Rearing, development, and early life history of the California Needlefish, *Strongylura exilis*

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Abstract

Fertilized eggs were obtained from field-caught specimens of California needlefish, *Strongylura exilis*, and incubated in an experimental aquarium to obtain developmental series of embryos, larvae, and juveniles. The spherical eggs are 2.4-2.7 mm in diameter and have 28-40 elongate filaments evenly spaced over the shell. At hatching (10-19 days after fertilization) the larvae have functional eyes, jaws, digestive tracts and caudal fins and are covered with xanthic and melanistic pigment. Newly hatched larvae fed immediately on larvae of brine shrimp and grew rapidly (1 mm/day). Late larvae and early juveniles continued rapid growth on a diet of frozen adult brine shrimp and chopped squid. Allometric growth of the upper and lower jaws produces a "halfbeak" stage which reaches a maximum at 24 mm body length when the relative difference in "beak" length is 27 % of body length. During the developmental period the sheath of melanophores and xanthophores which covers the body changes to a zonal pattern consisting of a greenish black dorsum and two lateral silvery zones.

Introduction

The California needlefish, *Strongylura exilis*, is the most common representative of the family Belonidae in the California Current region. It ranges from Peru to San Francisco (including the Galapagos Islands) usually inhabiting bays and harbors at or near the surface in small schools (**Fitch & Lavenberg** 1971; **Eschmeyer** et **al.** 1983). This excellent food fish can grow as large as 91 cm and is occasionally taken on hook and line by sport fishermen, but is not fished commercially.

Although eggs and larvae of other needlefish species have been described (**Ryder** 1882 ; **D'Ancona** 1931 ; **Mito** 1958 ; **Breder** 1959 ; **Masurekar** 1967 ; **Foster** 1973 ; **Rosenthal & Fonds** 1973 ; **Hardy** 1978) early life history information on *S. exilis* is scanty. In their review of beloniform ontogeny, **Collette** et **al.** (1984) illustrated the egg and an 8.6 mm larva of *S. exilis* and listed the egg diameter and filament arrangement in a summary table. The purpose of this paper is to describe the eggs, larvae, and juveniles of a complete developmental series of *S. exilis* reared in the experimental aquarium of the Southwest Fisheries Center, with special emphasis on the ontogenetic changes in color pattern.

Methods and Materials

Five adult specimens of *S. exilis* were collected in a 24 m beach seine over sandy substrate north of Scripps Institution of Oceanography (SIO) pier on June 13, 1979. The two males (435 and 480 mm SL) and three females (500-636 mm SL) were mature and free-running eggs from the largest female were artificially fertilized at 0830 hrs. with sperm from macerated testes of the largest male. The five specimens were preserved and deposited in the SIO fish collection (cat. no. 79-88).

The fertilized eggs were taken to the Southwest Fisheries Center experimental aquarium for incubation. The incubation container was a white plastic cylinder (diameter = 28 cm, depth = 8 cm) with a 500 μm nylon mesh bottom. This was partially immersed in a 100 l cylindrical black fiberglass container that was placed in a large water bath. The eggs were bathed in a constant stream of sea water which ranged from 19° to 21 °C during the incubation period. After hatching the larvae were placed in a 100 l rearing container in the water bath. Sea water volume in the rearing container was maintained at about 80 l and a liter of dense algal culture (*Tetraselmis suesica* or *Dunaliella* sp.) was added every few days to maintain water quality. Since the rearing container was non-circulating, gentle aeration was used to prevent stratification. The tanks were illuminated by four 40 watt fluorescent lamps about 1 m from the surface on a 12 hour day/12 hour night cycle.

After hatching, the larvae were fed nauplii of brine shrimp (*Artemia* sp.) daily at a minimum concentration of one nauplius/ml. Late stage larvae and juveniles were fed frozen brine shrimp, chopped squid, and occasionally larvae of the queenfish, *Seriphus politus*. Eggs and larvae were regularly sampled and preserved in 4 % formalin. Some were photographed before preservation to record xanthic pigmentation.

The sequence and timing of egg developmental events was described using stages formulated by Oppenheimer (1937). A developmental series of larvae and juveniles was established to study ontogenetic changes in morphology, morphometrics and pigmentation. Subsequently, selected specimens from this series were stained with Alizarin Red-S and cleared in a graded series of KOH and glycerin to determine the sequence of formation of ossified fin rays. For larger specimens, X-radiographs were also used to determine fin ray development.

