey (*Entosphenus tridentatus* Gairdner, 1836) from the American River, California

**5a. CONTRACT NUMBER**

**5b. GRANT NUMBER**

**5c. PROGRAM ELEMENT NUMBER**

**6. AUTHOR(S)**
René C. Reyes

**5d. PROJECT NUMBER**

**5e. TASK NUMBER**

**5f. WORK UNIT NUMBER**

**7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)**
Bureau of Reclamation, Tracy Fish Collection Facility, TO-410,
16650 Kelso Road, Byron CA 94514-1909

**8. PERFORMING ORGANIZATION REPORT NUMBER**
Tracy Technical Bulletin 2008-3

**9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)**
Bureau of Reclamation, Tracy Fish Collection Facility, TO-410,
16650 Kelso Road, Byron CA 94514-1909

**10. SPONSOR/MONITOR'S ACRONYM(S)**

**11. SPONSOR/MONITOR'S REPORT NUMBER(S)**

**12. DISTRIBUTION/AVAILABILITY STATEMENT**
Available from the National Technical Information Service (NTIS)
Operations Division, 5285 Port Royal Road, Springfield VA 22161

**13. SUPPLEMENTARY NOTE**

**14. ABSTRACT**

Early life stages of Pacific lamprey (*Entosphenus tridentatus*) from the American River in northern California are described. Pacific lamprey eggs hatch between 18 to 23 days at 12 °C (± 1 °C). First feeding was observed as early as the gill stage when they were approximately 8 millimeters (mm) (0.314 inches [in]) total length (TL). Ammocoetes burrowed into the substrate 12 to 14 days after hatching when they were approximately 9 mm (0.354 in)TL. Functional digestive tract, apparent when the gut tissue became transparent and remaining yolk mass excreted, was observed when ammocoetes were greater than 20 mm (0.787 in) or about 30 days after hatching. Early stage development of the Pacific lamprey was similar to the well-studied sea lamprey (*Petromyzon marinus*) and other lamprey species. Egg and larval development of the Pacific lamprey in California are not well-documented. This paper briefly describes the egg development and larval morphological development of Pacific lamprey from the American River and contains images and enumeration of stages corresponding to Piavis' (1961) sea lamprey embryological and ammocoete study.

**15. SUBJECT TERMS**
Pacific lamprey, American River, ammocoetes, lamprey, larvae, early life stages, embryogenesis, sea lamprey, egg development

| **16. SECURITY CLASSIFICATION OF:** | | | **17. LIMITATION OF ABSTRACT** | **18. NUMBER OF PAGES** | **19a. NAME OF RESPONSIBLE PERSON** |
|---|---|---|---|---|---|
| | | | | | Donald E. Portz, Ph.D. |
| **a. REPORT** | **b. ABSTRACT** | **a. THIS PAGE** | | 34 | **19b. TELEPHONE NUMBER** *(Include area code)* |
| | | | | | 303-445-2220 |

# Tracy Fish Facility Studies
# California

## Embryogenesis and Ammocoete Morphological Development of the Pacific Lamprey (*Entosphenus tridentatus* Gairdner, 1836) from the American River, California

Tracy Technical Bulletin 2008-3

by

René C. Reyes[1]

November 2008

U.S. Department of the Interior
Bureau of Reclamation
Mid-Pacific Region
Denver Technical Service Center

[1] Bureau of Reclamation
Tracy Fish Collection Facility, TO-410
16650 Kelso Road
Byron CA 94514-1909

## MISSION STATEMENTS

The mission of the Department of the Interior is to protect and provide access to our Nation's natural and cultural heritage and honor our trust responsibilities to Indian tribes and our commitments to island communities.

---

The mission of the Bureau of Reclamation is to manage, develop, and protect water and related resources in an environmentally and economically sound manner in the interest of the American public.

## TRACY FISH FACILITY IMPROVEMENT PROGRAM

Ron Silva, Manager

## TRACY SERIES EDITOR

Donald E. Portz, Ph.D.
U.S. Department of the Interior – Bureau of Reclamation
Technical Service Center
Fisheries and Wildlife Resources Group, 86-68290
PO Box 25007
Denver CO 80225-0007

## COVER

Fish photography by René Reyes, Tracy Fish Collection Facility, Tracy, California.
Design by Doug Craft.

## DISCLAIMER

Mention of commercial products does not constitute endorsement.

# TABLE OF CONTENTS

*Page*

**Abstract** ..... **iv**
**Introduction** ..... **1**
**Materials and Methods** ..... **2**
Study Area ..... 2
Pacific Lamprey Eggs ..... 2
Pacific Lamprey Ammocoetes ..... 4
**Results** ..... **4**
Embryogenesis ..... 4
Ammocoete Development Stages ..... 13
**Discussion** ..... **19**
**Acknowledgments** ..... **22**
**References** ..... **22**
**Glossary and Abbreviations** ..... **26**

## Table

*Table* *Page*

1 Comparison of Pacific lamprey early life stages with other lamprey ..... 20

## Figures

*Figures* *Page*

1 Map of the study area ..... 3
2 Generalized embryology and terminology for Pacific lamprey ..... 5
3 Pacific lamprey developing eggs. ..... 6
4 Morula stages. ..... 7
5 Blastula stage ..... 8
6 Gastrula stage ..... 9
7 Neurula to neural rod stage. ..... 10
8 Head stage. ..... 11
9 Prehatching stage. ..... 12
10 Hatching. ..... 13
11 Morphology of a Pacific lamprey ammocoete ..... 14
12 Pigmentation stage. ..... 15
13 Gill stage ..... 16
14 Burrowing stage ..... 16
15 Larva. ..... 17
16 Ammocoete head development sequence. ..... 18
17 Eggs of other species found in lamprey redds. ..... 21

# ABSTRACT

Early life stages of Pacific lamprey (*Entosphenus tridentatus*) from the American River in northern California are described. Pacific lamprey eggs hatch between 18 to 23 days at 12 °C (± 1 °C). First feeding was observed as early as the gill stage when they were approximately 8 millimeters (mm; 0.314 inches [in]) total length (TL). Ammocoetes burrowed into the substrate 12 to 14 days after hatching when they were approximately 9 mm (0.354 in) TL. Functional digestive tract, apparent when the gut tissue became transparent and remaining yolk mass excreted, was observed when ammocoetes were greater than 20 mm (0.787 in) or about 30 days after hatching. Early stage development of the Pacific lamprey was similar to the well-studied sea lamprey (*Petromyzon marinus*) and other lamprey species. Egg and larval development of the Pacific lamprey in California are not well-documented. This paper briefly describes the egg development and larval morphological development of Pacific lamprey from the American River and contains images and enumeration of stages corresponding to Piavis' (1961) sea lamprey embryological and ammocoete study.

# INTRODUCTION

The Pacific lamprey (*Entosphenus tridentatus*) is a parasitic, eel-like aquatic vertebrate restricted to the Pacific coast of North America from the Aleutian Islands to Baja California (Scott and Crossman, 1973; Morrow, 1980; Ruiz-Campos and Gonzalez-Guzman, 1996; Moyle, 2002). In California, they are found in the Sacramento-San Joaquin River Delta system from below the Friant Dam on the San Joaquin River (Moyle and Nichols, 1973) to the upper drainages of the Sacramento River including the Red Bluff diversion dam (Wang, 1986). Pacific lampreys go through a larval stage (ammocoete) and an adult stage. After hatching, the ammocoetes spend a short time in the gravel nest, eventually swim up into the current, and are washed downstream to a suitable area of soft sand or mud (Moyle, 2002). Ammocoetes have undeveloped eyes (although eyespots are present), teeth, and a sucking disk. They filter feed by straining organic material from the water column and diverting it into the mouth by a scoop-shaped oral hood (McPhail and Lindsey, 1970; Meeuwig *et al*., 2004) and by sucking organic matter and algae off the substrate surface (Moore and Mallat, 1980; Moyle, 2002). Eventually ammocoetes develop large eyes and a sucking disk with teeth, and metamorphose into a parasitic adult. The length of the ammocoete stage has not been verified but is believed to be about 3–7 years (Hardisty and Potter, 1971) or 5–7 years (Scott and Crossman, 1973; Hammond, 1979; Moyle, 2002).

Pacific lamprey are anadromous. Recently observed presence of bile acids produced by feeding ammocoetes may drive adult migratory behavior in Pacific lamprey (Sorensen and Close, 2000), similar to the sea lamprey (*Petromyzon marinus*; Vrieze and Sorensen, 2001). Adults usually migrate to spawning streams between early March and late June (Moyle, 2002). In the American River, Pacific lampreys were observed spawning from January to June. During the 3 years of lamprey egg collection (2003–2005), the peak lamprey spawning occurred late March to early April (Hannon and Deason, 2004). Nests are built by moving rocks to the downstream end of the depression (Moyle, 2002) leaving much of the sand and smaller gravel in the depression (Hannon and Deason, 2004). Female fecundity is high, from a low range of 10,000–106,000 eggs (Pletcher, 1963) to the high range of 98,000–240,000 eggs (Kan, 1975).

The early life stages of Pacific lamprey play an important role in the river ecosystem. Numerous fishes, including salmon fry, have been observed feeding on lamprey eggs and ammocoete in lamprey redds during and after spawning (Pletcher, 1963; Pfeiffer and Pletcher, 1964; Manion, 1968). In Oregon, speckled dace (*Rhinichthys osculus*) feed heavily on Pacific lamprey eggs (Brumo, 2006). White sturgeon (*Acipenser transmontanus*) and several species of salmonids have been known to utilize Pacific lamprey ammocoetes (Hammond, 1979; Claire, 2004). The ammocoetes live in habitats where they feed on diatoms, which are unexploited by other vertebrates (Pletcher, 1963; Kan, 1975). Ammocoetes drift almost exclusively at night throughout the spring and summer at rates exceeding several thousand per hour (White and Harvey, 2003). This large amount of prey could be a significant source of food for fishes of special concern

such as salmonids. Juvenile lampreys migrating downstream may have buffered salmonid juveniles from predation by predacious fishes and sea gulls (Close *et al*., 1995).

Embryonic development (embryogenesis) and ammocoete morphological development of Pacific lamprey are similar to the well-studied sea lamprey. The objective of this study is to document and describe the embryology of Pacific lamprey and the morphological development of the Pacific lamprey ammocoete in the American River in northern California, applying the staging enumeration used by Piavis (1961) for sea lamprey. Although ecological and biological information for the Pacific lamprey is known from studies conducted in Canada and the Pacific Northwest (e.g., Pletcher, 1963; Beamish, 1980; Richards, 1980; Claire, 2004; Meeuwig *et al*., 2005), most of the studies emphasized adult migration and fish passage with little targeted research elsewhere, especially in early life histories (Brumo, 2006). Information on the early life history and stages of this species in California is deficient.

# MATERIALS AND METHODS

## Study Area

The American River is a tributary of the Sacramento River located near Sacramento in northern California (Figure 1). Just like other rivers in California, water flow from the American River is regulated by dams built for irrigation, municipal, and industrial uses. The Folsom Dam (not pictured in map), constructed by the U.S. Army Corps of Engineers and transferred to the Bureau of Reclamation (Reclamation), is an integral part of the Central Valley Project. Nimbus Dam, 11 kilometers (6.8 miles) downstream from Folsom Dam, regulates the water releases for power made through the Folsom Power Plant. Power generated from both Folsom and Nimbus power plants is marketed by the Western Area Power Administration. The American River and Nimbus fish hatcheries were built to compensate for the loss of salmonid spawning habitat due to the dams. Pacific lamprey spawn using oxbows and shallow locations composed of rock and gravel throughout the stretch of the river below the dams and hatcheries.

