Larval development of *Symphurus williamsi* (Cynoglossidae: Pleuronectiformes) from the Gulf of California

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Abstract.—The larval development of *Symphurus williamsi* Jordan and Culver, 1895 (Cynoglossidae: Pleuronectiformes) is described from 69 specimens from the Gulf of California, Mexico. Diagnostic characteristics used to identify larvae of this species are 3–5 pigment spots situated on the dorsal region of the body of the base of the pterygiophore of the dorsal fin and 3–4 pigment spots on the ventral region of the body on the base of the pterygiophore of the anal fin. In early stages, a pigment is present on the base of each anal-fin ray. These pigments also appear at the bases of the dorsal-fin rays in the posterior third of the dorsal fin. The first three dorsal-fin rays are elongated in larvae less than 11.2 mm body length.

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Symphurus is a world-wide genus distributed predominantly in temperate and tropical seas and oceans. The genus has 71 recognized species, 17 of which are found in the American region of the Pacific Ocean (Munroe, 1992). Thirteen species have been found in the Gulf of California: *S. atramentatus*, *S. atricaudus*, *S. callopterus*, *S. chabanaudi*, *S. elongatus*, *S. fasciolaris*, *S. gorgonae*, *S. leei*, *S. melanurus*, *S. melasmatotheca*, *S. oligomerus*, *S. prolatinaris*, and *S. williamsi* (Munroe and Mahadeva, 1989; Munroe, 1990; Munroe and Nizinski, 1990; Mahadeva and Munroe, 1990; Munroe et al., 1991; Munroe et al., 1995). Specimens of *Symphurus* are usually captured in large quantities by shrimp trawls in some tropical regions, but they are not exploited commercially because of their relatively small size (Pérez and Findley, 1985; Van der Heiden, 1985; Van der Heiden et al., 1986).

The taxonomy of the eastern Pacific species was poorly defined until the recent study of Munroe (1992), who concluded that it was possible to identify each of these species by a combination of the dorsal-, anal-, and caudal-fin ray counts and by the interdigitation patterns of dorsal proximal pterigyophores and neural spines (ID pattern).

Symphurus williamsi Jordan and Culver, 1895, can be found from the southern region of the Gulf of California, Mexico, to Panama in shallow waters with sandy bottoms (Munroe et al., 1995). Larvae occur throughout the Gulf of California. Large numbers were found during the summer in collections made south of Islas Tiburón and Angel de la Guarda (Aceves, 1992).

Of all species found in the American region of the Pacific, only the larvae of *S. atricaudus* (the only species of this genus distributed north as far as California) and *S. elongatus* have been described (Moser, 1981; Ahlstrom et al., 1984; Matarese et al., 1989; Charter and Moser, 1996). In this study, we offer a description of the larval stages of *S. williamsi* from preflexion through prejuvenile stages. Observations made on the larval development of *S. williamsi* are compared with those made previously on *S. atricaudus* and *S. elongatus*.

Table 1

Meristics for species of *Symphurus* of the Gulf of California with the same pterygiphore interdigitation pattern (1-5-3-2-2) taken from Munroe (1992).

	S. williamsi	*S. atricaudus*	*S. chabanaudi*	*S. elongatus*	*S. melasmatotheca*	*S. melanurus*	*S. prolatinaris*
Dorsal-fin rays	89–95	94–102	98–109	99–107	90–98	96–104	103–110
Anal-fin rays	73–79	77–83	82–92	83–90	74–80	79–87	86–93
Caudal-fin rays	12	12	12	12	11	12	12
Total vertebrae	47–51	50–53	52–57	53–56	49–52	50–54	54–58

Materials and methods

Plankton samples were taken during eight oceanographic expeditions made in the Gulf of California in April, July–August, and November–December 1984, June and August 1986, July 1991, September 1993, and June 1994. Samples were obtained by using oblique tows with 60-cm diameter bongo nets equipped with nets of 333-µm and 505-µm mesh, as detailed in Kramer et al. (1972). All larvae and juveniles used in this study were deposited in the larval fish collection of the Plankton and Marine Ecology Department of Centro Interdisciplinario de Ciencias Marinas of the Instituto Politecnico Nacional (CICIMAR-IPN).