Because of allometric growth of the snout during development the anterior margin of the eye, rather than the anterior tip of the snout was used as the reference point in making longitudinal morphometric measurements. Thus, for morphometric comparisons, body length (BL) is defined as the distance from the anterior margin of the eye to the posterior margin of the hypural plate. Snout length and lower jaw length are measured from the tip of each jaw to the anterior margin of the eye. Head length is measured from the anterior margin of the eye to the cleithrum and the anterior margin of the eye is the anterior reference point for measurements to the anus and fin origins. Standard length (SL) is the distance from the tip of the upper jaw to the posterior margin of the hypural plate. All other measurements follow the definitions of **Ahlstrom** et **al.** (1976).

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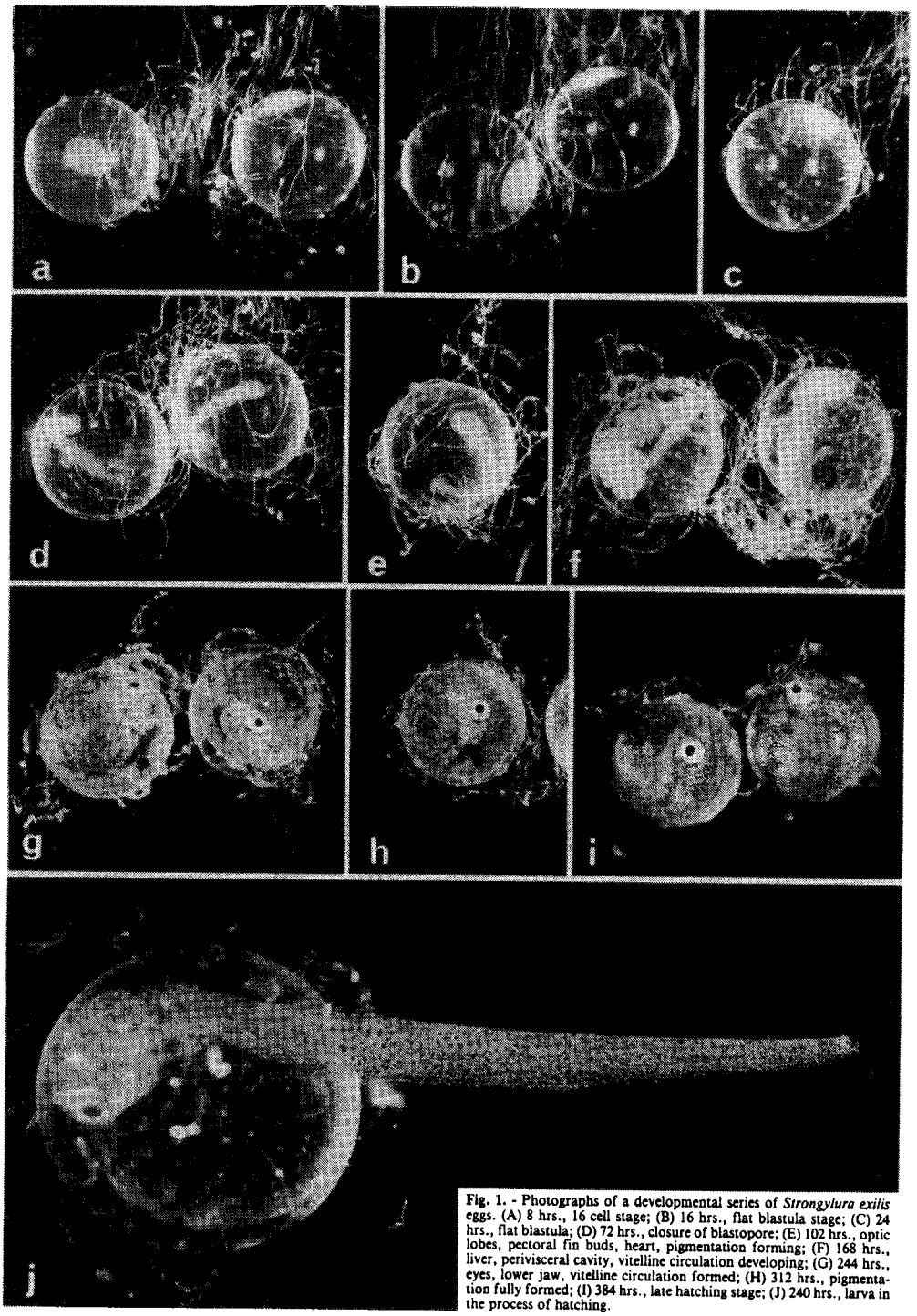