## Pacific Lamprey Eggs

Fertilized lamprey eggs were obtained from the American River Steelhead Survey conducted by Reclamation's John Hannon and Brian Deason. Additional eggs were obtained from nests shallow enough to be accessed on foot. Pacific lampreys were observed spawning in the American River from January to May. Eggs were collected early spring of 2003–2005. Soon after collection, eggs were placed into labeled 1-liter (L; 0.26 gallons [gal]) Nalgene containers, which were kept in 38-L (10-gal) coolers with ice for the 2-hour transport to the laboratory.

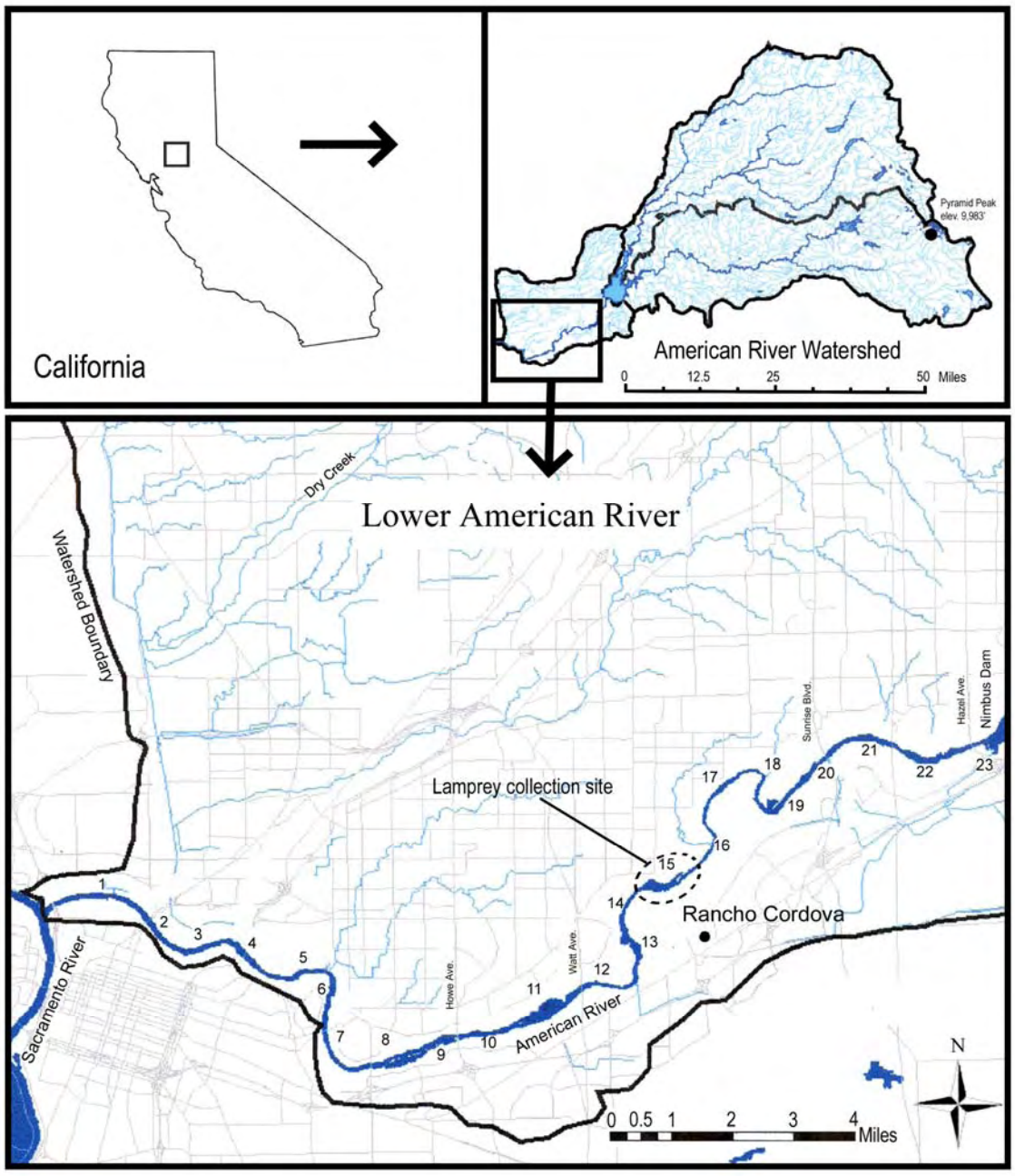


FIGURE 1.—Map of the study area. Pacific lamprey eggs were collected from the lower American River above Rancho Cordova, CA. The numbers are river miles measured from the Sacramento River confluence. Map courtesy of John Hannon, Bureau of Reclamation.

Only wild-spawned newly fertilized eggs were used for the embryological observations. These eggs were used for determining hatch-size range and larval morphological descriptions. Newly fertilized eggs were identified by the presence of the animal and vegetal poles and also by the beginning of the visible furrows. Because eggs were collected from the wild, determination of time of fertilization can only be estimated. Only eggs at the morula or earlier stages were used. Eggs were incubated at a

temperature of 12 °C ± 1 °C in 1-L (0.26-gal) bowls of freshwater. Twenty eggs were placed in each bowl. Water was changed daily by siphoning out half and replacing with water of the same temperature to avoid shock.

Eggs were digitally photographed using a 5.0-megapixel Polaroid camera attached to a stereomicroscope (Leica MZ7, Leica Microsystems, Inc., Bannockburn, Illinois). Photographs were calibrated, labeled, and archived for future reference. Because of the accumulation of images over time, an image database of the egg and larvae development was created. During the incubation process, measurements and observations were made. Imaging analysis software (Image-pro© version 6.2, Media Cybernetics, Inc., Bethesda, Maryland) was used to obtain accurate measurements. Eggs and larvae were preserved in buffered formalin for future reference. Additional eggs were preserved and sent to University of California at Davis for histology. However, attempts at slicing the eggs and obtaining proper stains of the embryos were unsuccessful.

## Pacific Lamprey Ammocoetes

Soon after hatching, ammocoetes were measured. Anesthesia (Tricaine Methanesulfonate [MS-222], Argent Laboratories, Redmond, Washington) was not used for day 0 ammocoetes since they are not very active at this stage. Measurements and observations were taken along with several calibrated images for future analysis. Image-pro© was used for accurate measurements of archived and calibrated images.

The ammocoetes were slowly acclimated to room temperature of 18 °C ± 1 °C within 7 days (increase of 1 °C/day). The ammocoetes were kept in labeled 5.2-L (1.4-gal) trays, and their growth was monitored. Morphology changes as well as their behavior were noted daily. After 10 days, ammocoetes were placed on a substrate consisting of mud and sand in order to observe burrowing behavior and length of time until burrowing. Observations on lamprey behavior were limited once burrowing was initiated. Newly hatched ammocoete are sometimes called “proammocoete” (Potter, 1980); however, in this paper, the life stages after hatching will be called “ammocoete.”

# RESULTS

The results section is divided into two parts: Embryogenesis and Ammocoete Development Stages. There are 14 stages for the embryogenesis of Pacific lamprey and 4 stages of ammocoete development. After each stage, except for stage 0–1, images immediately follow the stage description.

## Embryogenesis

Pacific lamprey eggs are deposited in redds made of rocks, stones, and gravel (Moyle, 2002; Hannon and Deason, 2004). Eggs are not adhesive and stay buried until ammocoetes emerge. In the laboratory, eggs hatched between 18–23 days post spawn

(dps) at 12 °C (± 1 °C). Unlike teleost fishes, which have meroblastic cell division, initial egg division of Pacific lamprey is holoblastic, meaning the entire egg divides. Eggs slightly dilate from newly fertilized eggs with egg-size range of 1.4–1.5 mm (0.055–0.059 in) to prehatching size range of 1.5–1.6 mm (0.059–0.063 in). Eggs were spherical, sometimes elliptical to irregular, slightly adhesive, and are deposited singly. The embryo is mostly white at the zygote to morula stages. The yolk mass becomes defined at the head development stage and is mostly yellow to greenish in color. A generalized sequence of egg development and some common terminology is shown in Figure 2. A more detailed egg development sequence is summarized in Figure 3.

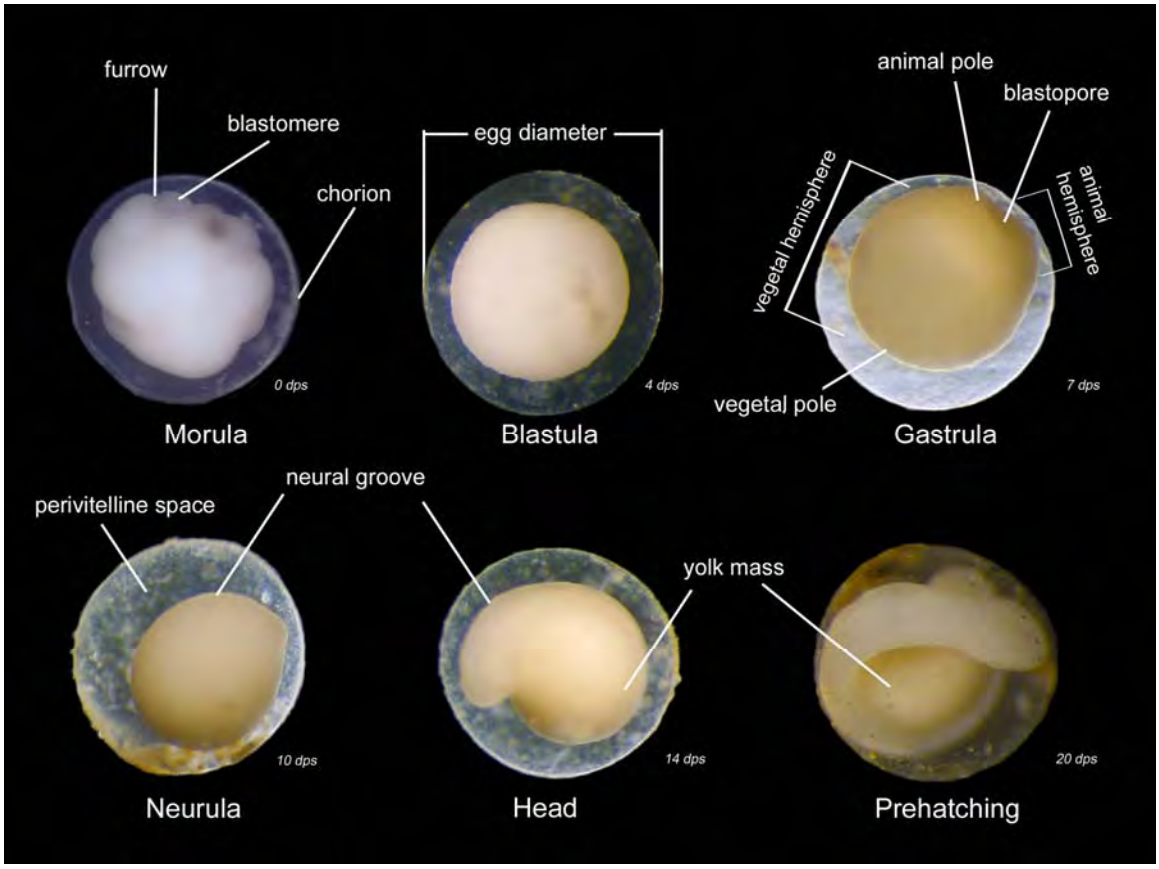


FIGURE 2.—Generalized embryology and terminology for Pacific lamprey.