All *Symphurus* larvae collected with the 505-µm net were separated from the other net contents. Flexion, postflexion, and juvenile specimens were cleared, stained (Potthoff, 1984), and identified on the basis of meristic characteristics (Munroe, 1992). Subsequently, a developmental series of preflexion larvae showing similar pigmentation patterns and meristic features was assembled. Counts of the dorsal- and anal-fin elements were sometimes extrapolated from pterygiophore counts, which occasionally appeared earlier in development than did corresponding rays. The following measurements were done on the left side of the body of the specimens:

Body length (BL): anterior end of snout to end of notochord in young larvae, or to posterior margin of hypural plate in more developed larvae.

Head length (HL): anterior end of snout to cleithral margin in small specimens, or to posterior margin of the opercle in larger ones.

Snout-anus length (Sn-A): anterior end of snout to posterior margin of anus.

Body depth (BD): vertical distance between dorsal and ventral margins (dorsal- and anal-fin pterygiophores excluded) at origin of pelvic fin.

Body depth at anus (BDA): vertical distance between dorsal and ventral margins (dorsal- and anal-fin pterygiophores excluded) at origin of anal fin.

Eye diameter (ED): horizontal distance between anterior and posterior margins of left eye (Moser, 1996).

The description of larval development was based on 69 specimens (2.2–13.2 mm BL). None of these larvae were in the yolksac stage, indicating that eclosion must have taken place at a smaller size. To characterize larval development intervals, divisions proposed by Ahlstrom et al. (1976) were followed.

Results

Cleared and stained larval and prejuvenile specimens (n=17, between 7.7–13.2 mm BL) showed the following pterygiophore patterns: 1-5-3-2-2 (41.2%), 1-5-2-3-2 (35.2%), 1-5-2-2-2 (11.8%), 1-4-2-2-2 (5.9%), and 1-5-4-2-2 (5.9%). There are seven species in the area with the same main pterygiophore pattern (Table 1). Using these 17 specimens and the remaining 52 larvae (Table 2), we counted 9 precaudal vertebrae, 38–42 caudal vertebrae (mode=40), 89–97 dorsal rays (mode=92 and 94), 71–80 anal rays (mode=75), and 12 caudal-fin rays. The combination of these characteristics indicates that the species is *S. williamsi*.

Description of the larvae

Diagnosis *Symphurus williamsi* larvae typically have a pigmentation pattern of 5 spots along the middorsal line at the bases of the dorsal-fin pterygiophores and 2 to 3 similar spots located on the bases of the dorsal-fin rays. There are also 3 to 4

Table 2

Symphurus williamsi larvae and juvenile measurements (mm): body length (BL), snout-anus length (Sn-A), head length (HL), eye diameter (ED), body depth (BD), body depth at anal fin (BDA), and individual counts: dorsal rays (DR), anal rays (AR), caudal rays (CR), caudal vertebrae (CV), and total vertebrae (TV). Start of flexion stage (═══); start of postflexion stage (– – –); start of juvenile stage (───).