Fig. 1. - Photographs of a developmental series of *Strongylura exilis* eggs. (A) 8 hrs., 16 cell stage; (B) 16 hrs., flat blastula stage; (C) 24 hrs., flat blastula; (D) 72 hrs., closure of blastopore; (E) 102 hrs., optic lobes, pectoral fin buds, heart, pigmentation forming; (F) 168 hrs., liver, perivisceral cavity, vitelline circulation developing; (G) 244 hrs., eyes, lower jaw, vitelline circulation formed; (H) 312 hrs., pigmentation fully formed; (I) 384 hrs., late hatching stage; (J) 240 hrs., larva in the process of hatching.

Développement des oeufs de *Strongylura exilis*, de 8 à 384 heures.

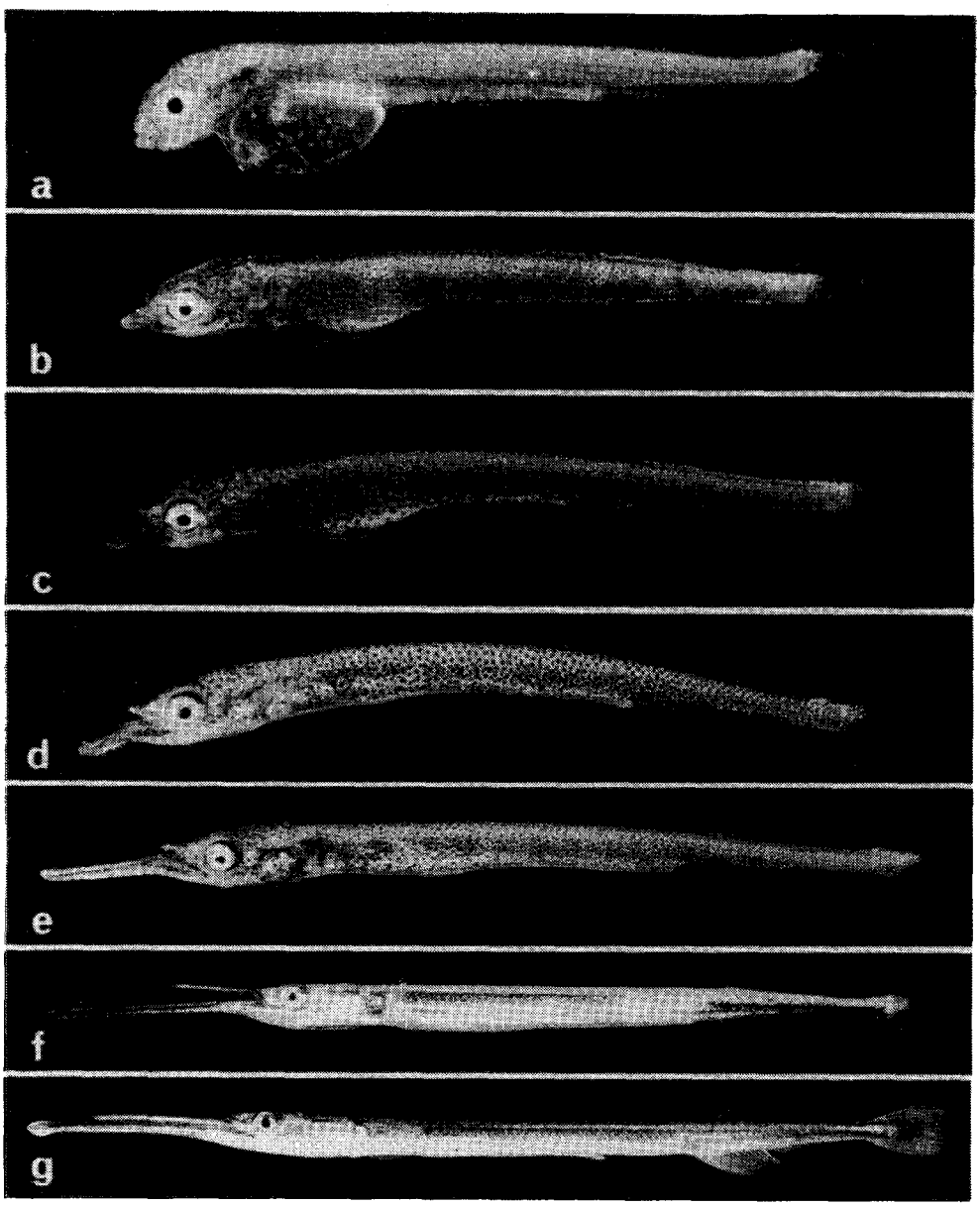

Fig. 2. - Photographs of developmental series of *Strongylura exilis*. (A) 9.1 mm BL, new hatched; (B) 9.6 mm BL, day 1; (C) 10.6 mm BL, day 2; (D) 12.6 mm BL, day 3; (E) 16.5 mm BL, day 6; (F) 32.5 mm BL, day 18; (G) 44.4 mm BL, day 28.

Développement de *Strongylura exilis*, de l'éclosion à 28 jours.

Table 1
Developmental features of *Strongylura exilis* eggs

Hours after fertilization	Stage (Oppenheimer 1937)	Developmental features
2-1/4	2	Fertilized
4	3- 4	2 and 4 cell stages
8	5- 6	16-cell stage
12-1/2	8- 9	Early to late high blastula
16	10	Flat blastula
20	10	Flat blastula
24	10-11	Flat blastula and expanding blastula
32	12	Early gastrula
49-1/2	13-14	Mid to late gastrula
72	15-17	Closure of blastopore; embryo, central nervous systems, optic vesicles, somites forming
102	20-22	Midbrain expanded to form optic lobes; heart forming and beating; pectoral fin bud forming; pigment forming on yolk and embryo
120	23-24	Xanthophores and melanophores scattered over yolk and beginning to cover embryo; embryo showing axial flexion
145	25	Formation of urinary vesicle
168	27-28	Liver and perivisceral cavity forming; pectoral fin buds rounded; xanthic pigment solid over embryo, except over dorsal midline and less concentrated over brain; perivisceral walls becoming pigmented
193-1/2	29	Notochord flexion; pectoral fins beating and fish flipping; xanthic and melanistic pigment over entire head and body
222-1/2	30	Lower jaw forming
244	31	Fin rays in caudal fin; lower jaw formed; jaws, eyes, and body moving
day 10-19	32	Hatching

Description of Development

Eggs