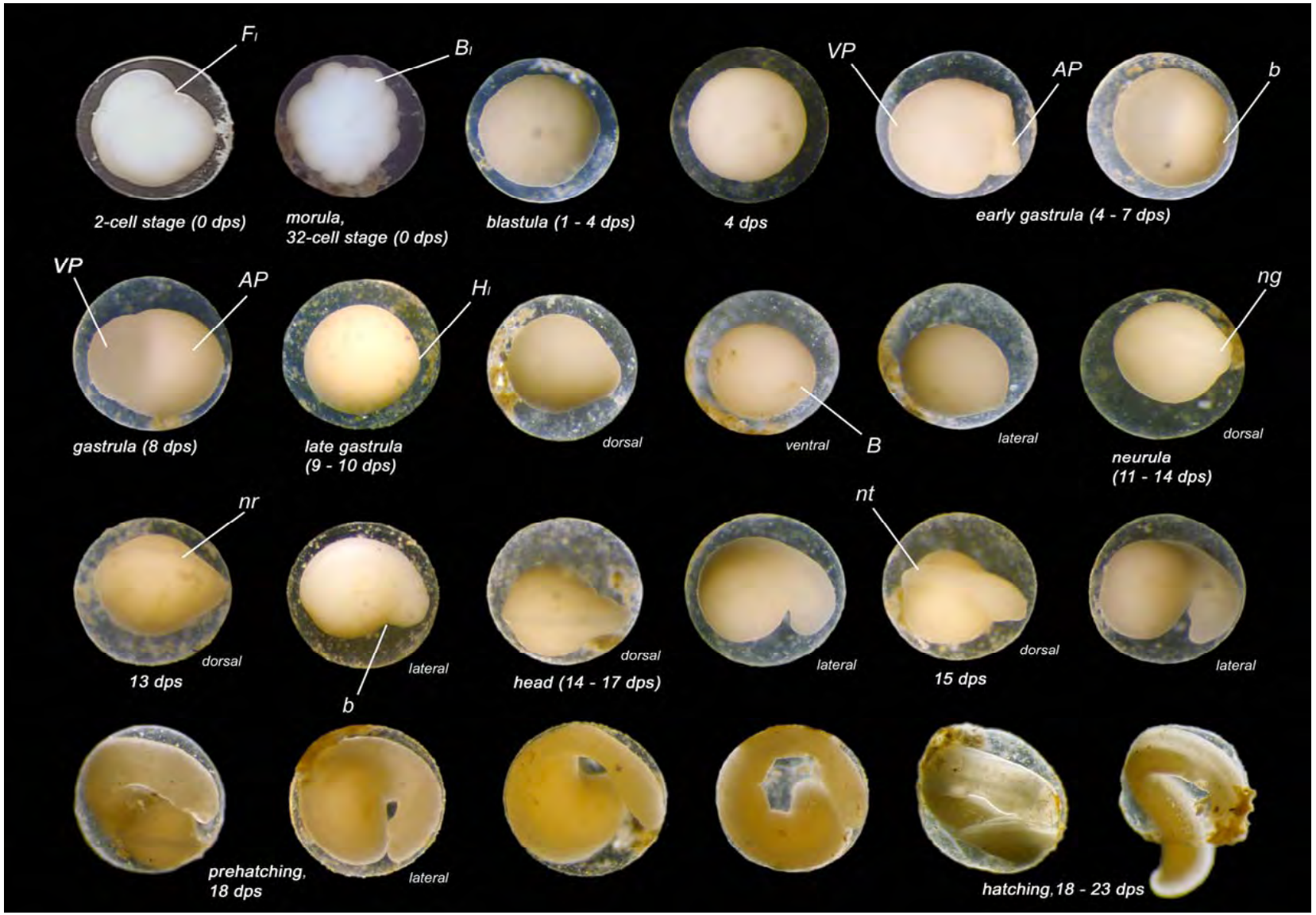


FIGURE 3.—Pacific lamprey developing eggs positioned so that the animal pole and developing head are pointed to the right. $F_I$ = furrow of the 1st cleavage, $B_I$ = irregular blastomeres, AP = animal pole, VP = vegetal pole, b = blastopore, $H_I$ = developing head, ng = neural groove, nr = neural rod, nt = neural tube. Eggs incubated at 10–13 °C.

**Stage 0–1**: Ovulated but unfertilized egg to Zygote, 0 dps.

*Egg size:* ~ 1.0 mm (0.039 in).

*Description:* The egg at these stages is circular or oval, has a smooth surface, and is not adhesive. Eggs are telolecithal, meaning the egg has a large amount of yolk. A depression at the animal pole becomes visible where the cleavage will occur.

**Stage 2–7**: Morula stages (2-cell to 64 cells), 0 dps (Figure 4).

*Egg size:* 1.4–1.5 mm (0.055–0.059 in) in diameter, $n$ = 20.

*Description:* Morula stage begins when the first cleavage appears at stage 2. Cell division of the egg is holoblastic. Cleavage begins as a small furrow at the animal pole. The furrows (white arrows) are unequal in length during division, therefore, the blastomeres are irregular and the embryo looks "bumpy." The embryo is white and opaque. The chorion and perivitelline space are clear. Stages 1 to 7 are complete within 24 hours. The end-point of stage 7 is reached when there are more than 64 cells.

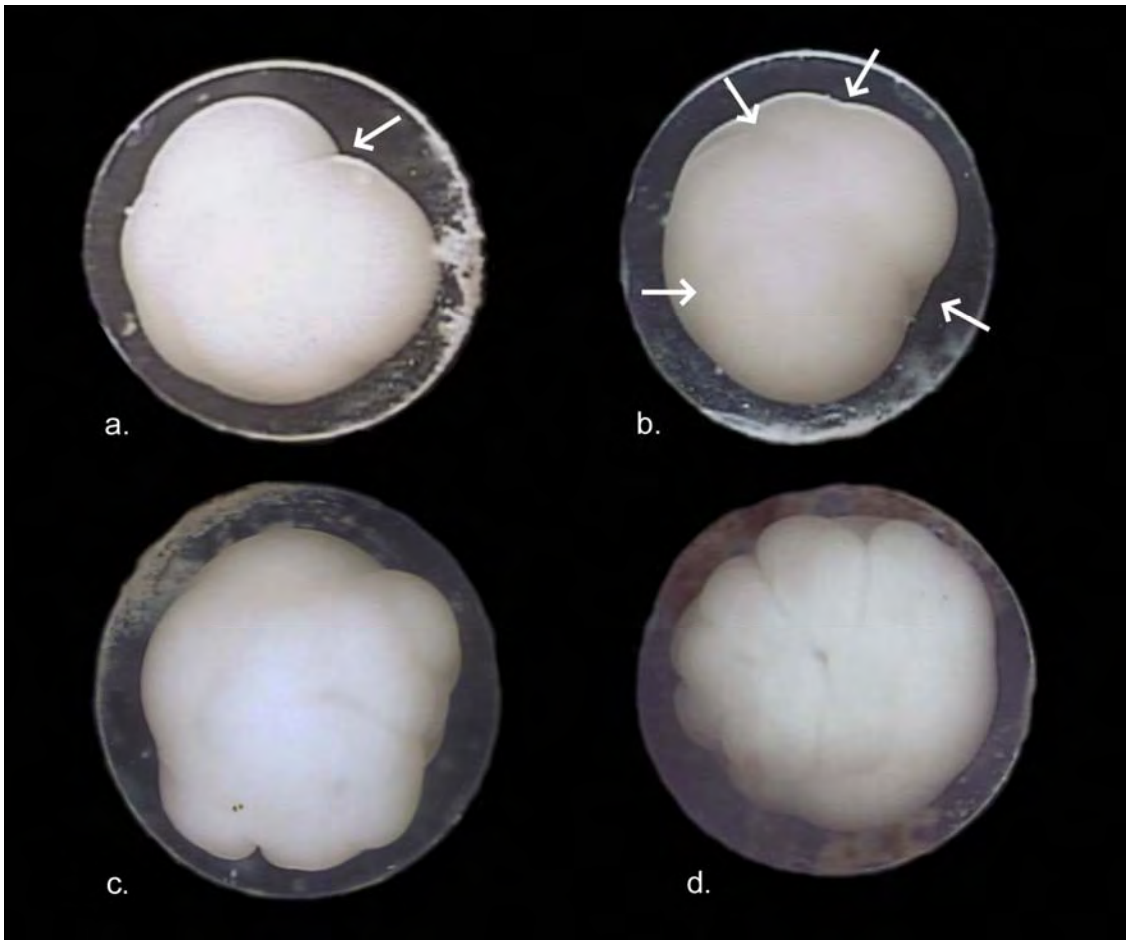


FIGURE 4.—Morula stages showing irregular shaped embryos at 0 dps. White arrows point at the location of the cleavage or furrow: a. 2-cell stage (Stage 2) showing the first cleavage dividing the egg into 2 unequal blastomeres; b. 4-cell stage (Stage 3) with 4 unequal blastomeres; c. 16-cell stage (Stage 5); d. 32-cell stage (Stage 6). Not pictured are 8-cell stage (Stage 4) and 64-cell stage (Stage 7).

**Stage 8**: Blastula, 1–4 dps (Figure 5).

*Egg size:* 1.41–1.59 mm (0.055–0.062 in), avg. size of 1.49 mm (0.058 in), *n* = 33.

*Embryo:* avg. size of 1.17 mm (0.046 in).

*Description:* As the number of cell division increases, blastomere size decreases. Therefore, the embryo's surface looks progressively more smooth and spherical. Blastocoel, an opening within the embryo (Romer, 1962), is visible through the animal cells. This stage ends when the blastopore appears and the animal pole differentiates.

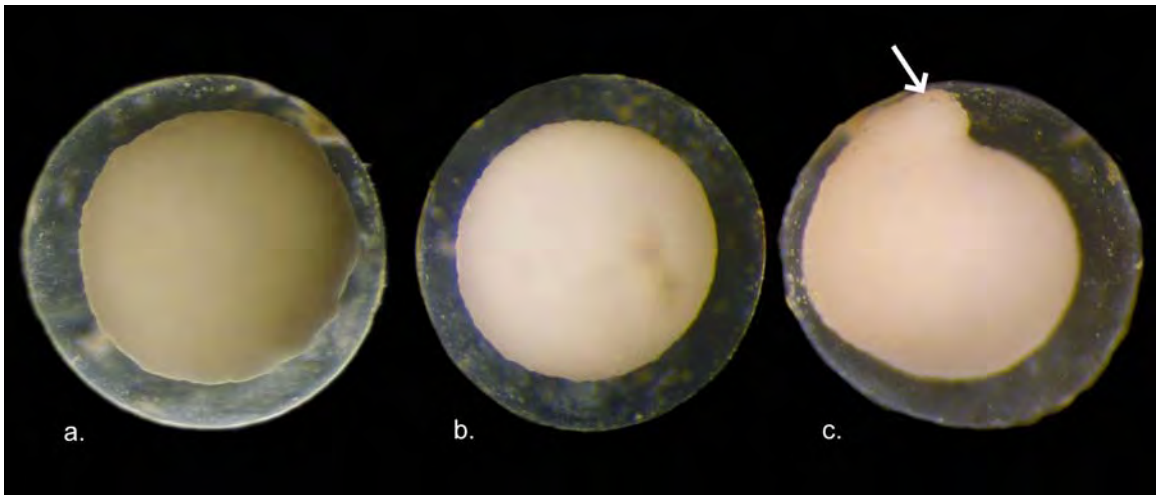


FIGURE 5.—Blastula stage at 1–4 dps: a. Early blastula with small blastomeres; b. Blastula stage showing smooth surface; c. Late blastula with differentiating animal pole (white arrow) and blastopore appearing (not visible in this image).

**Stage 9:** Gastrula, 4–10 dps (Figure 6).

*Egg size:* 1.46–1.64 mm (0.057–0.064 in) in diameter, avg. of 1.53 mm (0.06 in), *n* = 81.

*Embryo:* avg. size of 1.2 mm (0.047 in).