BL	Sn-A	HL	ED	BD	BDA	DR	AR	CR	CV	TV
2.2	1.1	0.6	0.2	0.5	0.3				22	31
2.4	1.1	0.6	0.2	0.5	0.3				37	46
2.6	1.1	0.6	0.2	0.7	0.3				32	41
2.8	1.2	0.7	0.2	0.9	0.6				38	47
2.8	1.2	0.7	0.2	0.8	0.4				34	43
2.9	1.3	0.7	0.2	0.9	0.7				40	49
3.1	1.5	0.8	0.2	1.1	0.7				38	47
3.2	1.4	0.9	0.2	1.2	0.8				39	48
3.3	1.7	1.1	0.2	1.4	1.1				38	47
3.5	1.5	0.9	0.2	1.1	0.7				40	49
3.7	1.5	1.1	0.2	1.3	0.9				40	49
3.8	1.8	1.1	0.2	1.2	0.9				38	47
4.0	1.9	1.2	0.2	1.3	0.9				38	47
4.1	1.9	1.3	0.2	1.4	1.1				40	49
4.3	1.9	1.1	0.3	1.6	1.2				40	49
4.3	1.9	1.1	0.3	1.6	1.1				40	49
4.5	2.1	1.2	0.2	1.8	1.1				41	50
4.6	2.0	1.3	0.2	1.5	1.2				40	49
4.8	1.8	1.1	0.2	1.5	0.9				39	48
5.0	2.0	1.2	0.3	1.7	1.4				39	48
5.0	1.9	1.2	0.2	1.7	1.1				40	49
5.0	2.1	1.3	0.3	1.6	1.2				38	47
5.3	2.1	1.4	0.3	1.7	1.2				40	49
5.6	2.0	1.4	0.3	1.5	1.1				41	50
5.8	2.3	1.5	0.3	1.9	1.4				40	49
5.9	2.3	1.4	0.3	1.9	1.2				40	49
6.1	2.4	1.6	0.3	1.9	1.5				40	49
6.1	2.2	1.7	0.3	1.9	1.4		80		40	49
6.3	2.4	1.5	0.3	1.8	1.4				40	49
6.6	2.2	1.6	0.3	2.1	1.5				38	47
6.8	2.5	1.7	0.3	2.3	1.5	92	79		41	50
7.0	2.6	1.6	0.3	1.9	1.5	92	77		41	50
7.2	2.7	1.8	0.3	2.2	1.7	92	75		40	49
7.3	2.7	1.7	0.3	1.9	1.5	95	79		40	49
7.4	2.5	1.7	0.3	2.3	1.5	94	75		41	50
7.7	2.6	1.7	0.3	2.0	1.7	92	75	12	40	49
7.8	2.9	1.9	0.3	2.0	1.6	94	76	12	38	47
8.0	2.8	2.0	0.3	2.2	1.7	93	77		41	50
8.2	2.8	1.9	0.3	2.3	1.9	96	77	12	40	49
8.3	3.1	2.0	0.3	2.4	1.9	95	76	12	41	50
8.3	2.9	1.9	0.3	2.4	1.8	96	79	12	40	49
8.3	2.9	1.9	0.3	2.3	1.9	93	76	12	40	49
8.4	3.0	1.9	0.3	2.1	1.5	94	76	12	39	48
8.7	2.9	2.2	0.3	2.5	2.1	91	74	12	40	49
9.3	3.0	2.1	0.3	2.0	1.6	94	75	12	38	47
9.5	3.3	2.2	0.3	2.3	2.0	94	77	12	40	49
9.6	3.4	2.2	0.3	2.6	2.1	91	75	12	38	47
9.8	3.1	2.0	0.3	2.3	2.0	92	76	12	40	49
9.9	3.2	2.1	0.3	2.2	2.0	93	71	12	39	48
9.9	3.2	2.1	0.3	2.3	2.1	94	78	12	41	50
10.0	3.0	2.2	0.3	2.5	2.2	91	75	12	40	49
10.2	2.8	2.2	0.3	2.4	2.2	92	75	12	41	50

continued

Table 2 (continued)