S. exilis eggs are among the smallest known for Belonidae. The diameter for 25 measured eggs was 2.44-2.72 mm ($\bar{x}$ = 2.57 ± 0.061 SD). Each spherical egg has 28-40 ($\bar{x}$ = 33.3 ± 3.06 SD for 25 eggs) evenly spaced filaments singly attached to the thick chorion by a swollen truncated cone. The filament lengths of 13.5 > 26.7 mm are among the largest reported from this family. These filaments are intertwined with those of adjacent eggs forming adhesive clumped egg masses which attach to vegetation or floating objects. The clear yolk is unsegmented and oil globules are absent.

Developmental features of the egg of *S. exilis* conform closely to the stages of egg development of *Fundulus heteroclitus* described by Oppenheimer (1937). Using these criteria, the timing of developmental events in *S. exilis* eggs is summarized in Table 1. Early cleavage stages are completed within 12 hours after fertilization (fig. 1A, B). The blastula undergoes epiboly at about 24 hours, marking the beginning of gastrulation (fig. 1C). By 72 hours after fertilization the blastopore has closed and the embryo is well established, with a central nervous system, optic vesicles, and somites forming (fig. 1D). At 102 hours the heart is beating and xanthic (yellow) and melanistic (black) pigment is forming on the embryo and yolk (fig. 1E). At 168 hours the embryo is advanced, has well developed eyes, brain lobes and pectoral fins. Xanthic pigment covers the entire embryo except the mid-dorsal line and is scattered evenly over the yolk. Melanophores also cover the embryo except for the region over the medulla and the dorsal midline of the body. They are concentrated over the developing perivisceral region at the sides of the body and over the vitelline circulatory vessels on the surface of the yolk (fig. 1F). By 193-1/2 hours, the developing fish is flipping its tail, the pectoral fins are beating, and the tip of the notochord is flexing. At 244 hours the eyes are fully formed, the caudal fin rays and median finfold are developing and the jaws and digestive tract are formed. The eyes are silvery and the head and body are covered with xanthophores and melanophores. Xanthophores are distributed sparsely over the yolk and melanophores remain concentrated along the vitelline vessels. The pectoral and caudal fins and the median finfold lack pigment (fig. 1G).