*Description:* As the unevenness of the animal hemisphere (see above Figure 5c) becomes less, the embryo appears divided by two sections: an opaque animal hemisphere and a translucent vegetal hemisphere. Initially, the animal hemisphere becomes rounded, and a large, circular blastopore appears at the apex of the animal hemisphere. During gastrulation, embryonic cells migrate through the blastocoele. The translucent part (vegetal hemisphere) becomes smaller and appears to be engulfed (epiboly) by the movement of the ectoderm of the opaque animal hemisphere. This migration of the animal cells is evident by the advancing margin of the epibolizing cells. The engulfed cells, the mesoderm and endoderm, go on to form the somites (J. Wang, 2008, personal communication) and the lining of the gut (Romer, 1962), respectively. At completion of epiboly, the embryo is opaque and is white to cream in color. The blastopore decreases in size, becomes more elliptical, and begins its migration beneath the developing crescent-shaped dorsal lip. The migration seems to be along the midsagittal plane of the embryo or ventrally towards the rear. In sea lamprey, the apparent migration of the

blastopore resulted from the reduction in the size of the blastocoele (Piavis, 1961). The dorsal lip over the blastopore marks the end of the gastrula stage.

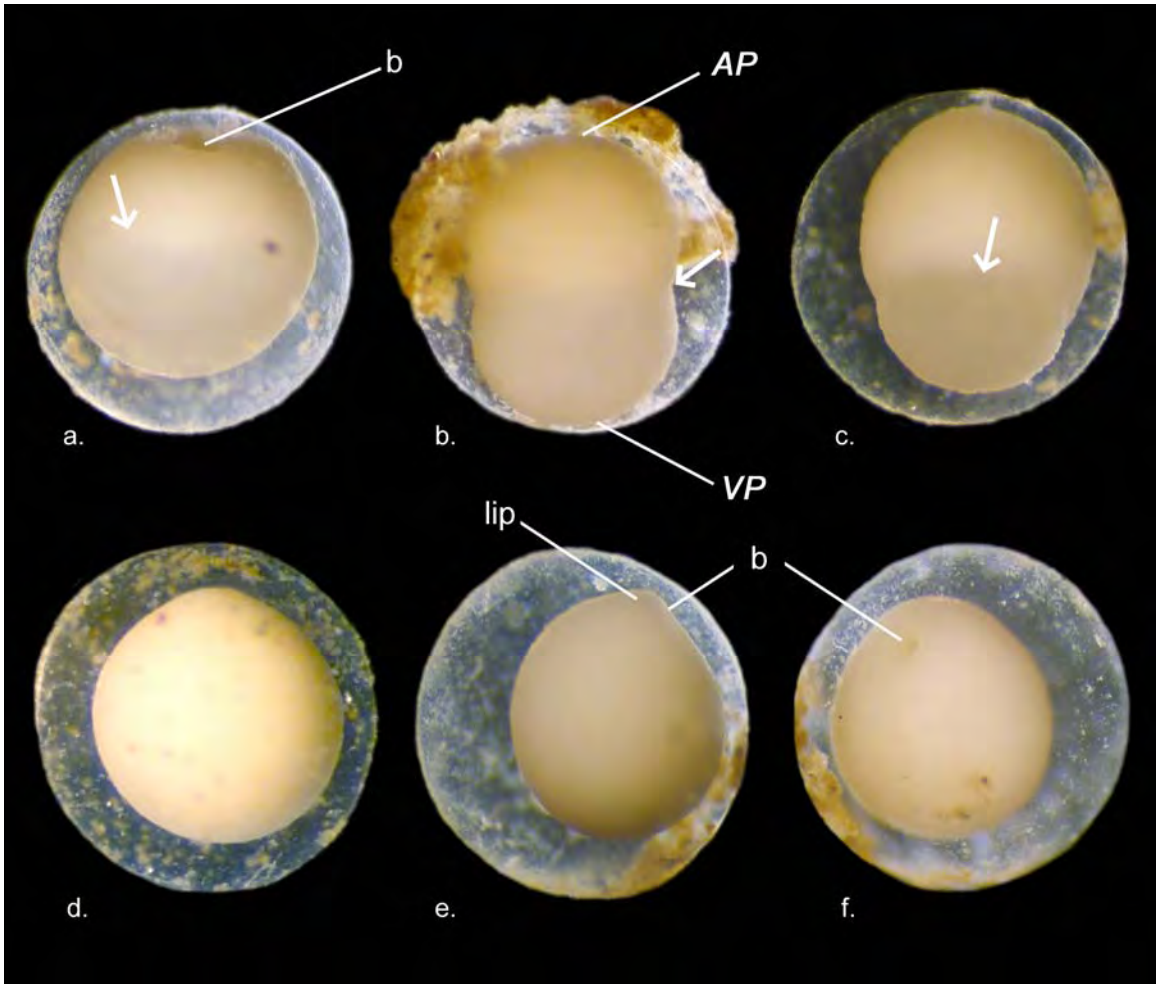


FIGURE 6.—Gastrula stage at 4–10 dps. The eggs are aligned so that the animal pole (AP) is facing north and the vegetal pole (VP) is facing south. a–c illustrates the epibolization or epidermal cell migration. The white arrows point at the advancing margin of the epibolizing cells: a. The initial blastopore (b) is large and located at the AP; b. 50% epiboly; c. 75% epiboly. d-e illustrates the shape of the 100% epiboly, gastrulated embryo at three different views: d. Dorsal view of the embryo showing the protruding dorsal lip at the AP; e. Lateral view of the embryo showing crescent-shaped dorsal lip covering the blastopore; f. Ventral view of the embryo showing the smaller, elliptical blastopore.

**Stage 10–11:** Neurula to neural rod**,** 11-14 dps (Figure 7).

*Egg size:* 1.54-1.55 mm (0.06-0.061 in) in diameter, avg. size of 1.52 mm (0.059 in), $n = 29$.

*Embryo:* about 1.0 mm (0.039 in) at the short axis to 1.2 mm (0.047 in) at the long axis.

*Description:* Neural groove is observed at the middle of the thickening neural plate. Neural folds on both side of the neural groove become elevated. As it becomes more elevated, the folds unite to form a single neural rod. Neurula stage ends at the first fusing

of the folds. At the neural rod stage, the neural rod becomes prominent across the dorsum of the embryo, for about three quarter the length of the embryo. The blastopore is now at the uppermost point of its initial migration along the midsagittal plane. Laterally, the embryo is shaped like a bean.

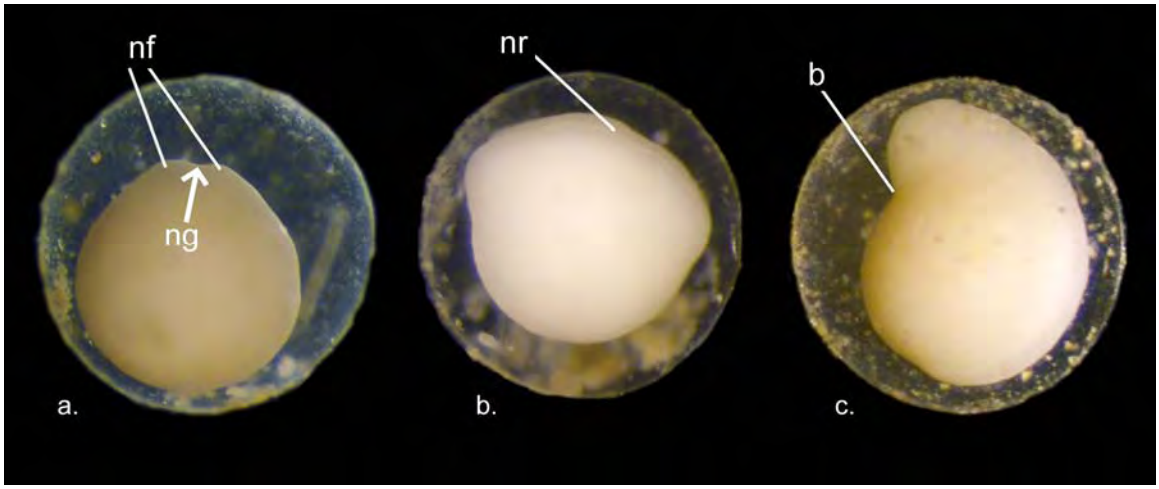


FIGURE 7.—Neurula to neural rod stage at 11–13 dps: a. Dorsal view of the neurula embryo which begins with the appearance of the neural groove (ng) located between the two neural folds (nf); b. Neurula embryo illustrating the nf beginning to fuse to create the neural rod (nr). Neurula stage ends when the first union of the two folds occurs; c. Lateral view of the nr embryo illustrates initial location of the blastopore before it starts migrating posteriorly along the midsagittal plane.

**Stage 12:** Head, 14–17 dps (Figure 8).

*Egg size:* 1.45–1.64 mm (0.057–0.064 in) avg. diameter of 1.55 mm (0.061 in), $n = 29$.

*Length of head:* about 0.27 mm (0.01 in) at 14 days to 0.54 mm (0.021 in) at 17 dps (taken from tip of head to anterior-most part of yolk mass).

*Description:* The head at this stage is now elevated from the yolk mass. The yolk mass is spherical. "Cheeks" on head are developing. The neural rod runs almost the full length of the embryo. The blastopore, difficult to see, has migrated posteriorly and is located at the posterior-most point of the neural rod, right below the ventral side of head. Somites are faintly visible. First signs of muscle movements (neck and head moving laterally) occur at this stage of head development. The stage ends at the first sign of muscle movement.

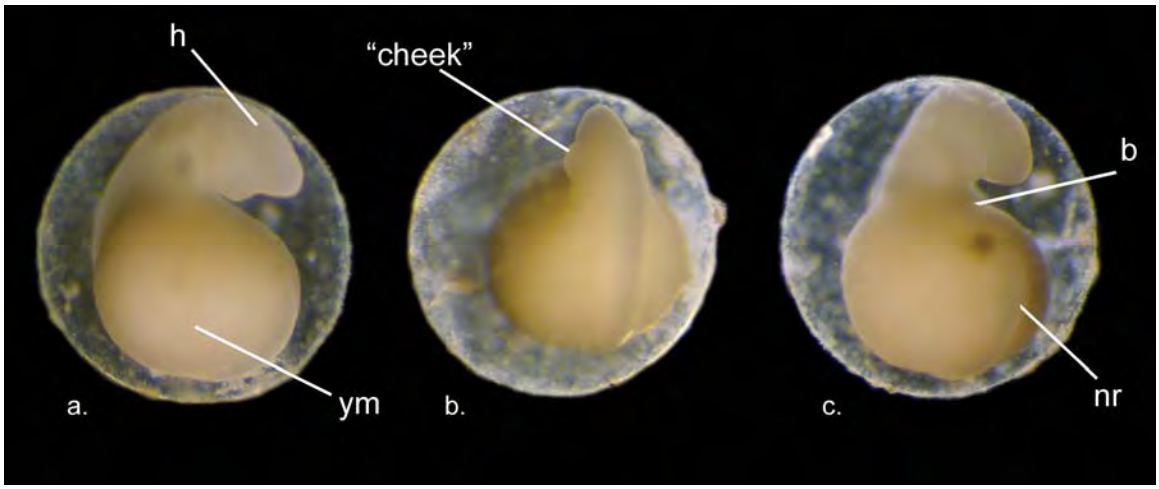


FIGURE 8.—Head stage at 14–17 dps: a. Lateral view of the head stage embryo. The head (h) is protruded and elevated from the yolk mass (ym); b. Dorsal view of the head stage embryo illustrating the spherical shape of the ym and prominent cheeks on the head; c. Ventral view of the embryo illustrating the neural rod (nr) extending almost the full length of the embryo. At the end of the nr is the blastopore (b), not visible in this image.