BL	Sn-A	HL	ED	BD	BDA	DR	AR	CR	CV	TV
10.4	3.1	2.2	0.4	2.5	2.3	92	76	12	41	50
10.6	3.4	2.3	0.4	2.3	2.1	93	74	12	38	47
10.6	3.3	2.3	0.3	2.2	2.2	91	75	12	39	48
10.7	3.5	2.2	0.3	2.6	2.3	94	76	12		
10.8	3.3	2.5	0.4	2.6	2.4	91	73	12	39	48
11.1	3.4	2.4	0.3	2.5	2.2	94	77	12	39	48
11.1	3.6	2.5	0.3	2.7	2.7	90	75	12	38	47
11.1	3.7	2.6	0.3	2.4	2.4	97	80	12	39	48
11.1	3.7	2.5	0.3	2.4	2.4	93	76	12	42	51
11.3	3.5	2.5	0.3	3.0	2.3	92	77	12	39	48
11.4	3.3	2.3	0.3	2.5	2.3	94	79	12	40	49
11.7	3.4	3.2	0.4	3.5	3.3	93	73	12		
11.9	3.8	2.8	0.3	2.5	2.3	92		12	40	49
12.7	3.2	2.5	0.4	2.3	2.7	91	75	12	38	47
12.9	3.9	3.0	0.3	2.4	2.6	89	74	12	39	48
13.1	3.9	3.0	0.3	3.1	2.4	94	74	12		
13.2	3.4	2.9	0.3	2.2	2.9	92	75	12	39	48

spots along the midventral line at the bases of the anal-fin pterygiophores, and 1 to 2 similar spots located on the anal-fin ray bases. At time of formation of the anal-fin rays, a melanophore appears at the base of each fin ray. A similar pigment is also found at the base of each dorsal- fin ray in the posterior third of the body in larvae less than 11.2 mm BL. The first 3 dorsal rays are elongated in larvae less than 11.2 mm BL, with the second and third of these longer than the first.

Morphological features The body is compressed and ribbonlike and has a deep head. The gut extends beyond the ventral profile. The intestine is noticeably coiled and its terminal end is directed towards the right side of the body. Larvae attain the appearance of juveniles when the protruding gut is incorporated within the ventral body profile at approximately 12 mm BL. At metamorphosis, a fleshy rostral beak is formed anterior to the dorsal-fin origin.

Migration of the right eye starts at 6.1 mm BL and eye migration is completed in larvae of 11.1 mm BL. The migrating eye crosses anterior to the dorsal-fin origin, between the rostral beak and the interorbital region. Notochord flexion begins at 5.0 mm BL and is completed near 8.0 mm BL. The juvenile stage begins at about 11.9 mm BL (Table 2).

Growth is not isometric throughout larval development (Table 3). Head length, snout-anus length, and body depth decrease with respect to body length from preflexion to juvenile stages. Body depth at the anal-fin origin remains constant throughout development. Eye diameter in relation to head length decreases from preflexion to juvenile stages.

Table 3

Symphurus williamsi larvae and juvenile body proportions (in percent of BL): body length (BL), head length (HL), snout-anus length (Sn-A), body depth (BD), body depth at anal fin (BDA), and eye diameter (ED).

Body proportions	Average	Standard deviation	Interval
HL:BL			
Preflexion	27	2.8	23–33
Flexion	25	1.3	23–28
Postflexion	23	1.5	20–27
Juvenile	22	1.4	20–24
Sn-A:BL			
Preflexion	45	3.3	38–52
Flexion	38	2.2	33–42
Postflexion	33	2.4	28–37
Juvenile	29	2.6	25–32
BD:BL			
Preflexion	33	5.2	21–42
Flexion	31	2.5	26–34
Postflexion	25	2.6	21–30
Juvenile	20	2.5	17–24
BDA:BL			
Preflexion	22	5.5	12–33
Flexion	23	2.0	20–28
Postflexion	22	2.0	17–28
Juvenile	20	1.3	18–23
ED:HL			
Preflexion	24	6.2	15–33
Flexion	19	2.5	15–25
Postflexion	14	1.8	12–18
Juvenile	11	2.3	10–12

Formation of scales begins at 7.7 mm BL over the cephalic region, and by about 10.3 mm BL, scales are evident over the entire body.

Pigmentation Early preflexion larvae typically have three melanophores along the middorsal line and two or three on the dorsal-fin fold. Three other melanophores are present along the midventral line, and one or two similar spots are found on the anal-fin fold. A melanophore is located over the coiled intestine in anterior and posterior positions. The ventral surface of the coiled intestine shows numerous smaller and dispersed melanophores. Two other melanophores appear in the anterior region: one on the cleithrum near the base of the pectoral bud; the other on the ventral margin of the preopercle. The dorsal surface of the swimbladder is also pigmented (Fig. 1A).