Hatching (fig. 1J) began at 244 hours (day 10) and most of the eggs had hatched by day 16, however, a few eggs remained unhatched until day 19.

Larvae

General morphology: The yolksac of newly hatched larvae is oblate in shape and ranges in length from 2.0 to 2.5 mm, in height from 1.2 to 1.7 mm, and in volume from 2.77 to 5.56 cu. mm. Yolk sac dimensions for a larva 1 day after hatching were 1.9 x 1.1 mm with a volume of 2.08 cu. mm and a larva 2 days old had a yolk sac 0.65 x 0.50 mm with a volume of 0.89 cu. mm. By day 3 the yolk sac is resorbed (fig. 2). Length of the larvae at hatching ranges from 6.1 mm to 9.1 mm BL.

Larvae are well differentiated at hatching with functional eyes, jaws and digestive tract (fig. 2A). The most pronounced morphological change during development is the increase in length of the snout and lower jaw (table 2; fig. 2). At hatching the mouth is slightly subterminal to subequal. The lower jaw grows rapidly, attaining a length 33 to 41 % of the body length in specimens 23.8 to 54.8 mm BL and 42 to 47 % of the body length for the 55.1 to 111.0 mm BL size range. The upper jaw grows more slowly and is about 1/2 the length of the lower jaw at 32.0 mm BL (fig. 2F). Thereafter growth is rapid, with upper jaw length reaching 88 to 92 % of lower jaw length in specimens ranging from 68.5 mm to 111.0 mm BL. Allometric growth of the upper and lower jaws produces a "halfbeak" stage which reaches a maximum at about 24 mm BL when the relative difference in "beak" length reaches 27 % of BL.

Table 2
Measurements (mm) of early stages of *Strongylura exilis*

Body length	Age (days)	Standard length	Snout length	Lower jaw length	Head length	Eye to anus distance	Eye to anal fin origin	Eye to dorsal fin origin	Eye to pelvic fin origin	Pelvic fin length	Body depth	Pectoral fin length	Pectoral fin depth	Eye width	Eye height
6.2	0	6.3	0.1	0	0.9	4.2	–	–	–	–	0.4	0.4	0.4	0.5	0.4
6.8	0	7.0	0.2	0.08	1.1	4.7	–	–	–	–	0.6	0.6	0.4	0.5	0.4
8.2	0	8.4	0.2	0.2	1.3	5.6	–	–	–	–	0.7	0.7	0.4	0.6	0.5
9.9	1	10.2	0.3	0.7	1.5	6.8	7.2	7.7	–	–	1.4	0.8	0.4	0.6	0.6
10.2	2	10.6	0.4	0.9	1.6	7.3	7.5	8.0	–	–	1.2	1.0	0.5	0.7	0.6
12.3	3	13.0	0.7	1.8	1.9	8.6	8.7	9.7	–	–	1.3	0.9	0.5	0.8	0.6
13.4	4	14.2	0.8	2.4	2.0	9.7	9.8	10.4	–	–	1.4	1.1	0.6	0.8	0.7
16.2	6	17.2	1.0	3.8	2.3	11.0	11.2	11.8	–	–	1.4	1.4	0.6	0.9	0.7
17.5	8	18.8	1.2	4.8	2.6	12.0	12.2	12.8	–	–	1.6	1.5	0.7	1.0	0.8
23.0	10	25.4	2.4	5.4	3.6	16.2	16.5	17.0	12.3	0.5	1.9	2.1	0.8	1.2	1.1
23.8	10	26.1	2.2	8.6	3.6	16.2	16.7	17.7	12.0	0.5	2.0	1.9	0.8	1.2	1.1
27.0	12	29.9	2.9	9.2	3.9	18.4	18.7	19.7	14.2	0.5	1.9	2.3	0.8	1.3	1.1
32.0	17	38.4	6.4	13.0	5.0	21.8	22.2	23.4	16.8	0.9	2.4	2.5	1.0	1.7	1.5
32.5	18	38.5	6.0	12.3	5.0	22.5	22.9	24.0	17.2	0.8	2.3	2.8	1.2	1.5	1.4
48.8	39	63.1	14.3	17.3	7.9	32.8	33.0	36.5	24.0	2.3	2.8	4.6	1.5	2.7	2.2
50.7	39	65.2	14.5	19.0	8.3	35.1	35.9	38.1	27.0	2.1*	2.7	4.6*	1.4	2.7	2.3
54.8	35	70.5	15.7	18.0	8.9	37.9	38.6	40.4	28.9	2.6*	3.6	5.2	1.5	2.8	2.5
55.1	39	73.6	18.5	23.3	9.6	38.3	39.0	41.3	29.0	2.4	3.2	5.2	1.6	2.8	2.2
55.8	36	72.3	17.1	24.6	9.2	39.3	40.2	42.5	29.6	2.6	3.8	5.1	1.7	2.7	2.3
58.1	44	79.1	21.0	26.7	9.8	39.3	39.6	41.8	30.1	2.6*	3.8	5.2	1.6	2.9	2.8
68.5	57	87.3	18.8*	20.6	11.2	47.4	48.2	50.4	36.6	2.9*	4.1	6.2	1.7	3.5	3.2
79.2	73	109.3	30.1	34.1	11.7	54.0	55.0	56.7	40.3	3.5	5.7	7.7	2.3	4.0	3.8
79.9	96	113.5	33.6	37.8	13.8	56.2	57.4	60.2	43.4	4.2	6.1	8.6	2.1	4.2	3.9
80.0	81	112.7	32.7	35.9	12.8	56.1	57.1	59.3	43.1	4.0	5.5	8.0	2.2	4.2	3.8
111.0	120	155.8	44.8	48.6	17.0	75.3	77.0	81.0	57.6	5.5	7.7	11.7	3.3	5.7	5.7