**Stage 13:** Prehatching, 18–21 dps (Figure 9).

*Size:* 1.53–1.63 mm (0.060–0.064 in).

*Length of head and "neck":* 1.4–1.6 mm (0.055– 0.062 in) taken from tip of head to anterior-most part of yolk mass at the midline.

*Description:* Embryos are very active. The "neck" (distance between yolk mass and head) is longer. Somites are more visible. Perivitelline space is almost fully occupied by the active embryo which is pushing itself against the inside wall of the chorion. The neural rod is now a true neural tube (Piavis, 1961). The dorsal fin is elevated. Active head movement from side to side causes the egg membrane to slowly tear. The heart is visible towards the end of the stage. The stage ends when the head breaks through the chorion membrane to initiate hatching.

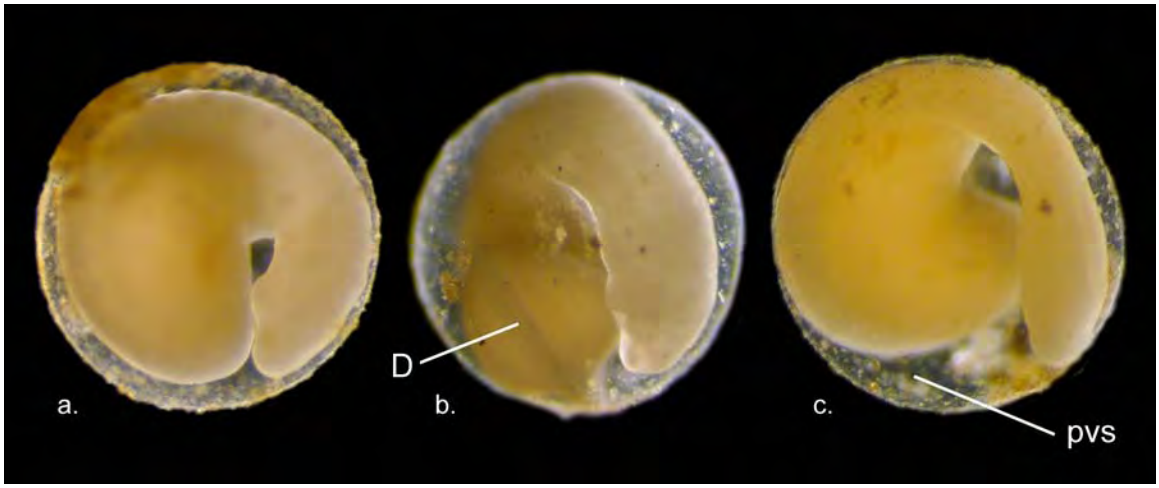


FIGURE 9.—Prehatching stage at 18–21 dps: a. Lateral view of embryo with yolk mass that is more slender; b. Ventral view of the yolk mass showing elevation of dorsal fin (D); c. Prehatching embryo occupying most of the perivitelline space (pvs).

**Stage 14:** Hatching, 18–23 dps, 0 dph (Figure 10).

*Size:* 4.5–6.0 mm (0.177–0.236 in) total length (TL), mostly 5.6 mm (0.220 in) TL at hatching.

*Preanal length (PAL) / TL:* 93–97%, mostly 95%, anus is located near the posterior end.

*Blastopore:* Located at the ventral flexion of the posterior and is very tiny.

*Head:* Eyes are not developed and with no visible pigments.

*Description:* Hatching begins when embryo breaks through the chorion, usually head first. The first day the newly hatched embryo is outside of the chorion is called 0 day post hatch (dph). The heart is beating and the yolk mass is elongated. Gill slits and oral opening are visible but are not functional (Figure 16a). Eyes are not yet developed. There are no pigments on the body. Body coloration ranges from white or cream to green. Ammocoetes hatch initially as curled larvae but become straighter in a few hours. Movement of the body is mainly anterior and is restricted by the heavy yolk-filled gut. Ammocoetes are on their sides, inactive, on the bottom substrate. Thirty to 40 preanal somites are visible. Hatching stage ends when melanophores appear on the embryo.

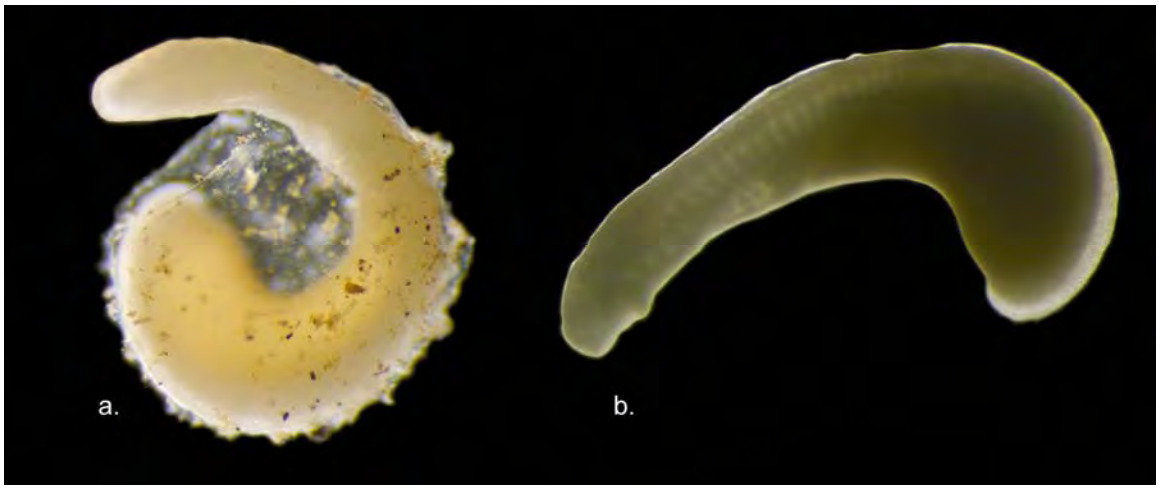


FIGURE 10.—Hatching at 18–23 day post hatch (dph): a. Head normally tears through the chorion first; b. Greenish colored newly hatched ammocoete (0 dph) with no pigments on the body.

## Ammocoete Development Stages

Pacific lamprey eggs hatch between 18–23 dps at 12 °C (± 1 °C) in the laboratory. In the wild, newly hatched ammocoetes have been collected in the nest, between stones and gravel. In the laboratory, newly hatched ammocoetes are inactive and remain on their side. The stages of development for the ammocoete show a gradual migration of the anus anteriorly. PAL / TL changes from a high of 93% at the newly hatched stage to a low of 87% at the burrowing stage. Oral opening develops from a slit during newly hatched to a functional mouth with a large oral hood during the burrowing stage. Refer to Figure 11 for locations and names of body structures of an ammocoete. Ammocoete head development sequence is summarized in Figure 16 a–f.

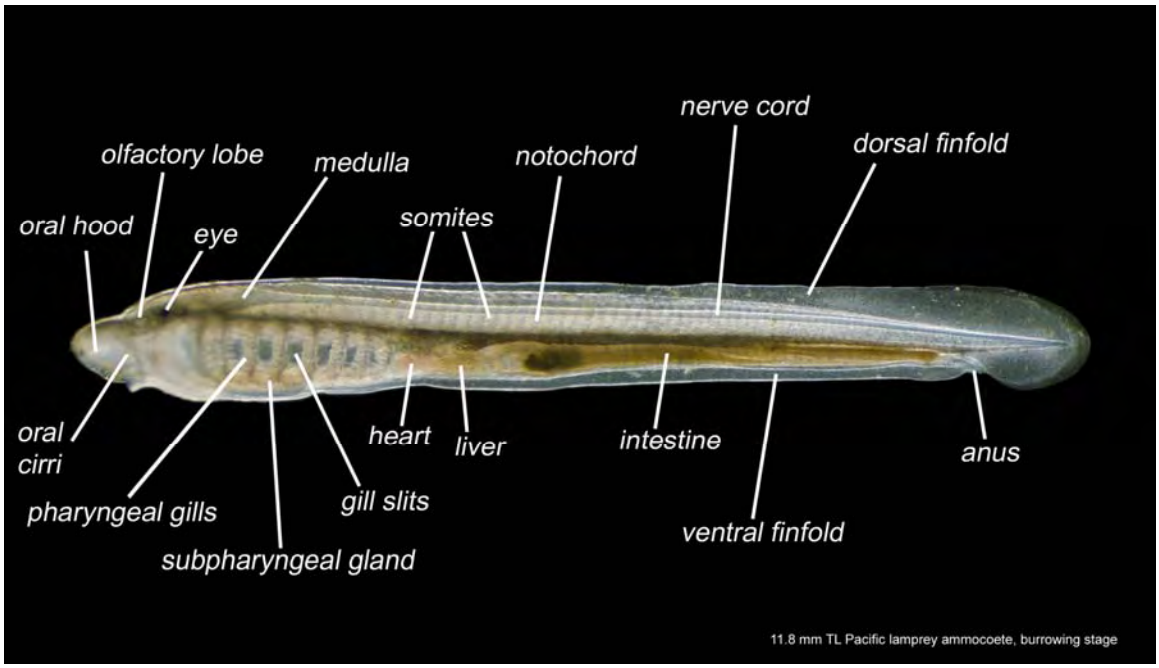


FIGURE 11.—Morphology of a Pacific lamprey ammocoete (after Hardisty and Potter, 1971).

**Stage 15:** Pigmentation, 1–4 dph (Figure 12).

*Size:* 5.8–6.8 mm (0.228–0.267 in).

*PAL / TL:* 92–93%.

*Head:* Initial pigments on midbrain (Figure 16b) and on the undeveloped eyes (Figure 16c), oral flap becoming prominent (Figure 16d).

*Description:* Ammocoetes at 1 and 2 dph are still on their sides and are active only when disturbed. Ammocoetes are nearly straightened by 1 dph. First pigments appear dorsally on the mid-head area and progressively along the mid-lateral line. Dorsal and ventral areas of the body are mainly pigment-free. Initial pigments appear on the eye. Oral flap is developing but not yet functional. The liver is visible and the light pinkish heart is apparent. Toward the end of the stage, the caudal finfold differentiates and elevates from the caudal peduncle. The stage ends with the appearance of functional gill slits.


FIGURE 12.—Pigmentation stage at 1–4 days post hatch (dph). a. 6.8 mm (0.268 in) total length (TL) ammocoete (1 dph) shows location of the first pigments (white arrow). Dorsal view shows the first pigmentations prominently appearing on the head; b. 7.6 mm (0.299 in) TL ammocoete (3 dph) with pigments appearing on the undeveloped eye and along the mid-lateral body; c. 7.8 mm (0.307 in) TL ammocoete (4 dph) with an enlarging oral flap and more pigments all over body. The caudal finfold is also differentiating.

**Stage 16**: Gill, 4–12 dph (Figure 13).

*Size:* 7.6–9.3 mm (0.299–0.366 in).

*PAL / TL:* 90–92%.

*Description:* At about 8 mm (0.315 in) TL, ammocoetes develop seven gill slits, eyes are fully pigmented, and otoliths are visible behind the eyes (Figure 16e). The oral opening is functional and exogenous feeding can begin. Their body is less opaque and more translucent. Melanophores extend along dorsum and sides of ammocoete from anterior to posterior. Eyes are pigmented. The oral flap is enlarging into a hooded functional mouth. Pharyngeal gills are slightly visible.