With finfold disappearance (late preflexion larvae), the characteristic pigmentation pattern is established: five spots located along the middorsal line at the bases of the dorsal-fin pterygiophores and two or three spots on the bases of dorsal-fin rays. Three or four spots appear along the midventral line at the bases of the anal-fin pterygiophores, and one or two spots are present on the bases of anal-fin rays.

When formation of the dorsal- and anal-fin rays is complete, a pigment spot appears on the base of each anal ray. Similar pigments are found on the bases of the fin rays in the posterior third of the dorsal fin. On the head, an inner melanophore appears over the forebrain and another over the otic region. Finally, a melanophore is present on the distal margin of the peduncle of the pectoral fin (Fig. 1B).

During the flexion stage, the pigmentation pattern of preflexion larvae remains, but the spots on the bases of anal- and dorsal-fin rays sometimes disappear. The pigment over the otic region, that on the opercle margin, and the melanophore on the posterior part of the intestine also disappear. In this stage there are additional pigments that appear. A series of dots are found over the ventral margin of the head, and a melanophore appears over the inferior portion of the base of the ventral fin. Flexion larvae are similar to those of postflexion larvae (Fig. 2A).

At the postflexion stage, three melanophores appears on the bases of the caudal-fin rays, and at 11.2 mm BL, the cephalic and opercular pigments may disappear (Fig. 2A).

In early juveniles, four spots appear on the midline of the body. Their positions with respect to the melanophores already present on the dorsal margin are one between second and third spots, one between third and fourth, one directly ventral to the fourth spot, and one posterior to the fourth spot. There is now pigment on the base of every dorsal-fin ray throughout the entire fin. A series of small spots also develop on the rays on the anterior part of the anal fin (Fig. 2B).

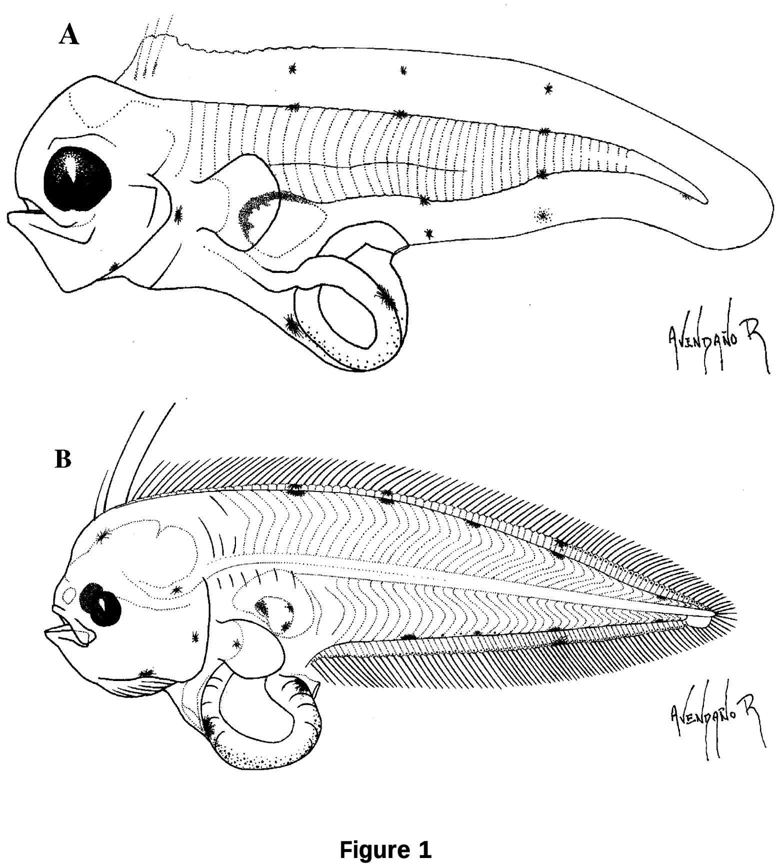

Figure 1
Symphurus williamsi: (**A**) 2.2-mm preflexion larva; (**B**) 6.3-mm flexion larva.