* Indicates damaged fin or other structure.

Teeth begin to form on the lateral margins of the lower and upper jaws at day 2. Tooth development increases rapidly and by day 10 a pattern of widely spaced dagger-like teeth with smaller closely spaced teeth between them is apparent. Initially, teeth are formed on the lower jaw somewhat anterior to the tip of the upper jaw but by about day 18 (32.5 mm BL) teeth are forming simultaneously as the jaws elongate. The upper jaw is narrower than the lower jaw and, when closed, fits into a groove in the latter. Only the fleshy tip of the lower jaw lacks teeth in our largest specimens.

In contrast to the allometry of jaw growth most other body proportions remained remarkably constant through the growth series. This is shown by the mean values and standard deviations for proportions measured over the entire growth series: (1) head length/BL = 15.7 % ± 0.88, (2) eye to anus/BL = 69 % ± 1.37, (3) eye to anal fin origin/BL = 70.5 % ± 1.50, (4) eye to dorsal fin origin/BL = 74.6 % ± 1.99, and (5) body depth/BL = 7.9 % ± 2.02. Eye width is initially about 1/2 the head length and undergoes a relative decrease to about 1/3 the head length in specimens larger than 23.0 mm BL. At hatching eye height is about 75 % of eye width and undergoes a relative increase throughout the developmental period until the eye becomes round in our largest specimens.

Fin development/meristics: Notochord flexion and the initial ossification of the principal caudal rays occurs approximately 2 days before hatching; however, the full complements of 7 + 8 principal and 6 + 6 procurrent rays are not ossifying until about 11.3 mm and 32.5 mm BL, respectively (table 3). Dorsal, anal, and pectoral fin ray elements and the vertebral centra are ossifying during the first

Table 3
Meristics of larvae and early juveniles of *Strongylura exilis*

Body length	Age (days)	Vertebrae	Caudal fin rays		Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays
			Principal	Procurrent				
6.4	unhatched	–	1 + 2	0 + 0	–	–	–	–
6.7	"	–	1 + 2	0 + 0	–	–	–	–
8.3	0	42	4 + 5	0 + 0	X	5	1	–
11.3	3	70	7 + 8	0 + 0	15	16	3	–
13.4	4	69	7 + 8	1 + 1	15	17	5	–
16.2	6	69	7 + 8	2 + 2	14	18	8	–
17.5	8	69	7 + 8	3 + 3	15	18	8	–
23.8	10	69	7 + 8	4 + 4	16	18	11	–
27.0	12	69	7 + 8	4 + 4	14	18	12	X
32.0	17	69	7 + 8	5 + 6	15	18	12	5
32.5	18	68	7 + 8	6 + 6	16	18	13	5
80.5	49	69	7 + 8	6 + 6	16	18	12	6

X = présent
– = absent

day after hatching. Full fin ray complements for dorsal (12-16) and anal (15-20) are ossifying by 11.3 mm BL (3 days after hatching). The entire vertebral column (68-74 centra) is ossifying by 13.4 mm BL (day 4). The paired fin ray elements ossify later. Full pectoral fin ray complements (12-13) are formed by 27.0 mm BL (12 days after hatching). Pelvic fins are last to achieve the full complement of 6 rays usually between 32.5 mm (day 18) and 48.8 mm BL (day 39). The pelvic fins develop later in *S. exilis* than in any other known belonid species.