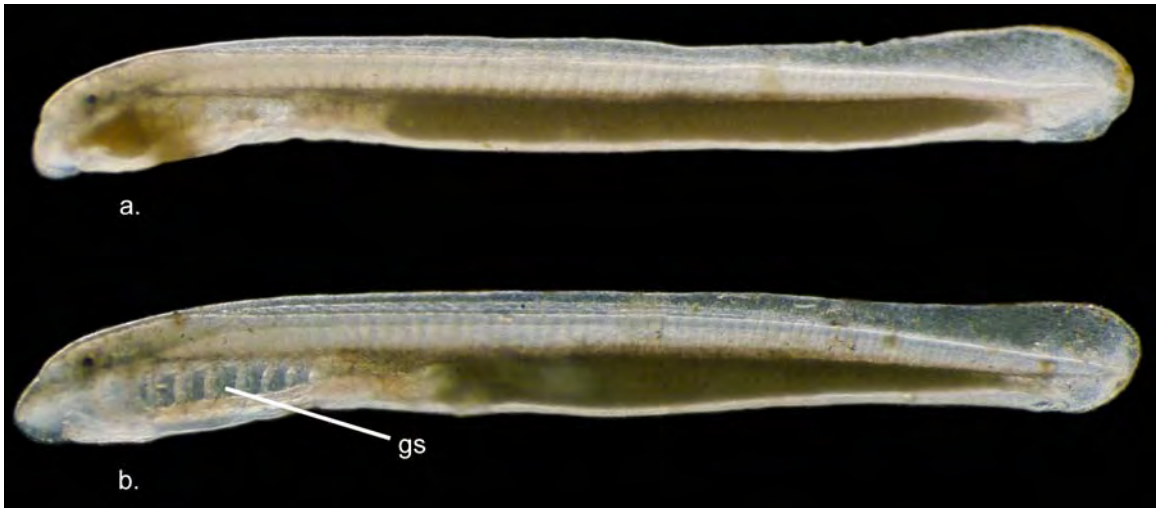


FIGURE 13.—Gill stage at 4–10 days post hatch (dph). a. 8-mm (0.315-in) total length (TL) ammocoete (6 dph) with pigmenting eye and functional oral opening; b. 8.5-mm (0.335-in) TL ammocoete (10 dph) with seven functional gill slits (gs).

**Stage 17**: Burrowing, 12–14 dph (Figure 14 and 16f).

*Size:* > 9.1 mm (0.358 in) TL.

*PAL / TL:* 87–90%.

*Description:* The stage begins when the ammocoete burrow into the mud. At ~ 9 mm (0.354 in) TL, ammocoetes are actively burrowing in mud and have gill slits that are functional. Pharyngeal gills with the gill filaments develop and the gill slits expand to create a large branchial basket. Oral hood around the mouth is protruded and inferior. Oral cirri are visible. The ammocoete has prominent eyespots. The anus migrates anteriorly; PAL / TL decreases to ~ 89%. Body is translucent except for the yolk that is being absorbed and the intestines.


FIGURE 14.—Burrowing stage at ≥ 12 days post hatch. a. 16.7-mm (0.657-in) total length ammocoete shows oral cirri (oc) around the mouth and well-developed pharyngeal gills with large gills slits; b. same ammocoete ventrally shows the shape of the large oral hood and the expanded branchial basket (bb).

**Stage 18**: Larva, ~ 30 dph (Figure 15).

*Size:* > 20 mm (0.787 in) TL.

*Description:* At this stage, the stellate pigmentations that dominated the earlier ammocoete stages have become circular and numerous, covering the body dorsally and laterally including the oral hood; ventrally, however, the ammocoete remains pigment-free. Pigmentation also covers the well-developed branchial gills. Green bile is observed marking the presence of a gall bladder (Piavis, 1961). The yolk remaining in the lumen of the gut eventually passes through the anus. The gut tissue becomes transparent marking the completion of the digestive tract. At this point, the ammocoete becomes age 0.

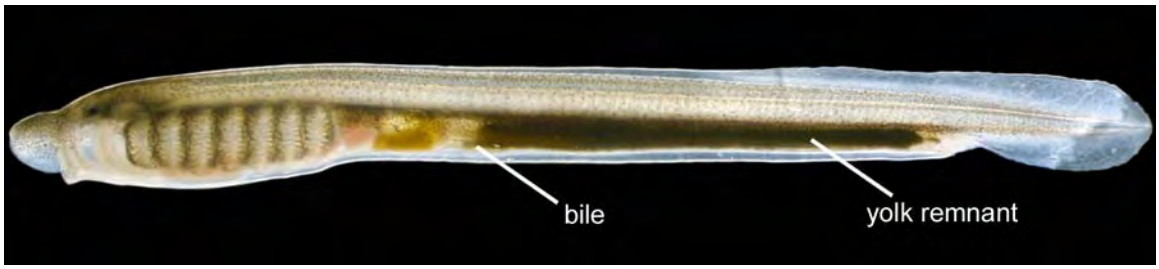


FIGURE 15.—Larva. 19.7-mm (0.775-in) total length ammocoete with pigmentation throughout the body including the pharyngeal gills, green bile produced by gall bladder, and remnants of the yolk passing the gut through the anus.

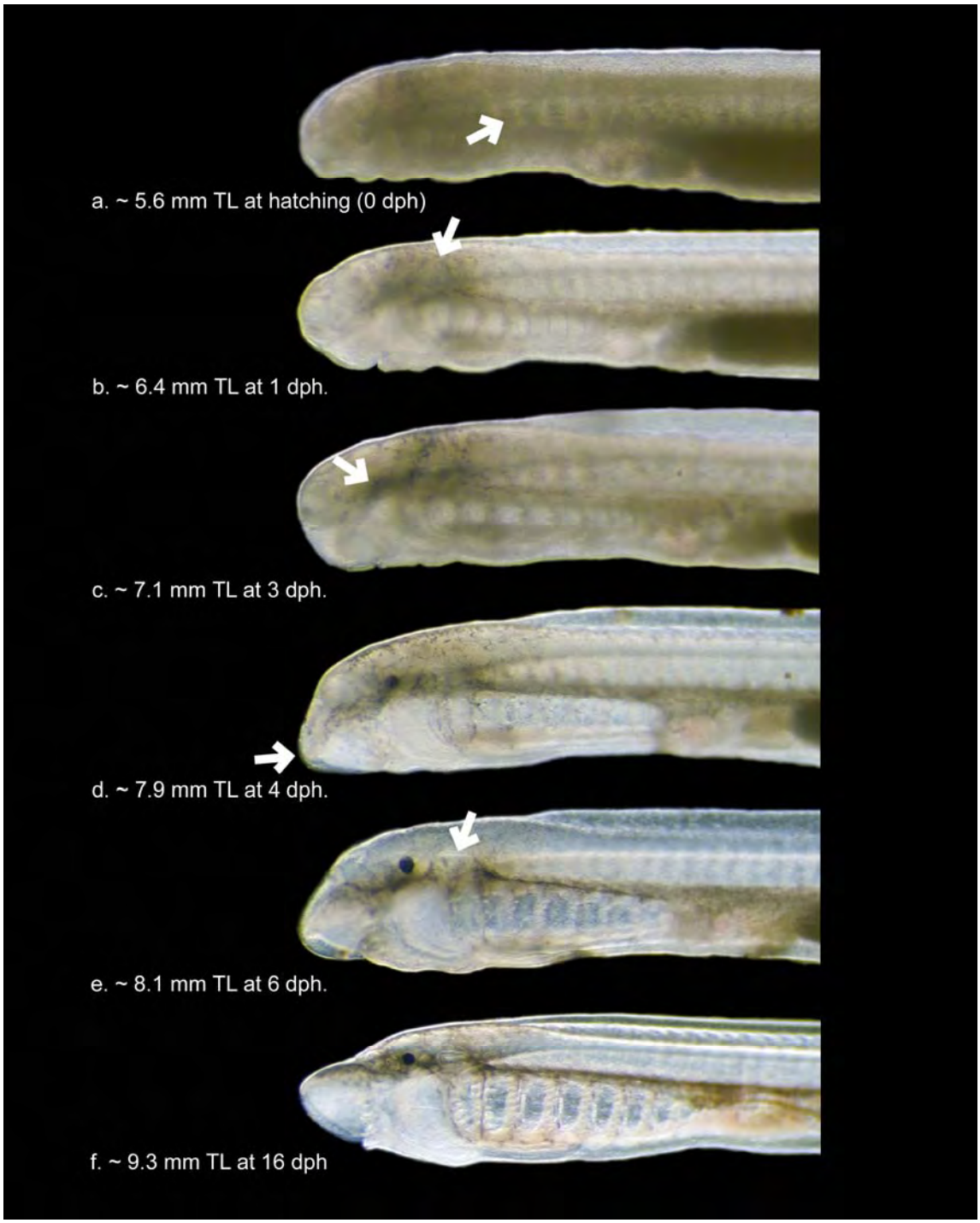


FIGURE 16.—Ammocoete head development sequence: a. gill slits are visible but not yet functional; b. first pigments appear at the midbrain area; c. pigments appear on the undeveloped eye; d. oral flap becomes more prominent; e. otoliths visible; f. burrowing stage with functioning gill slits.

# DISCUSSION

The early life stages of lamprey *spp*., including Pacific lamprey, in California are not well-studied. Although geographically overlapping in the study area, the eggs and ammocoete of the river lamprey (*Lampetra ayresii)* and western brook lamprey (*Lampetra richardsoni)* were not collected and therefore no comparisons with Pacific lamprey were made. Since lampreys possess few morphological characteristics that are variable between species (Gill *et al.,* 2003), differentiating the early stages is difficult. Morphological differences such as trunk myomeres and body proportions are not reliable characteristics for separating these different species at the ammocoete stage (Richards *et al.,* 1982). Furthermore, the early life stages of river lamprey are virtually unknown (Meeuwig *et al.,* 2004). For western brook lamprey, both mean egg diameter and emergent larval length are significantly smaller than those of Pacific lampreys (Meeuwig *et al.,* 2004). Mitochondrial DNA tests have indicated that Pacific lampreys are distinctly different from the other two lampreys. River lamprey and western brook lampreys only recently diverged from each other (70,000 years ago) and therefore are considered satellite species and genetically inseparable (Docker *et al*., 1999).

Although stages described are based mainly on external features, Pacific lamprey embryonic and ammocoete developmental intervals are visible and easily demarcated. Initial cell divisions during the morula stage are holoblastic and completed in about a day. The epibolization of the embryo during the gastrula stage is visible by the advancing margin of the opaque animal cells over the translucent vegetal cells. The open blastopore persists throughout embryogenesis. The blastopore was believed to eventually become the anus (Shipley, 1885; Piavis, 1961). Although beyond the scope of this paper, a recent study suggests that the anus actually develops by secondary canalization and proctodeum formation at the former site of the blastopore (Richardson and Wright, 2003). During the neural stage, the neural folds fuse and become elevated, forming the neural rod. During the head stage, the blastopore is located below the ventral side of the head. Head movement breaks the chorion and ammocoete usually exits head first. Once hatched, ammocoete is curved and inactive. The body eventually straightens in 1–2 days. Eyes become pigmented within 4 dph and gills develop within 4 to 10 dph. Exogenous feeding commences during the gill stage. Burrowing stage occurs as early as 12 dph but usually around 9 mm (0.35 in). Meeuwig *et al*. (2005) found that survival of the larvae was greatest at 18 °C and that higher proportion of abnormalities can be expected at 22 °C. Larval stage is reached when the digestive tract is functional and the remnant of the yolk is excreted.