Fin formation

Unpaired fin development Incipient dorsal-fin rays are present in the anterior dorsal finfold at 2.8 mm BL. At 4.0 mm BL, about one half of the dorsal and anal rays are formed in a posterior direction. Complete formation of these fins occurs at about 6.8 mm BL. The 3 elongated dorsal-fin rays, present since this fin originated, disappear at 11.4 mm BL.

Paired fin development Pectoral-fin buds are present in the smallest larvae we have seen (2.2 mm BL). This fin is reabsorbed at the postflexion stage (10.3 mm BL). Pelvic fins are developed at 5.7 mm BL. Only in early juveniles is a blind-side pelvic fin located on the midventral line and the ocular pelvic fin is in a more dorsal position.

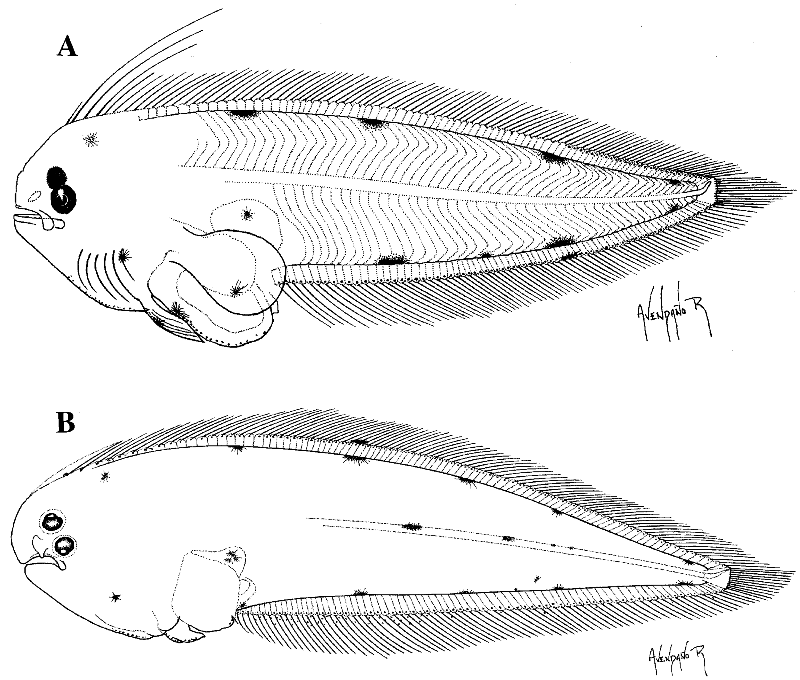

Figure 2
Symphurus williamsi: (**A**) 10.0-mm postflexion larva; (**B**) 11.9-mm transformation larva.

Discussion

Larvae of *S. williamsi* are easily distinguishable from those of *S. atricaudus* by differences in pigmentation patterns. During early preflexion stage, *S. williamsi* has two or three pigments over the dorsal and midventral lines, and the pigments over the finfold are in the middle. *S. atricaudus* has a series of small melanophores along the midventral line. The pigments over the finfold are in blotches and are on the ventral and dorsal margins. There are also several pigments over the ventral margin of the head and the gut that *S. williamsi* does not have.

At the flexion stage, *S. williamsi* has the spot pattern along the dorsal and ventral profile. In contrast, *S. atricaudus* has a series of melanophores along the dorsal- and anal-fin margins and a series of pigments along the midbody line that never develop in *S. williamsi*.

In *S. williamsi*, three elongated rays are characteristic. In *S. atricaudus*, five rays appear first in the dorsal fin but never become elongated. The intestine in *S. williamsi* projects only ventrally, whereas in *S. atricaudus* the projection is ventroposterioriad.