A prominent median finfold is present at hatching. The dorsal and anal finfolds begin at the level of the anus and join posteriorly with the caudal finfold. A pre-anal finfold is present between the yolk sac and the anus. The dorsal, anal, and caudal finfolds are lost as the rays develop, however, the pre-anal finfold persists until about 30 mm BL.

Pigmentation: At hatching the larva is covered with a sheath of melanophores and xanthophores. Both surfaces of the pectoral fin base are covered and the body sheath fans out onto the caudal fin rays. Areas which lack pigment are the branchiostegal membrane, the pectoral fin blades, the median finfold, and the terminus of the gut (fig. 2A). An internal melanistic streak lies above the gut and extends anteriad into the head beneath the otic region. Posterior to the gut the streak continues as heavy melanistic lines on each side of the anal fin. In hatchlings with large yolk sacs the melanophores are concentrated along the vitelline blood vessels and the xanthophores are scattered over the yolk sac. As the yolk sac decreases the melanophores and xanthophores gradually cover the entire region (fig. 2B, C).

At about day 3 guanine begins to form on the opercle and in the lining of the perivisceral cavity and these regions develop an aquamarine color that persists throughout the growth series (fig. 2D). By day 12 (27 mm BL) the melanistic pigment begins to diminish on the trunk region above the gut and this region develops a shiny guanine layer. The dorsum and upper trunk retains the melanistic and xanthic covering and by day 17 (32 mm BL) three distinct pigment zones are apparent on the trunk: (1) a dorsal zone extending about a third of the way down the trunk consisting of heavy melanistic pigment infused with residual xanthic pigment that is beginning to be replaced by bright green pigment, (2) a middle silvery zone with some melanophores, and (3) a ventral silvery aquamarine zone (fig. 2F). These zones continue posteriorly and converge towards the caudal fin. By day 28 (44 mm BL) the dorsal zone is bright green with a black background and yellow pigment is absent (fig. 2G). With continued development the lateral silvery zone widens and in our largest specimens (120 days; 110 mm BL) the dorsal zone is about 1/4 of the body depth and is entirely black.

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RESUMÉ

Elevage, développement et premiers stades du Poisson-aiguille californien *Strongylura exilis*

Strongylura exilis est le Bélonidé le plus commun en Californie. On le trouve d'ordinaire en petits bancs dans les eaux superficielles des criques et des ports. C'est un excellent Poisson de consommation, pouvant atteindre 91 cm, mais dont la pêche n'est pas commercialisée. Les documents sur les premiers stades de cette espèce sont rares et le présent travail se propose de décrire les œufs, les larves et les juvéniles obtenus par élevage dans un aquarium expérimental du *Southwest Fisheries Center*. Les géniteurs ont été pris dans la nature, mais l'insémination a été pratiquée artificiellement. Les œufs, sphériques, sont parmi les plus petits de la famille (2,4-2,7 mm) et ont 28 à 40 longs filaments régulièrement disposés sur leur coque. A l'éclosion, 10 à 19 jours après la fécondation à 19-20 °C, les larves sont nourries immédiatement de nauplies d'Artémias et leur croissance sera rapide (1 mm/jour) ; les yeux, les mâchoires, le tractus digestif et la nageoire caudale sont fonctionnels dès la naissance, et le corps est revêtu d'une couche de mélanophores et de xanthophores. Les derniers stades larvaires et les juvéniles poursuivent leur croissance rapide avec un régime d'Artémias adultes congélées et de Calmars hachés. La croissance allométrique des mâchoires la mandibule s'allongeant plus rapidement que la mâchoire supérieure aboutit à un stade "demi-bec" qui atteint un maximum lorsque la longueur du corps est de 24 mm et que la différence de longueur entre les deux mâchoires est égale à 27 % de la longueur du corps.

Au cours du développement, la couverture uniforme de chromatophores (mélanophores et xanthophores) évolue vers un patron rayé en long, comportant une région dorsale noire-verdâtre et des flancs argentés.