The stages of development of the embryo and ammocoete are similar to the development observed for the well-studied sea lamprey and to other studied lamprey species (Table 1). Pacific lamprey ammocoetes hatched between 18–23 days after fertilization at 12 °C (± 1 °C) which is in line with Moyle's (2002) observation of 19 days at 15 °C. Compared to other studies of lamprey early stages, the Pacific lamprey hatched 7 or more

TABLE 1.—Comparison of Pacific lamprey early life stages with other lamprey

| **Stages** | ***E. tridentatus*** | ***E. tridentatus*** [1] | ***L. reissneri***[2] | ***P. marinus*** [3] |
|---|---|---|---|---|
| Two-cell to Morula | < 24 hr | 26 hr | 28 hr | 19 hr |
| Blastula | 24–96 hr | 32 hr | 48 hr | 24 hr |
| Gastrula | 96–240 hr | 74 hr | 78 hr | 64 hr |
| Neurula | 11–14 d | 5.5 d | 5 d | 4 d |
| Head | 14–17 d | 7.5 d | 7.5 d | 6 d |
| Hatching | 18–23 d | 11 d | 11 d | 10 d |
| Pigmentation | 1–4 dph | 15 d | 16 d | 13 d |
| Burrowing | 12–14 dph* | – | 24 d | 17 – 33 d |
| Larva | ~ 30 dph* | 32 d | 31 d | 33 d |
| Temperature | 12 °C (± 1 °C)<br>*18 °C (± 1 °C) | 18 °C | 15 °C | 18.4 °C |

[1] Pacific Lamprey in Japan (*Entosphenus tridentatus;* Yamazaki *et al*., 2003)
[2] Far East Brook Lamprey (*Lampetra reissneri;* Tahara, 1988)
[3] Sea Lamprey (*Petromyzon marinus;* Piavis, 1961)

days later because the temperature was cooler. Despite temperature differences, embryogenesis progressed similarly.

The spawning of Pacific lamprey overlaps geographically and temporally with other species in the Sacramento-San Joaquin River Delta system. In the American River, Pacific lamprey eggs have been collected with eggs from steelhead trout (*Oncorhynchus mykiss)*, Sacramento sucker (*Catostomus occidentalis)*, and Sacramento pikeminnow (*Ptychocheilus grandis)*; therefore, distinguishing species redds and eggs are important. Pacific lamprey redds are generally smaller and often have no "tail spill" compared to steelhead redds. During the act of spawning, Pacific lampreys pick up larger rocks with their sucking discs and carry them to the tail spill leaving much of the sand and gravel in the pot (main nest depression). Therefore, more fine particles were present in the pots of Pacific lamprey redds than in the pots of steelhead redds (Hannon and Deason, 2004). Pacific lamprey eggs were also collected in redds that had fertilized eggs of Sacramento sucker and Sacramento pikeminnow. Distinct egg size and color difference distinguish the Pacific lamprey from other species (Figure 17): Sacramento sucker eggs were 3.0–3.9 mm (0.118–0.153 in) in diameter and are yellowish; Sacramento pikeminnow were 2.5–3.2 mm (0.098–0.126 in) in diameter and pale yellow; steelhead are large at 4.6–6.2 mm (0.181–0.244 in) in diameter and are orange to yellow; and Pacific lamprey eggs were 1.4–1.9 mm (0.055–0.074 in) in diameter and are mainly white.

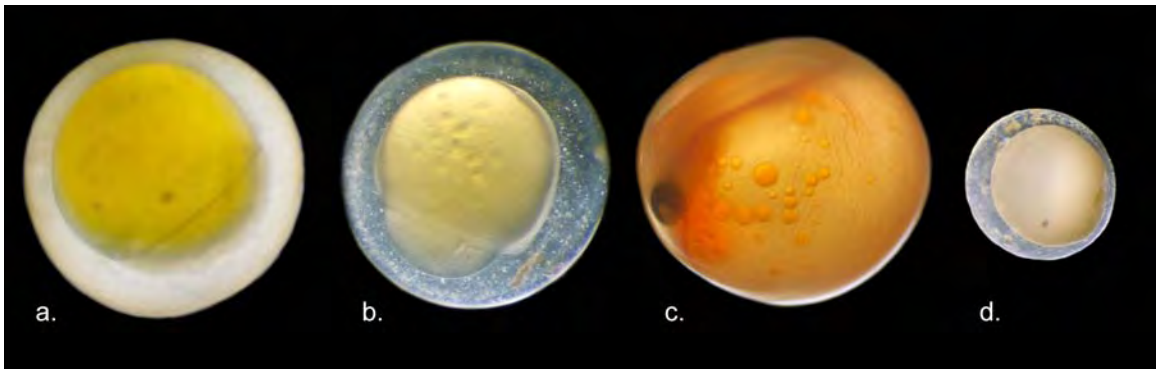


FIGURE 17.—Eggs of other species found in lamprey redds: a. Sacramento sucker (*Catostomus occidentalis)*; b. Sacramento pikeminnow (*Ptychocheilus grandis)*; c. Steelhead (*Oncorhynchus mykiss)*; d. Pacific lamprey (*Entosphenus tridentatus*) egg for comparison.

The dependence of native species on flow regimes and habitat structure is well established (Close *et al.*, 1995; Renaud, 1997; Feyrer *et al.*, 2004; Brown and May, 2006; Feyrer *et al.*, 2006; Moyle *et al.*, 2007) and also applies with Pacific lamprey. Adult lampreys rely on water releases from the reservoirs to spawn and ammocoetes rely on low water velocities and substrate size to burrow (Pletcher, 1963). In the American River, dams not only block access to natural spawning grounds of Pacific lamprey but also trap sediments, such as silt and clay particles (Arthur *et al.*, 1996), which the ammocoetes use for burrowing. Ammocoete prefer finer sediments and substrates (Close *et al.*, 1995; Torgersen and Close, 2004) and their densities increase with densities of finer substrates (Claire, 2004). Water velocity presumably must be fast enough to provide a steady influx of food and yet slow enough to promote the deposition of soft sediments needed for ammocoete burrowing (Torgersen and Close, 2004). Finally, shoreline boulder-created calm water pockets commonly support increased ammocoete densities (Claire, 2004).

Pacific lamprey is considered "vulnerable" by the 2008 American Fisheries Society Endangered Species Committee due to habitat destruction and modification and to over-exploitation (Jelks *et al.*, 2008). Conservation interest in Pacific lamprey has grown in recent years, with increasing attention from Tribes, local, state, and federal agencies, non-governmental organization (NGOs), and academia (USFWS, 2007) because of the apparent population decline (Close *et al*., 2002; Petersen, 2006). Due to similarities in habitat requirements and life histories between the Pacific lamprey and anadromous salmonids, it is likely that many of the same factors are limiting their survival (Brumo, 2006). Habitat disturbance due to river channelization and dams has caused significant declines along the Oregon coast and in the Columbia River Basin (Close, 2001; Close *et al.*, 2002; Moser *et al*., 2002) and in California (Moyle, 2002). A few Native Americans collect adult lampreys for food in the American River (J. Hannon, 2003, personal communication). In the Pacific Northwest, Pacific lamprey is still used by Native Americans as a religious food, subsistence food, and as medicine (Close *et al.*, 2002). In California, Pacific lampreys are still present in most of their native areas but large runs have almost disappeared (Moyle, 2002). In the South Delta, ammocoetes and newly

transformed adults are collected from the Tracy Fish Collection Facility in great numbers between January and March. They are salvaged and released back to the Sacramento-San Joaquin River Delta, however, salvage efficiencies for this species are unknown. It is likely that ammocoetes are lost to the pumps during these months. Habitat degradation and water flow regulation remain a major impediment to lamprey *spp*. conservation (Renaud, 1997).

## ACKNOWLEDGMENTS

I would like to thank Reclamation's John Hannon and Brian Deason for providing the bulk of the eggs used for this study; Dr. Johnson Wang for explaining embryologic processes and larval anatomy; Reclamation's Zachary Sutphin for supplying eggs; Brandon Wu for technical editing; my lead Brent Bridges and supervisor Ron Silva for providing additional technical and financial support; and to Reclamation's librarians Alba Scott and Patricia Stewart.

## REFERENCES

Arthur, J.F., M.D. Ball, and S.Y. Baughman. 1996. *Summary of federal and state water project environmental impacts in the San Francisco Bay-Delta estuary, California.* Pages 444–495 *in* J.T. Hollibaugh (editor). San Francisco Bay: the Ecosystem. Pacific Division of the American Association for the Advancement of Science, San Francisco, California.

Beamish, R.J. 1980. *Adult biology of the river lamprey (Lampetra ayresi) and the Pacific lamprey (Lampetra tridentata) from the Pacific coast of Canada.* Canadian Journal of Fisheries and Aquatic Sciences 37:1906–1923.

Brown, L.R., and J. May. 2006. *Variation in spring nearshore resident fish species composition and life histories in the lower Sacramento-San Joaquin watershed and Delta (California).* San Francisco Estuary and Watershed Science. Volume 4, Issue 1 (July 2006). http://repositories.cdlib.org/jmie/sfews/vol4/iss2/art1

Brumo, A.F. 2006. *Spawning, Larval Recruitment, and Early Life Survival of Pacific Lampreys in the South Fork Coquille River, Oregon.* Master's thesis. Oregon State University, Corvallis.

Claire, C.W. 2004. *Pacific lamprey larvae life history, habitat utilization, and distribution in the South Fork Clearwater River drainage, Idaho.* Master's thesis. University of Idaho, Moscow.

Close, D.A. 2001. *Effects of acute stress and tagging on the swimming performance and physiology of Pacific lampreys (Lampetra tridentata).* Master's thesis. Oregon State University, Corvallis.

Close, D.A., M.S. Fitzpatrick, and H.W. Li. 2002. *The ecological and cultural importance of a species at risk of extinction, Pacific lamprey.* Fisheries 27:19–25.

Close, D.A., M.S. Fitzpatrick, H.W. Li, B. Parker, D. Hatch, and G. James. 1995. *Status Report of the Pacific Lamprey Lampetra tridentata in the Columbia River Basin.* U.S. Department of. Energy. Bonneville Power Administration. Project Number 94-026, Contract Number 95BI39067, 40 pages (BPA Report DOE/BP-39067-1). Portland, Oregon.

Docker, M.F., J.H. Youson, R.J. Beamish, and R.H. Devlin. 1999. *Phylogeny of the lamprey genus Lampetra inferred from mitochondrial cytochrome b and ND3 gene sequences.* Canadian Journal of Fisheries and Aquatic Sciences 56:2340–2349.

Feyrer, F., T.R. Sommer, and W. Harrell. 2006. *Importance of flood dynamics versus intrinsic physical habitat in structuring fish communities: evidence from two adjacent engineered floodplains on the Sacramento River, California.* North American Journal of Fisheries Management 26:408–417.

Feyrer, F., T.R. Sommer, S.C. Zeug, G. O'Leary, and W. Harrell. 2004. *Fish assemblages of perennial floodplain ponds of the Sacramento River, California (USA), with implications for the conservation of native fishes.* Fisheries Management and Ecology 11:335–344.

Gill, H.S., C.B. Renaud, F. Chapleau, R.L. Mayden, and I.C. Potter. 2003. *Phylogeny of living parasitic lampreys (Petromyzontiformes) based on morphological data.* Copeia 4:687–703.

Hammond, R.J. 1979. *Larval biology of the Pacific lamprey, Entosphenus tridentatus (Gairdner), of the Potlach River, Idaho.* Master's thesis. University of Idaho, Moscow.

Hannon, J., and B. Deason. 2004. *American River Steelhead (Oncorhynchus mykiss) Spawning 2001–2004.* U.S. Bureau of Reclamation internal report.

Hannon, J. 2003. Fish Biologist, U.S. Bureau of Reclamation, Sacramento, California.

Hardisty, M.W., and I.C. Potter. 1971. *The behaviour, ecology, and growth of larval lampreys.* Pages 85–126 *in* M.W. Hardisty and I.C. Potter (editors). The Biology of Lampreys, Volume 1, Academic Press, New York, New York.