Larvae of *S. williamsi* can be distinguished from those of *S. elongatus* by the pigmentation patterns. In the preflexion stage, *S. elongatus* does not have spots at the bases of the dorsal-fin rays, and these larvae do not have pigments at the bases of each of the anal- and dorsal-fin rays. Later in their development, the pigmentation of *S. elongatus* consists of a few distal pigments on the anal fin, twelve dashes along the lateral midline, and a small blotch on the caudal-fin rays, not observed in *S. williamsi*. In the early transformation stage, *S. elongatus* has a series of melanophores over the anterior part of the head, which never appear in *S. williamsi*. Like *S. atricaudus*, *S. elongatus* never develops elongated rays.

Yevseyenko (1990) described *Symphurus* sp. larvae. Its meristic characters have led us to believe it is *S. callopterus*, principally because of its ID pattern. These larvae are different from those of *S. williamsi* in pigmentation pattern because on the caudal section of the body an accumulation of pigment in the form of two oblique bands and two belts are found. These pigments are approximately equidistant from one other and never are found in *S. williamsi*.

Instead of three elongated dorsal-fin rays, like *S. williamsi*, *Symphurus* sp. have the first 7 dorsal-fin rays elongated from 7.5 to 25.4 mm BL (Yevseyenco, 1990). The presence of elongated fin rays in pleuronectiform larvae has phylogenetic interpretations only in bothids and appears to be apomorphic within the order and this family (Hensley and Ahlstrom, 1984). However the use of this characteristic for phylogenetic interpretations in cynoglossids does not allow proper comparisons because most larvae remain unknown.

Adults of *S. williamsi* (7.5 to 11.6 cm BL) are smaller than those of *S. atricauda* (13 to 18 cm BL) and *S. elongatus* (13.5–15 cm BL) (Munroe et al., 1995), and this size difference is observed in larvae also. All stages of development in *S. williamsi* occur at smaller sizes (flexion between 5.0 and 8.0 mm and transformation >11.9 mm) than in other species. The flexion stage in *S. atricaudus* occurs between 8.6 and 10.8 mm BL (Ahlstrom et al., 1984; Matarese et al., 1989), and the transformation stage between 19 and 24.2 mm BL (Kramer, 1991). The flexion stage in *S. elongatus* is >6.8 mm and <18.9 mm BL and transformation takes place from >18.9 mm to <28.3 mm BL (Charter and Moser, 1996). In *Symphurus* sp. transformation occurs between 21 and 38 mm BL (Yevseyenko, 1990).

Usually the size range at metamorphosis that is plesiomorphic for the order is ca. 10 to 25 mm BL because most pleuronectiforms metamorphose in this range (Hensley and Ahlstrom, 1984).

Metamorphosis in *S. williamsi* occurs at ca. 11.9 mm BL; however, as described by Hensley and Ahlstrom (1984), size at metamorphosis is an important characteristic for larval identification, but its use for inferring phylogenetic relations in most instances is premature.

Symphurus williamsi has a larger head at all developmental stages, compared with those of *S. atricaudus* and *S. elongatus*. The distance from snout to anus in *S. williamsi* is relatively longer than it is in *S. atricaudus* but is similar to that of *S. elongatus*. In the juvenile stage, this distance is longer in *S. williamsi* than it is in *S. elongatus*. Larvae of *Symphurus* sp. as described by Yevseyenko (1990) have an abdominal cavity extending downward. This projection has the form of a greatly elongated sac, and the lower end terminates in a wormlike process that *S. williamsi* does not have. The loop of the intestine in *Symphurus* sp. is almost one half of the body length.

The body depth at the preflexion stage is greater in *S. williamsi* compared with that in *S. atricaudus* but is similar to that of larvae of *S. elongatus*. In postflexion and prejuvenile stages, this proportion is smaller in *S. williamsi* than in both of these other species.

Finally, body depth at the anus is shallower in *S. williamsi* than it is in *S. elongatus* at all stages in *S. atricaudus* during flexion and juvenile stages.

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