Jelks, H.L., S.J. Walsh, N.M. Burkhead, S. Contreras-Balderas, E. Diaz-Pardo, D.A. Hendrickson, J. Lyons, N.E. Mandrak, F. McCormick, J.S. Nelson, S.P. Platania, B.A. Porter, C.B. Renaud, J.J. Schmitter-Soto, E.B. Taylor, and M.L. Warren, Jr. 2008. *Conservation status of imperiled North American freshwater and diadromous fishes.* Fisheries 33:372–407.

Kan, T.T. 1975. *Systematics, variation, distribution, and biology of lampreys of the genus Lampetra in Oregon.* Doctoral dissertation. Oregon State University, Corvallis.

Manion, P.J. 1968. *Production of sea lamprey larvae from nests in two Lake Superior streams.* Transactions of the American Fisheries Society 97:484–486.

McPhail, J.D., and C.C. Lindsey. 1970. *Freshwater Fishes of Northwestern Canada and Alaska*. Bulletin of the Fisheries Research Board Canada 173.

Meeuwig, M.H., J.M. Bayer, and R.A. Reiche. 2004. *Identification of larval Pacific lampreys (Lampetra tridentata), river lampreys (L. ayresi), and western brook lampreys (L. richardsoni), and thermal requirements of early life history stages of lampreys.* Amended Final Report for 2002–2004. Bonneville Power Administration. Project Number 2000-029. Portland, Oregon.

Meeuwig, M.H., J.M. Bayer, and J.G. Seelye. 2005. *Effects of temperature on survival and development of early life stage Pacific and western brook lampreys.* Transactions of the American Fisheries Society 134:19–27.

Moore, J.W., and J.M. Mallat. 1980. *Feeding of larval lamprey.* Canadian Journal of Fisheries and Aquatic Sciences 56:1658–1664.

Morrow, J.E. 1980. *Freshwater Fishes of Alaska.* Anchorage: Alaska Northwest Publishing, Anchorage, Alaska.

Moser, M.L., P.A. Ocker, L.C. Stuehrenberg, and T.C. Bjornn. 2002. *Passage efficiency of adult Pacific lampreys at hydropower dams on the lower Columbia River, USA.* Transactions of the American Fisheries Society 131:956–965.

Moyle, P.B. 2002. *Inland Fishes of California.* University of California Press, Berkeley, California.

Moyle, P.B., and R. Nichols. 1973. *Ecology of some native and introduced fishes of the Sierra-Nevada foothills in Central California.* Copeia 3:478–490.

Moyle, P.B., P.K. Crain, and K. Whitener. 2007. *Patterns in the use of a restored California floodplain by native and alien fishes.* San Francisco and Estuary Watershed Science. Volume 5, Issue 3 (July 2007). http://repositories.cdlib.org/jmie/sfews/vol5/iss3/art1

Petersen, R.S. 2006. *The role of traditional ecological knowledge in understanding a species and river system at risk: Pacific lamprey in the Lower Klamath Basin.* Master's thesis. Oregon State University, Corvallis.

Pfeiffer, W., and T.F. Pletcher. 1964. *Club cells and granular cells in the skin of lampreys*. Journal of the Fisheries Research Board of Canada 21:1083–1088.

Piavis, G.W. 1961. *Embryological stages in the sea lamprey and effects of temperature on development.* Fisheries Bulletin 61:111–143.

Pletcher, T.F. 1963. *The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada.* Master's thesis. University of British Columbia, Vancouver, Canada.

Potter, I.C. 1980. *The ecology of larval and metamorphosing lampreys.* Canadian Journal of Fisheries and Aquatic Sciences 37:1641–1657.

Renaud, C.B. 1997. *Conservation status of Northern Hemisphere lampreys (Petromyzontidae).* Journal of Applied Ichthyology 13:143–148.

Richards, J.E. 1980. *Freshwater biology of the anadromous Pacific lamprey Lampetra tridentata.* Master's thesis. University of Guelph, Ottawa, Canada.

Richards, J.E., R.J. Beamish, and F.W.H. Beamish. 1982. *Descriptions and keys for ammocoetes of lampreys from British Columbia. Canada.* Canadian Journal of Fisheries and Aquatic Sciences 39:1484–1495.

Richardson, M.K., and G.M. Wright. 2003. *Developmental transformations in a normal series of embryos of the sea lamprey Petromyzon marinus (linnaeus).* Journal of Morphology 257:348–363.

Romer, A.S. 1962. *The Vertebrate Body*. Third Edition. W.B. Saunders Company, Philadelphia, Pennsylvania.

Ruiz-Campos, G., and S. Gonzalez-Guzman. 1996. *First freshwater record of Pacific lamprey, Lampetra tridentata, from Baja California, Mexico.* California Department of Fish Game 82:144–146.

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

Shipley, A.E. 1885. *On the Formation of the Mesoblast, and the Persistence of the Blastopore in the Lamprey.* Proceedings of the Royal Society of London 39:244–248.

Sorensen, P.W., and D.A. Close. 2000. *The olfactory system of migratory adult Pacific lampreys (Lampetra tridentata).* Pages 14–27 *in* D.A. Close (editor). Pacific Lamprey Research and Restoration Project, Annual Report 1998. U.S. Department of Energy, Bonneville Power Administration, Portland, Oregon.

Tahara, Y. 1988. *Normal stages of development in the lamprey, Lampetra reissneri (Dybowski).* Zoological Science 5:109–118.

Torgersen C.E., and D.A. Close. 2004. *Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (Lampetra tridentata) at two spatial scales.* Freshwater Biology 49:614–630.

U.S. Fish and Wildlife Service. 2007. *Pacific Lamprey Conservation Initiative.* http://www.fws.gov/pacific/fisheries/sp_habcon/lamprey/pdf/101107%20FINAL%20Lamprey%20Conservation%20Initiative.pdf

Vrieze, L.A., and P.W. Sorensen. 2001. *Laboratory assessment of the role of a larval pheromone and natural stream odor in spawning stream localization by migratory sea lamprey (Petromyzon marinus).* Canadian Journal of Fisheries and Aquatic Sciences 58:2374-2385.

Wang, J.C.S. 1986. *Fishes of the Sacramento-San Joaquin Estuary and Adjacent Waters, California: A Guide to the Early Life Histories.* Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary, Technical Report 9.

Wang, J.C.S. 2008. Ichthyologist, National Environmental Sciences, Inc., Byron, California.

White, J.L., and B.C. Harvey. 2003. *Basin-scale patterns in the drift of embryonic and larval fishes and lamprey ammocoetes in two coastal rivers.* Environmental Biology of Fishes 67:369–378.

Yamazaki, Y., N. Fukutomi, K. Takeda, and A. Iwata. 2003. *Embryonic development of the Pacific lamprey, Entosphenus tridentatus.* Zoological Science 20:1095–1098.

# GLOSSARY AND ABBREVIATIONS[1]

**Ammocoete** The larval stage of lampreys (Petromyzontiformes) which is characterized by the presence of an oral hood and the lack of a sucking disk, teeth and developed eyes. For this paper, ammocoete stage begins at hatching.

**Animal pole** The location on the fish egg where polar bodies emerge. It corresponds to the point of fertilization just below where the sperm penetrates the chorion through the micropyle.

**Anterior** Towards the front end. *Antonym* Posterior.

**Bile** Yellow or green alkaline fluid secreted from the liver.

**Blastocoele** The cavity of the blastula.

**Blastomere** Individual cells forming the early embryo.

**Blastopore** Circular opening on the yolk of eggs not covered by the advancing germ ring during epiboly.

**Blastula** The single-layered, hollow ball of cells; the final product of cleavage stages in the embryo characterized by the formation of the blastocoel.

**Branchial basket** The network-like cartilaginous skeleton of the gill region of Petromyzontiformes and Holocephali. Also called gill basket.

**Caudal** Referring to the tail.

**Chorion** The embryonic membrane enclosing the egg.

**Cleavage** Divisions during the initial stages of embryonic development where blastomere divisions are clearly marked.

**Dorsal lip** Tissue above the blastopore marking the end of the gastrula stage.

**Dorsum** Back region.

[1] Most definitions derived from "Dictionary of Ichthyology" by Brian W. Coad and Don E. McAllister.

**dph** Abbreviation for day post hatch.

**dps** Abbreviation for day post spawn.

**Ectoderm** Outermost germ layer which later forms the nervous system and epidermis.

**Embryo** Developmental stages up to the moment of hatching.

**Embryogenesis** Process of embryo development.

**Endoderm** A germ layer formed during embryogenesis which later forms the lining of the gut.

**Epiboly** The thinning and spreading movement of the embryonic cell mass over the surface of the yolk, eventually encompassing the yolk completely.

**Exogenous feeding** Feeding through the mouth and digested in the intestine. *Antonym* Endogenous feeding.

**Eyespot** A photosensitive structure (like an eye) containing primitive homologues of rods and cones and is probably able to detect differences in quantity of light but incapable of forming an image.

**Finfold** Median integumentary fold of embryos of fishes.

**Furrow** Depressions between blastomeres created by the divisions of the cells. *Synonym* Cleavage.

**Gall bladder** Small sac associated with the liver used for storing the bile which is used in digestion.

**Gastrula** Embryonic stage in which an archenteron (primitive gut) forms by invagination of cells through a blastopore, and in which germ layers appear and the embryonic axis is formed.

**Gill slits** Gill openings.

**Holoblastic** A description of cell division when a whole egg undergoes cleavage.

**Lumen** The cavity of any organ, duct or sac.

**Melanophore** Black pigment.

**Meroblastic** A description of cell division when only part of an egg undergoes cleavage.

**Mesoderm** A germ layer formed during gastrulation that later forms bones and muscles.

**Metamorphose** To change from larvae to adult.

**Midsagittal plane** A plane that divides exactly at the middle the left and right sides.

**Morula** Stage in egg development where the blastomere forms a mulberry-like cluster.

**Neural fold** Ridge formed from the neural plate located on both sides of the neural groove.

**Neural groove** Midsagittal depression on the surface of the anterior neural plate present during early segmentation.

**Neural plate** Thickened epithelium forming the earliest dorsal ectodermal primordium of the central nervous system.

**Neural rod** A solid ridge which projects ventrally towards the yolk and later becomes a hollow neural tube. Neural rod formation occurs during primary neurulation in teleosts.

**Neural tube** The primordium of the central nervous system characterized by a cavity and developing from the neural rod.

**Neurula** The process of forming a dorsal ectodermal neural tube. *Syn*onym Neurulation.

**Oral cirri** Fringe-like appendages located at the oral opening; *Singular* cirrus.

**Oral hood** A scoop-like structure formed by prolongation of the lips around the oral opening.

**Oral opening** The vestibule which leads to the mouth.

**Otoliths** Structure in the inner ear used for perception of acceleration including gravity. *Synonym* Ear stones.

**Ovulated** The discharge of a mature ovum (egg) from the ovary.

**Perivitelline space** The fluid-filled space between the embryo and chorion of an egg.

**Pharyngeal gills** Developing respiratory organ consisting of gill filaments.

**Posterior** Towards the back end. *Antonym* anterior.

**Proctodeum** The back ectodermal part of the digestive tract.

**Redd** A depression often on gravel where fish eggs are deposited.

**Somite** A body segment; in the embryo, an undifferentiated mesodermal component of an early trunk.

**Stellate** Star-like melanophore.

**Tail spill** The posterior part of a redd.

**Telolecithal** Description of an egg with a large amount of yolk at one end.

**Vegetal pole** Opposite to the animal pole on the egg. Later in embryonic development corresponds to the point on the yolk cell furthest from the developing blastodisc.

**Ventral(ly)** Pertaining to the lower surface or abdomen, opposite to the back or dorsal side.

**Zygote** Fertilized egg.